Perspectives on Dog–Human Interactions

Habilitation Thesis

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Summary

In comparative psychology we draw inferences about the evolution of cognition by investigating the similarities and differences between human and non-human animals. I am especially interested in which cognitive skills have evolved in different species that allow them to be optimally adapted to their environment. Dogs, due to their high sociality and the fact that they were subject to a special domestication process, represent a highly promising model to investigate social cognition from a comparative perspective. Studying dog cognition not only sheds light on the question on what skills humans share with other animal species, but also what kind of selection pressures lead to human-like skills. Dogs are not simply pets that live in the human environment, but they also form a close relationship to humans and cooperate with them. Thus, studying dogs living in that special niche will not only inform us about their cognitive skills but might also help us to better understand the selection pressures that led to the unique cognition of humans.

The aim of this habilitation thesis is to characterize the dog-human relationship taking diverse perspectives on dog cognition and the dog-human bond. During their long domestication process, dogs have evolved special cognitive skills that help them to function effectively in human societies. In this thesis, I present experimental evidence for these skills and I suggest that the skills have evolved in a domain-specific manner, independently from each other. Dogs show outstanding cognitive skills in the domain of (1.) communication, (2.) perspective taking, (3.) cooperation and (4.) olfaction processing, but perform poorly or average in other domains such as (5.) metacognition and (6.) behavioral matching.

Regarding (1.) **communication** I present experimental evidence that dogs without special training are able to successfully show a human a hidden object and that this showing behavior in dogs is a means to communicate the location of that hidden object. I argue that successful communication between dog and humans in general is the consequence of four preconditions in dogs: (i) they are extremely attentive and interested in what humans are doing, (ii) they have excellent learning abilities, (iii) they are able to read subtle cues of human behavior and (iv) they have extensive experience with different communicative situations.

Furthermore, I present an experiment about (2.) **perspective taking** – defined as the ability to assess what others can perceive. Here I found that dogs are able conceal auditory but not visual information from humans when they approach forbidden food. Taken together with findings from previous studies, I conclude that dogs use certain strategies when they assess what a human can and cannot perceive.

I studied (3.) **cooperation** both within dogs and between dogs and humans. Within dogs I used a problem-solving paradigm that involved aspects of a hunting-like situation. I compared the performances of dogs with those of wolves. My results suggest that the abilities needed to coordinate their actions were already present in the dog-wolf ancestor. Dogs and wolves may show similar cooperative skills when cooperating with their conspecifics, but dogs might cooperate better with humans than wolves do, as it is likely that during the domestication process dogs have been selected to cooperate specifically with humans. Consequently, I investigated the cognitive and motivational skills required for a dog to support a human. From the results I conclude

that dogs display a number of prosocial behaviors towards a human when they are able to infer the goal of the human and when they understand how to fullfill it.
In contrast to communicative, cooperative and perspective taking skills, (4.) the special **olfactory skills** of dogs probably did not evolve during domestication, but could be one of the reasons why dogs were domesticated. Here I present evidence that dogs can use olfactory information in an adaptable way: Dogs were presented with a violation-of-expectation paradigm in which they could track the odor trail of one target, but at the end of the trail, they found another target. I found that they are able to represent what they smell—that is, when they follow a trail they have an expectation of something or someone at the end of the trail. Thus, not only is dogs' sense of smell itself quite outstanding, but so are also their related cognitive skills.

In contrast, in their (5.) **metacognitive skills** and in (6.) **behavioral matching,** dogs do not show unique skills but perform similarly to other social mammals. Regarding (5.) **metacognition** I investigated whether dogs were sensitive to the information that they themselves had or had not acquired. I found that dogs seek additional information in uncertain situations, but their behavior in these situations is less flexible compared to great apes or human children. Finally, I did not find evidence for (6.) **behavioral matching,** ie. whether dogs develop an increased affiliation towards a human who mimics them. Dogs in my study showed no increased preference for one of two human experimenter who matched the dogs' walk.

In this thesis I present a view on dog cognition that differentiates individual cognitive skills, pointing out how exactly they are adapted to their special human environment. Thus, I emphasize the unique closeness of the dog-human relationship. I also point out where current findings are incomplete or show limits of their paradigms and call for further research. Firstly, I criticize the fact that most data on dogs' understanding of their social and physical environment is based on performance in the visual or sometimes in the auditory modality. As dogs' olfaction is their most relevant sense, I therefore call for more dog studies that are based on olfaction. Secondly, regarding the dog-human relationship, there are many open questions that have not yet been considered well enough: for example, whether dogs are capable of skills like empathy, the human perspective on dogs, and cultural differences in dog-human interactions. Thirdly, to better understand the dog-human bond it is crucial to further investigate when, where and how domestication started. This is also needed in order to understand why dogs were domesticated and what made and makes them valuable for humans. To answer the above mentioned questions, an interdisciplinary approach is crucial, in which scientists from the fields of archaeology, linguistics, paleoclimatology, genetics, anatomy, ethology, psychology, sociology, and anthropology work together.

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1. Introduction

One of the most fascinating questions in contemporary behavioral science concerns which cognitive skills humans share with other animal species and which are uniquely human (i.e. Bräuer, Hanus, Pika, Gray, & Uomini, 2020; Byrne, 1996; Premack & Woodruff, 1978; Tomasello, 2019). A useful approach to this question is the comparative approach, which pinpoints similarities and differences between human and non-human animals to then draw informed inferences about the evolution of human behavior and cognition (i.e. Bräuer et al., 2020; Call, Burghardt, Pepperberg, Snowdon, & Zentall, 2017; Heyes & Huber, 2000; Tennie, Call, & Tomasello, 2009). Following Shettleworth, the term 'cognition' refers to "adaptive information processing in the broadest sense, from gathering information through the senses to making decisions and performing functionally appropriate actions, regardless of the complexity of any internal representational processes that behavior might imply" (Shettleworth, 2000, p.43).

1.1. Dogs as a model species in Comparative Psychology

Whereas in the early days of the field Comparative Psychology rats, pigeons and monkeys were the typical species studied (Beach, 1995; Bräuer et al., 2020; Kamil, 1987), the attention later shifted towards great apes, in particular chimpanzees (Call, 2003; Call et al., 2017; Rowell, 1999). Indeed, as our closest living relatives, they represent an obvious model to study human-like cognitive skills. One puzzling question that arose at the end of the last century was why chimpanzees had problems interpreting the human pointing gesture, in contrast to human children who start to use the gesture in their first year (Butterworth & Morissette, 1996). The paradigm typically used was the object choice task in which food is hidden in one of two cups out of view of the subject. The human experimenter then provides a cue about the location of the food by pointing at the correct cup (i.e. Krause & Mitchell, 2018). Great apes and other primates usually perform at chance level or slightly above (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Clark, Elsherif, & Leavens, 2019; Miklósi & Soproni, 2006; Mulcahy & Call, 2009).

Inspired by everyday observations, researchers from two different labs had the idea to test domestic dogs, who indeed outperformed our closest living relatives in that task and were able to use the human pointing gesture to locate hidden food (Hare & Tomasello, 1999; Miklósi, Pongracz, & Csanyi, 1997). These findings in the late 1990s contributed to a rapid change in the scientific view of dogs (Aria et al., 2020). Previously, dogs were conceived of merely as wolves that had lost some of the skills of their wild relatives (Serpell, 2016). But in the last 20 years, researchers agreed that dogs are not "unskilled wolves", but they are simply adapted to *another* environment: the human environment (Bräuer & Vidal Orga, in press; Hare & Tomasello, 2005; Kaminski & Marshall-Pescini, 2014).

Nowadays we regard the dog as a highly interesting model in comparative psychology for four reasons:

1. **Domestic animal:** Dogs were domesticated, and thus selected to live in the human environment. In order to survive in that niche they might have evolved human-like skills (Hare & Tomasello, 2005; Kaminski & Marshall-Pescini, 2014).

2. **Long domestication process:** Dogs were domesticated earlier than any other animal, about 30,000 years ago, even before humans settled down (see chapter 1.2). Thus, there was a very long time period in which they could adapt to the human environment.
3. **Social animal:** Similar to humans and other primates, dogs are highly social animals. Thus, they live in a complex social environment, and they face a number of social challenges. As social situations can change rapidly and can be unpredictable, flexible solutions to these social problems are more adaptive than fixed behavioral patterns (Tomasello & Call, 1997) and it is adaptive to develop sophisticated social skills (Byrne & Whiten, 1988; Humphrey, 1976; Tomasello & Call, 1997).
4. **Special relationship to humans:** In contrast to other domesticated animals, dogs are not used for one or few purposes (Zeder, 2012), but in various different ways – such as protection, hunting, herding, rescuing, searching, servicing, and guiding (Miklósi, 2007; Serpell, 2016). Most of these functions require a close cooperation with humans. This has probably led to a selection pressure for a close relationship between dogs and humans (i.e. Bräuer & Vidal Orga, in press). Indeed, new findings might support the idea of a coevolution of human-dog bonding: Dogs prefer humans to other dogs as social partners (Gácsi et al., 2005; Miklósi, Kubinyi, Gácsi, Virányi, & Csanyi, 2003; Topál et al., 2005), the dog-human bond is comparable to the bond between human infants and their mothers (see Prato Previde & Valsecchi, 2014 for a review). It was also shown that reward-related brain activation in dogs has occurred in response to human praise, but also to the odor of a familiar human (Berns, Brooks, & Spivak, 2015; Cook, Prichard, Spivak, & Berns, 2016). On the hormonal level, there is evidence for an interspecies oxytocin-mediated positive loop facilitated and modulated by gazing between dogs and humans. In particular, affiliate interaction such as petting the dog, or a friendly eye gaze without threat, can cause physiological synchronization across species, increasing oxytocin and also dopamine levels and simultaneously lowering cortisol levels in dogs and their owners (Handlin et al., 2011; Miller et al., 2009; Nagasawa et al., 2015; Odendaal & Meintjes, 2003). This seems to be specific for the dog-human relationship, as in wolves, who rarely engage in eye contact with their human handlers, this effect could not be detected (Nagasawa et al., 2015).

In sum, due to their sociality and the fact that they were subject to a special domestication process, dogs represent a promising model to investigate social cognition from a comparative perspective. Studying dog cognition not only sheds light on the question of what skills humans share with other animal species, but also what kind of selection pressures lead to human-like skills. In other words, studying dogs living in their special niche – the human environment – might also inform us about the selection pressures that led to cognitive skills that are typical for humans.

1.2. Dog domestication

Dogs derive from prehistoric wolves (Kaminski & Marshall-Pescini, 2014). The exact timing and location(s) of the original domestication event(s) are highly debated, but are believed to have begun about 15,000 to 30,000 years ago in Eurasia (see Bräuer & Vidal Orga, in press, for a review, Thalmann et al., 2013; Vila et al., 1997; Wang et al., 2013). There is agreement that dog domestication started *at least* 14,000 years ago, as there is clear social and cultural evidence of domesticated dogs from this time (as illustrated by the Bonn-Oberkassel dog mandible found in a late Paleolithic grave in Germany; (Janssens et al., 2018)). After dogs were domesticated, they spread all over the world (Kaminski & Marshall-Pescini, 2014, see also Mitchell, 2017; Ní Leathlobhair et al., 2018).

It is also clear that dogs are the first species domesticated by humans, and that they were domesticated before humans settled down (Bräuer & Vidal Orga, in press; Kaminski & Marshall-Pescini, 2014). One important question is *why* wolves were domesticated in the first place. Clutton-Brock (1977) has explained domestication as the exploitation of one group of social animals by another, more dominant group that maintains complete mastery over the breeding, organization of territory, and food supply of the domestic animals (Clutton-Brock, 1977). Selective breeding over the course of many generations enhances various behavioral and physical characteristics conducive to domestic harmony and utility (Price, 1984; Serpell, 2016). Other authors, such as Zeder (2012), see domestication from a more mutualistic approach, where both human and domesticate benefit from the relationship (Price, 1984; Zeder, 2012). If domestication leads to a symbiotic relationship, then we would expect there to be advantages for both species – humans and wolves/dogs.

There is no doubt what the advantage was for the dogs/wolves: they not only gained a new food resource in human camps but were also protected from predators. However, what was the initial advantage for the human to domesticate the wolf? To answer this question we have to know which behavioral characteristics facilitate the domestication process. Hale (1969) has proposed such typical features such as a hierarchical group structure, a critical period in development of species-bond, being omnivorous, and a short flight distance – meaning they do not run far from humans when they encounter them (Hale, 1969; see Diamond, 1997). However, a number of these characteristics do not apply to wolves, such as being precocial and having limited agility. Moreover, wolves and early humans competed for the same kinds of prey. So why did humans domesticate a species that was a food competitor before they settled down? A tentative answer to this question might rely on various hypotheses about how wolves/dogs were used at the beginning of the domestication process. Humans might have taken advantage of wolves´ attentiveness and hunting abilities. Wolves/dogs probably cleared camps of garbage and vermin and might have been used as a source of meat, of heat, and as a means of transportation (Miklósi, 2007; Paxton, 2000; Serpell, 2016). Therefore, wolves might have had specific traits that allowed humans to make advantageous use of them. This seems more likely than the possibility that they were coincidentally in the right place at the right time for being domesticated – but it remains an open question (Kaminski & Marshall-Pescini, 2014).

There are also multiple theories on how domestication started. Either the process was initiated by humans, with hunters bringing wolf pups into the camp, or by wolves, with the animals approaching human camps to feed on discarded food scraps. The first scenario paints a picture where humans actively selected particularly friendly and approachable wolf puppies for companionship (Kaminski & Marshall-Pescini, 2014; Zimen, 1992). In the second scenario, in line with the so-called self-domestication hypothesis, wolves that were less aggressive or less fearful towards humans would have had the selective advantage to approach and live in close proximity to humans, and so had the opportunity to exploit new and reliable food sources (Hare, Wobber, & Wrangham, 2012; Kaminski & Marshall-Pescini, 2014). Today, many researchers suggest that it was a combination of these two scenarios – that wolves lived in close proximity to humans, and that some of them were tamed by humans, who later selected for animals showing less aggression and fear (Coppinger & Coppinger, 2001; Galibert, Quignon, Hitte, & André, 2011; Kaminski & Marshall-Pescini, 2014; Miklósi, 2007).

No matter how the domestication process started, the newly established relationship between humans and dogs was obviously very adaptive, as they together colonized the whole world (Mitchell, 2017; Ní Leathlobhair et al., 2018). Today, there are over 470 million pet dogs worldwide (Bedford, 2020). The 400–450 dog breeds all over the world differ in size, shape but also skull and brain formation (Roberts, McGreevy, & Valenzuela, 2010) and behavioral features (i.e. Gnanadesikan et al., 2020; Hecht et al., 2019; McGreevy et al., 2013). While the genetic underpinnings of breed formation and variation are still being investigated (Ostrander et al., 2019), it is clear that today's dog breeds mostly derived from small numbers of founders within the last 200 years.

Whereas most people consider the dog-human bond as a symbiotic relationship, Archer (1997) has described dogs as parasites, as humans reduce their own fitness by attaching themselves and devoting resources to this other species (Archer, 1997; see also Serpell & Paul, 2012). According to this hypothesis, dogs manipulate human responses that had evolved to facilitate human relationships, like those between parent and child. In other words, humans invest a lot of energy into dogs instead of into their own offspring. Indeed, new studies have shown that humans prefer dogs that often show childlike neotenous characteristics like raising their inner eyebrow (Waller et al., 2013). Wolves do not possess the muscle to raise their inner eyebrow (Kaminski, Waller, Diogo, Hartstone-Rose, & Burrows, 2019), and dogs show this movement in particular when humans are looking at them (Kaminski, Hynds, Morris, & Waller, 2017).

However, in the following I will present evidence that, in general, the benefits for humans are much higher than the costs of keeping dogs. Thus, I will argue that the dog-human bond is best explained by mutualistic relationship, where each species has a benefit. For dogs, the benefits are clear: they gain food, and in many cases, care and protection. Estimating the benefits for the human side is more difficult. Only a very few studies have tried to directly quantify the benefit of dog keeping for early humans. Their evidence has been mixed and difficult to extrapolate to other contexts, environments, and modes of subsistence. For example, Ruisila et al. (2004) has shown that hunting dogs can have a big impact on hunting success, and thus argued for a clear benefit of the dog-human partnership (Ruusila & Pesonen, 2004; see also Perri, 2016; Shipman, 2017). On the other hand, Koster (2009) found that the hunters in Central American rainforests took on risk when raising dogs as hunting partners, as not all dogs provided a net benefit in terms of animals harvested, and many dogs died young (Koster, 2009).

Today working dogs provide a clear benefit, as they support humans in various tasks. In addition to the classical usages as guard, hunting and herding dogs, humans have recently developed ways to use them as rescue, assistance and police dogs (Miklósi, 2007; Serpell, 2016). In the last years, there have been developments that take more advantage of dogs' excellent noses: in detection tasks dogs indicate the presence of specific trained odors. They can be trained to discriminate and indicate the presence of odors from narcotics, explosives, plants, parasites and various diseases such as cancer and diabetes (Alasaad et al., 2012; Browne, Stafford, & Fordham, 2006; Dalziel, Uthman, McGorray, & Reep, 2003; Furton & Myers, 2001; Gazit, Goldblatt, & Terkel, 2005; Lim, Fisher, & Burns-Cox, 1992; Lippi & Cervellin, 2012). But what are the benefits of a normal family dog in the western world? For example, there are 6.9 million dogs in Germany, where owners invest about 4.5 billion EUR per year to keep their dogs (Ohr, 2014). These costs can be calculated, but it is much more difficult to quantify the benefits.

However, there is various evidence that dog ownership produces considerable physical and mental health benefits and provides an important form of social support that encourages dog owners to walk (see Cutt, Giles-Corti, Knuiman, & Burke, 2007 and Cherniack & Cherniack, 2014 for reviews). For example, dog ownership is associated with a lower risk of death over the long term, which is possibly driven by a reduction in cardiovascular mortality (see Kramer, Mehmood, & Suen, 2019 for a meta-analysis). Dog owners are nearly four times more likely than non-dog owners to meet daily physical activity guidelines (Westgarth et al., 2019). There were also positive effects regarding mental health: military veterans with PTSD living with a service dog exhibited significantly less PTSD severity as well as less anger, anxiety, sleep disturbance, and alcohol abuse symptoms than veterans with PTSD without a dog (Rodriguez, Bryce, Granger, & O'Haire, 2018). Whereas many of these studies can only state correlations between dog ownership and health benefits (i.e. Cherniack & Cherniack, 2014), others used experimental interventions. For example, reduced cortisol levels were observed in students after a session of dog petting, compared to control groups who watched others pet animals or viewed images of animals (Pendry & Vandagriff, 2019). Another study found that dog therapy improved depressive symptoms and cognitive function in residents of long-term care facilities with mental illness compared to a group without dog therapy (Moretti et al., 2011). It is likely that all these benefits exceed the overall costs for dogs. Therefore, humans` bond to family dogs can also be considered as a mutualistic relationship, the result of the long domestication process.

1.3. Are dogs really "special"?

It is generally accepted that through domestication, dogs have changed in their morphology (i.e. Kaminski et al., 2019), in their genes and behavior (Li et al., 2014; von Holdt et al., 2017) and in particular in their cognitive skills (Hare & Tomasello, 2005; Kaminski & Marshall-Pescini, 2014; Miklósi, 2007). In a recent paper, Lea and Osthaus (2018) question the latter claim by asking in what sense dogs are "special". They compare dogs' cognition with that of three groups: other carnivores, other social hunters, and other domestic animals. They review studies about sensory cognition, physical cognition, spatial cognition, social cognition and self-awareness. Lea and Osthaus (2018) conclude that dog cognition is simply shaped by the particular characteristics of the three groups, and therefore dog cognition would not be exceptional (Lea & Osthaus, 2018).

However, that argumentation does not disprove dogs' exceptional status for our purpose of comparative analyses. Of course, as dogs *are* social carnivores, social hunters and domestic animals – it is appropriate to make comparisons with species of these groups. And it is not surprising that dogs perform similarly to wolves (carnivores), chimpanzees (social hunters) and horses (domesticated animals) in some tasks. Dogs belong to these groups, they faced similar selection pressures and thus, they have evolved comparable skills. Also, dogs' encephalization quotient, the brain-to-body ratio, is relatively standard for a mammal its size (Roth & Dicke, 2017).

However, most researchers have not claimed that dogs have evolved special cognitive skills *per se,* but rather skills that help them to function effectively in human societies (Hare & Tomasello, 2005; Kaminski & Marshall-Pescini, 2014; Miklósi, 2007). That goes beyond the selection pressures during domestication for other animals such as goats or chicken. In contrast to those – dogs are considered as part of the family (Serpell, 2016) and form a special relationship to humans (see chapter 1.1).

In the last 20 years, findings of comparative psychology have shed light on which cognitive skills dogs were selected for during this special domestication process. These skills can be grouped into three categories: communicative, perspective taking, and cooperation-related skills (Bräuer & Vidal Orga, in press; Hare & Tomasello, 2005; Kaminski & Marshall-Pescini, 2014). In the following, I will a) describe the findings about dogs in these three areas and b) put them into a comparative perspective with a special emphasize on how these skills might have changed during domestication. In Table 1 I summarize the classical paradigms that are used to investigate these skills in dogs.

Table 1: Important paradigms to test dogs' social cognitive skills (E = experimenter). Note that here and in the text the classification into the three categories (communicative, perspective taking, and cooperation-related skills) is sometimes ambiguous, as some studies fall into more than one category (i.e. communicative and cooperation-related skills).

Paradigm	**Details**	**Main Results**	**References (Examples)**
Communicative skills			
Use of human gestures	In an object choice task, food is hidden under one of two cups – invisible for the dog. E gives a communicative cue by for example pointing/gazing at the correct cup. The dog can then select one cup by approaching it.	Dogs select the correct cup.	(Bräuer et al., 2006; Clark et al., 2019)
Showing	While the dog – but not E – is present, a reward for the dog (toy or food) is hidden in one of four hiding places out of reach for the dog. The dog is then asked by E to show him / her where the reward is hidden.	E chooses the correct hiding place / Dogs show communicative strategies such as gaze alternation.	(Miklósi, Polgardi, Topál, & V, 2000; Heberlein, Turner, Range, & Virányi, 2016; Henschel, Winters, Müller, & Bräuer, 2020)
Social Referencing	Dog and owner are confronted with a scary new object for 2 minutes. Owner shows whether s/he is scared by the object or not by using voice, mimic, body posture.	Dogs check back to the owner / Dogs avoid or approach object in accordance with the information from the owner.	(Isabella Merola, Prato-Previde, & Marshall-Pescini, 2011; Isabella Merola, Prato-Previde, & Marshall-Pescini, 2012)
A not B Task	In the view of the subject, E hides a reward under box "A" – and the dog retrieves the reward. This repeated several times, but then, E moves the reward under box "B".	Perseveration error: dogs select under box "A" even though they saw reward hidden under "B".	(Topál, Gergely, Erdohegyi, Csibra, & Miklósi, 2009)

Paradigm	**Details**	**Main Results**	**References (Examples)**
Perspective taking			
Begging	Dogs can beg for food from either an attentive or a non-attentive person.	Dogs beg more from an attentive person.	(Gácsi, Miklósi, Varga, Topál, & Csanyi, 2004)
Forbidden food	E places food in front of the dog and forbids the dog to eat food. Dog's visual access to the food is either blocked (by barriers, closed eyes or darkness) or not.	Dogs approach forbidden food more and earlier, when E's visual access is blocked.	(Bräuer, Call, & Tomasello, 2004; Call, Bräuer, Kaminski, & Tomasello, 2003; Kaminski, Pitsch, & Tomasello, 2013)
Toys behind barriers	Two toys are placed on the dog's side of two small barriers (one opaque, one transparent). E is on the opposite side of the barriers, such that only the toy behind the transparent barrier is visible to E. Then E asks the dog to fetch the toy.	Dogs fetch the toy that E can see.	(Kaminski, Bräuer, Call, & Tomasello, 2009)
Cooperation			
Prosocial Choice	Subjects are given a choice between two reward combinations, either food is delivered to subject and the recipient (prosocial choice) or food is only delivered to the subject (selfish choice).	Mixed results, task might be too complex for dogs.	(Dale, Quervel-Chaumette, Huber, Range, & Marshall-Pescini, 2016; M. Quervel-Chaumette, Dale, Marshall-Pescini, & Range, 2015)
Door Open	E tries to enter a target room in order to retrieve a key. Dog can open the door to the target room by pushing a button. E either shows that she wants to enter the target room or not.	Dogs open the door when E communicates his/her goal in a natural way. / Dogs continue to open the door in repeated trials.	(Bräuer, Schönefeld, & Call, 2013)
Unsolvable problem	Dog is confronted with an unsolvable problem: a desirable piece of food is in a box and the dog cannot reach it. Owner / Caregiver stands behind the dog.	Dogs look back to the owner / Latency to look to the owner depends on persistence of dogs.	(Miklósi et al., 2003) (Sarah Marshall-Pescini, Rao, Virányi, & Range, 2017)
String pulling	Pairs of subjects have to coordinate their actions in a string-pulling task in order to retrieve food from a board.	Pairs of dogs do not perform well. / When tested with humans, dogs adjust their behavior.	(Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017; Friederike Range, Marshall-Pescini, Kratz, & Virányi, 2019)
Hunting-like situation	Pairs of subjects can approach a food reward behind a fence with two openings in it. A sliding door can block one opening but not both simultaneously. Subjects need to coordinate their actions, so that each is in front of a different opening, if one of them is to cross through and get food.	Most pairs solve the problem with significant variation in their performance. /Subjects coordinate better when they share the reward.	(Bräuer, Bös, Call, & Tomasello, 2013; Bräuer, Stenglein, & Amici, 2020)

1.3.1 Communication

Definition. Communication is defined here as the transfer of information from one entity to another, described in terms of the *sender-receiver model* (Shannon & Weaver, 1949).

Performance of dogs. When we observe dogs as senders of a signal, barking might be the most obvious form of their communication to humans. This is considered a result of dogs' adaptation to the human social environment (Pongrácz, Molnár, & Miklósi, 2010). Humans have developed a sophisticated and unique system of verbal and non-verbal auditory communication (i.e. Frühholz & Schweinberger, 2020), and it is hypothesized that therefore dogs could have developed a tendency to vocalize more during interactions with humans. Thus, dogs were selected for developing novel forms of the pre-existing vocalizations, which acquired different acoustic and functional characteristics, facilitating their communication with humans (Pongrácz et al., 2010; Siniscalchi, d'Ingeo, Minunno, & Quaranta, 2018; Taylor, Ratcliffe, McComb, & Reby, 2014). Interestingly, there are observations that feral and stray dogs vocalize less than family dogs, which may suggest that dogs vocalize mainly in communicative situations with humans (Kaminski & Marshall-Pescini, 2014). Indeed, humans – as receiver of these vocalizations – are able to derive information from the signal. In playback experiments it was shown that humans could infer the body size of a growling sender dog (Taylor, Reby, & McComb, 2009), but also successfully rate what situation the vocalization was recorded in (Pongracz, Molnar, Miklósi, & Csanyi, 2005).

Dogs also produce more human-like communicative signals, such as gaze alternation (Henschel et al., 2020; Kaminski, Neumann, Bräuer, Call, & Tomasello, 2011; Miklósi et al., 2000; Piotti & Kaminski, 2016). A typical situation in which gaze alternation occurs is the showing paradigm, first developed by Miklósi et al. (2000). Dog subjects witness how a reward is hidden out of their reach. Afterwards a human enters the room and the dogs indicate where the reward was hidden – often by alternating gazes between the hiding place of the reward and the human (Miklósi et al., 2000). However, the study by Heberlein et al. (2016) demonstrated that hand-raised and extensively socialized wolves are also able to use gaze alternation in a showing task. This suggests that socialization might play a bigger role in developing that signal than domestication (Heberlein et al., 2016).

Dogs' communicative behaviors might be more unique when we regard them as receivers of communicative signals. In neuroanatomical studies, Andics and colleagues (2014) have detected areas in the dog brain that are sensitive to the human voice and show a similar pattern to anterior temporal voice areas in humans (Andics, Gácsi, Faragó, Kis, & Miklósi, 2014). Data from behavioral studies complement and support theses findings: Dogs can distinguish between male and female speakers (Ratcliffe, McComb, & Reby, 2014), recognize humans by their voice (Adachi, Kuwahata, & Fujita, 2007) and they are sensitive to the emotional information in human vocalization (Albuquerque et al., 2016; Custance & Mayer, 2012; Huber, Barber, Faragó, Müller, & Huber, 2017; Taylor et al., 2014). Through training some dogs can also learn a large number of vocal labels to specific objects (Kaminski, Call, & Fischer, 2004; Kaminski, Fischer, & Call, 2008). In addition, it was shown that these dogs are able to combine the labels of objects and commands. Thus, they can learn to respond appropriate to commands like "fetch ball" and "paw ring" (Pilley & Reid, 2011; Ramos & Ades, 2012).

The most studied communicative behavior is the ability of dogs to use human cues. For example, dogs can use their sensitivity towards humans to learn about a potentially dangerous object by social referencing (Merola et al., 2011; Merola et al., 2012). Similar to children with their parents, dogs seek information about an object from their owner to guide their actions. Especially when presented with an ambiguous object, dogs react in accordance with the information given by the owner. If owners show concern, dogs inhibit their movements towards the object, but if owners show positivity, dogs move toward the object and interact with it sooner (Merola et al., 2011; Merola et al., 2012).

The setup most often used to test dogs' signal reception skills is the so-called object choice design, in which a food reward is hidden in one of two cups, out of the dog's view. When a human provides a communicative cue, such as pointing or gazing at the correct cup, dogs use these cues to locate the hidden food (Bräuer et al., 2006; see Miklósi & Soproni, 2006; Topál, 2014 and Krause & Mitchell, 2018 for reviews). Importantly, dogs attend to the referential nature of the human's gaze during the interactions (Kaminski, Schulz, & Tomasello, 2012; Soproni, Miklósi, Topál, & Csanyi, 2001; Teglas, Gergely, Kupan, Miklósi, & Topál, 2012) and the communicative intent of the human (Kaminski et al., 2012; see also Kaminski, Tempelmann, Call, & Tomasello, 2009), and they take the contextual information into account rather than blindly following a pointing gesture (Scheider, Grassmann, Kaminski, & Tomasello, 2011; see Kaminski & Nitzschner, 2013 for a review).

Influence of domestication. Dogs' ability to interpret human gestures probably evolved during domestication (Hare & Tomasello, 2005; Kaminski & Marshall-Pescini, 2014; Miklósi, 2007). Although there is mixed evidence of how shelter dogs with limited human contact use these gestures to locate hidden food (D'Aniello et al., 2017; Hare et al., 2010; Udell, Dorey, & Wynne, 2008), dogs overall perform much better at this task than hand-reared wolves. Even six-week-old puppies are already able to use human pointing gestures to locate hidden food (Gácsi et al., 2009; Gácsi, Kara, Belényi, & Miklósi, 2009; Hare, Brown, Williamson, & Tomasello, 2002; Riedel, Schumann, Kaminski, Call, & Tomasello, 2008; but see also Lampe, Bräuer, Kaminski, & Virányi, 2017).

In general, dogs are attuned to human ostensive cues such as eye contact and specific intonation patterns. These signals consist of a set of verbal and non-verbal cues that provide evidence of the sender`s intention to convey information. For example, when dogs have a choice between two containers, they often chose the one a human has ostensively cued, although they have seen that there is food (or more food) in the other container (Erdohegyi, Topál, Virányi, & Miklósi, 2007; Prato-Previde, Marshall-Pescini, & Valsecchi, 2008; Szetei, Miklósi, Topál, & Csányi, 2003). Moreover, Topál et al. (2009) found that dogs show a perseverative search error in the so-called A-not-B-task. Similar to young children, dogs persistently search for a hidden object at its initial hiding place even after observing it being hidden in another location. Ostensive cues from the human experimenter are crucial to the emergence of this perseverative search error. Importantly, human-reared wolves *(Canis lupus)* do not show dog-like context-dependent differences of search errors (Topál et al., 2009, see also Kis et al., 2012), suggesting that the sensitivity for ostensive cues has emerged during dog domestication.

Finally, it is very likely that dogs' vocal behavior also underwent considerable changes during the domestication process, as dogs vocalize in a wider variety of social contexts than wolves (Feddersen-Petersen, 2000; Pongrácz et al., 2010; Siniscalchi et al., 2018; Taylor et al., 2014).

In sum, dogs possess special communicative skills relative to other social mammals, including their closest living relatives. In particular, there is clear evidence that dogs perform differently than wolves in their communication with humans, especially when they vocalize, when they respond to human speech and when they react to human cues. This suggests that these skills must have evolved during domestication.

1.3.2 Perspective taking

Definition. Perspective taking is defined as the ability to assess what others can perceive. This skill is highly adaptive in various social contexts, such as communication, food competition or mating, but also in interspecies relationships, such as between predator and prey (i.e. Hare, Call, Agnetta, & Tomasello, 2000; Kummer, 1982). Flavell, (2002) distinguishes between two levels of visual perspective taking. In level 1, subjects understand that someone sees an object when she is looking at this object and if there are no obstacles blocking her view. Level 2 knowledge is more sophisticated, and involves understanding that even though both self and other can see the same object, it looks different when it is viewed from different positions (Flavell, Miller, & Miller, 2002).

Performance of dogs. Visual perspective taking has been intensely investigated in dogs via three basic experimental approaches. First, dogs have been tested in a situation in which they can beg for food. It was found that dogs begged more from an attentive human than from an inattentive human, indicating that they were indeed sensitive to human attention (Gácsi et al., 2004). In the second experimental approach, dogs were given a command – either to perform a certain action (i.e. lie down) or to refrain from doing something (i.e. do not eat the food). In the critical condition, the human could not see what the dog did. Either the human did not look at the dog (for example because her back was turned) or something blocked her visual access to the dog (a barrier or darkness). Dogs obeyed the command better when the human was able to see them (Bräuer et al., 2004; Call et al., 2003; Gácsi et al., 2004; Kaminski et al., 2013; Schwab & Huber, 2006; Virányi, Topál, Gácsi, Miklósi, & Csanyi, 2004).

Kaminski et al. (2009) took a third approach that went beyond explanations based on the presence of certain stimuli to assess whether one is being watched. They tested dogs in a cooperative situation in which the subjects were asked to fetch a toy. Two toys were placed on the dog's side of two small barriers (one opaque, one transparent). In the experimental condition, a human sat on the opposite side of the barriers, such that only the toy behind the transparent barrier was visible to her. She then told the dog to fetch the toy. Dogs preferentially fetched the toy that the experimenter could see, namely from behind the transparent barrier. Dogs did not have this preference in the two control conditions, in which the human could see either both or none of the toys. The authors concluded that even in the absence of behavioral cues, dogs were sensitive to humans' visual access, even if it differed from their own (Kaminski, Bräuer, et al., 2009).

Thus, in each of these three approaches, there was evidence that dogs are sensitive to the visual perspective of humans. However, dogs are also capable of *auditory* perspective taking – the ability to assess what humans can hear. One example of this is silently approaching food they know is forbidden (Bräuer, Keckeisen, et al., 2013; Kundey et al., 2010). Both studies also presented evidence that it is unlikely that this behavior is simply learned by experience with the owner. Dogs only try to retrieve forbidden food silently when silence is germane to obtaining food unobserved by the human gate-keeper, but not when humans are watching them during the approach or when they have left the room (Bräuer, Keckeisen, et al., 2013; Kundey et al., 2010). Moreover, shelter dogs with reduced human contact show similar patterns (Kundey et al., 2010).

Although dogs perform very well in assessing the human perspective, this skill is not outstanding in the animal kingdom as it is documented in other species as well. Chimpanzees, for example, show a level 1 understanding of visual perspective, understanding whether something is seen or not, similar to 2–3 year old children (Flavell et al., 2002). Although it is not clear whether chimpanzees, like domestic dogs, are able to distinguish between situations in which humans have their eyes open or closed and behave accordingly (Call et al., 2003), they show more sophisticated perspective-taking abilities than dogs. First, they can assess what humans can see – even in situations when they themselves are unable to see the human (Bräuer, 2014; Bräuer, Keckeisen, et al., 2013; Melis, Call, & Tomasello, 2006). Second, in contrast to dogs, chimpanzees also know what humans have seen in the past, i.e. that seeing leads to knowing (Hare, Call, & Tomasello, 2001; Kaminski, Bräuer, et al., 2009; Kaminski, Call, & Tomasello, 2008). Dogs probably mainly rely on what they themselves can perceive and have perceived when they assess what humans see or hear (Bräuer, 2014; Bräuer, Keckeisen, et al., 2013; but see also Catala, Mang, Wallis, & Huber, 2017; Kaminski et al., 2013).

Influence of domestication. It remains unclear whether dogs' sensitivity for the human perspective has developed during domestication. For practical reasons it is not possible to test wolves in some of the above-mentioned paradigms – they would not obey a command and they do not fetch objects. Udell et al. (2011) have tested wolves and dogs in a begging task. They concluded that wolves can also take into account the human perspective when begging from humans; at least they avoid begging when the human's back is turned (Udell & Wynne, 2011). However, Virányi and Range (2011) have questioned these results due to methodical flaws. As subjects had a choice between two humans calling their names, Udell et al. (2011) have found that subjects simply obeyed a familiar command better in a familiar context than in an unfamiliar one. Virányi and Range (2011) concluded that there is no evidence that wolves are sensitive to the attentional states of humans (Virányi & Range, 2011).

In sum, although perspective taking is well studied in domestic dogs, it remains to be determined whether this ability is mainly affected by domestication or by ontogeny and socialization of the individual (Udell & Wynne, 2011).

1.3.3 Cooperation

Definition. Cooperation is here defined as a behavior that is beneficial to another individual or to both individuals involved in a task (Melis & Semmann, 2010). One kind of cooperation is prosocial behavior, defined as a cooperative behavior on the part of one individual (the actor) that benefits another individual (the recipient) and occurs voluntarily (see Bräuer, 2015 and Melis & Warneken, 2016 for reviews). Following this definition, prosocial behavior includes several kinds of behavior, such as informing, instrumental helping and providing others with food

(Bräuer, 2015; Warneken & Tomasello, 2009). Warneken and Tomasello (2009) first argued that prosocial behavior has two main components: (1) a cognitive and (2) a motivational component. The cognitive requirement is that the actor has to understand the situation, i.e. the actor must recognize the recipient's goal and know how to fulfill that goal. The motivational component contains the question of whether the actor is willing to benefit the recipient (Bräuer, 2015; Melis & Warneken, 2016; Warneken & Tomasello, 2009).

Performance of dogs. Dogs cooperate with humans towards various objectives including protection, hunting, herding, rescuing, searching, servicing, and guiding (Miklósi, 2007; Serpell, 2016, see also chapter 1.1 and 1.2). In all these scenarios, dogs behave beneficially towards humans. However, in most of these cases it is unclear whether dogs actually understand human intentions and are motivated to cooperate with them, or whether they have simply been trained to follow specific commands or react to particular situations in certain ways (Bräuer, 2015; Bräuer, Schönefeld, et al., 2013; Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016).

In the literature, a number of different approaches have been used to investigate prosocial behaviors in domestic dogs (see Marshall-Pescini et al., 2016 and Bräuer, 2015 for reviews). In the prosocial choice task, subjects are given a choice between two reward combinations, one of which delivers a food item to the subject *and* the recipient (prosocial choice) and the other, which rewards only the subject (selfish choice). Thus, the subject can opt to consider the recipient's welfare as well as their own without extra costs – or only to reward themselves (see also Bräuer & Hanus, 2012). In this task, Quervel-Chaumette et al. (2015) found that dogs showed prosocial preferences towards conspecifics when they had a choice between pulling a tray that contained food for themselves and for the recipient and a tray that contained food only for themselves (Quervel-Chaumette et al., 2015). In contrast, in another version of the prosocial choice task, the token exchange task, in which dogs had the choice between a prosocial and a selfish token, subjects' choice could be explained by social facilitation and not by prosocial preferences (Dale et al., 2016). It was concluded that the token exchange task was probably too complex for the dogs (Dale et al., 2016), reflecting a cognitively limited understanding of the situation.

But given that dogs prefer humans to other dogs as social partners (see above), it is likely that dogs might cooperate better in such a task with a human partner than with another dog. One approach that has been used to test prosocial behavior in dogs towards humans is the informing paradigm (Bräuer, 2015; Kaminski et al., 2011). Although dogs – even without special training – inform naïve humans about the location of hidden food or toys (see also chapter 1.3.1, Heberlein et al., 2016; Miklósi et al., 2000; Savalli, Ades, & Gaunet, 2014), this behavior is found only when the result is beneficial for the dog. Kaminski et al. (2011) did not find evidence that dogs *helpfully* inform a human about a hidden object when their action is beneficial for the human partner only. However, again it is possible that while the motivational component was there, the cognitive capacity was lacking, i.e. that the dogs were just unable to recognize the human's goal and to realize that the human was searching for the object (Kaminski et al., 2011; see also Bräuer, 2014, 2015).

Dogs may not only have difficulties recognizing that the recipient requires help or information. In some situations, dogs might simply lack the knowledge of how to fulfill this goal. Macpherson and Roberts (2006) tested whether dogs seek help in an emergency: dogs' owners feigned a heart attack, and a bystander was available to whom the dogs could go for help. Nonetheless, the dogs did not solicit help from the bystander, likely because they did not know how to intervene in such a situation (Macpherson & Roberts, 2006).

With the aim of making the human goal as obvious as possible for the dog, Bräuer et al. (2013) used a set-up in which a human tried to enter a target room in order to retrieve a key. The tested dog could open the door to the target room by pushing a button. The help conditions, in which the human expressed that she wanted to enter the target room, were compared to a control condition, in which the human did not try to enter the room. Bräuer et al. (2013) found that dogs helped when the human communicated her goal in a natural way. Dogs did not differentiate between a familiar and an unfamiliar recipient (in contrast to Quervel-Chaumette et al., 2015), see above). More importantly, the dogs continued to open the door for the human over multiple trials without receiving any reward, indicating a high motivation to support her (Bräuer, Schönefeld, et al., 2013). In sum, and despite a limited sample size (Marshall-Pescini et al., 2016), this study suggests that dogs are highly motivated to help but have problems inferring the human's goal if it is not communicated clearly (Bräuer, Schönefeld, et al., 2013).

Surprisingly, in another study that enabled dogs to deliver food to humans by pulling a tray, they did not show prosocial preferences toward either familiar or unfamiliar human recipients (Quervel-Chaumette, Mainix, Range, & Marshall-Pescini, 2016). However, when compared with the findings of the same set-up with a dog recipient (Quervel-Chaumette et al., 2015; see above), dogs spent more time gazing at human recipients than at dog recipients (Quervel-Chaumette et al., 2016). The human recipients were not allowed to communicate with the dogs in any way, but this lack of communication from the human may have been very unnatural to the dogs. Quervel-Chaumette et al. (2016) conclude that human communication in such contexts highly affects dogs' responses.

Thus, the findings of both Bräuer et al. (2013) and Quervel-Chaumette et al. (2016) underline the important role of the human partner's behavior, and of exactly how s/he communicates her/his goal in a cooperative interaction. Overall, dogs seem to possess high motivation, but insufficient understanding of the situation to engage in complex forms of cooperation, such as prosocial behavior (Bräuer, 2015; Bräuer, Schönefeld, et al., 2013). It is likely that the communicative interaction with the human recipient and experience with the situation is crucial for a dog to recognize and fulfill the recipient's goal. The motivation of the dog might be influenced by the relationship to the recipient and by breed differences.

Are dogs' cooperative skills outstanding among animals? Chimpanzees, for example, help others in a variety of situations, such as in agonistic and feeding contexts (see Bräuer, 2015; Melis & Semmann, 2010; Yamamoto & Tanaka, 2009 for reviews). But compared to dogs, our closed living relatives are not as motivated to please or benefit others. Thus, the reason why chimpanzees sometimes fail to behave prosocially is not their inability to recognize the recipient's goal, but rather a lack of motivation to benefit others. This is in contrast to dogs, which are motivated to help but sometimes lack the cognitive abilities to understand the situation (see Bräuer, 2015 for a review).

Another line of research asks how dogs behave as the recipient of potential help. Miklósi et al. (2003) tested dogs in a manipulation task, in which dogs are suddenly faced with an insoluble version of the same task. In that situation dogs looked at their owner. Miklósi et al. (2003) suggested that when dogs look into a human's face they are able to initialize and maintain communicative interaction that leads to positive feedback by the humans (Miklósi et al., 2003).

Influence of domestication. Whether dogs in that above-mentioned manipulation task intentionally request help remains highly speculative, but the comparison with hand-raised wolves is crucial here. Socialized wolves do not look to their caregiver in the same situation. It was concluded that the readiness of dogs to look at the human face in that situation that cannot be achieved in wolves even after extended socialization (Miklósi et al., 2003). Although there are differences within dogs' persistence in the unsolvable task, domestication seems to play an important role here as free-ranging dogs, despite little exposure to dog-human communication, behaved similarly to other dogs (Marshall-Pescini et al., 2017).

Thus, the question is whether dogs' cooperative skills have evolved during domestication (Bräuer et al., 2020; Marshall-Pescini et al., 2017; Friederike Range et al., 2019). Some authors have speculated that one reason dogs were domesticated was that social structure and hunting behavior were similar for early humans and the ancestors of dogs, as wolves also hunt and breed cooperatively (Clutton-Brock, 1977; Coppinger & Coppinger, 2001; Mech & Boitani, 2003). Cooperation skills probably already existed in dogs' ancestors, as recent studies with hand-reared wolves socialized with humans have confirmed that these wolves show high social attentiveness and tolerance and are highly cooperative. Such characteristics may have provided a good basis for the evolution of dog-human cooperation (see Range & Virányi, 2015 for a review). Dogs are sometimes outperformed by wolves in setups that require cooperation with conspecifics (Marshall-Pescini et al., 2017), whereas in other tasks both species perform similarly (Bräuer et al., 2020; Ostojić & Clayton, 2014). It is conceivable that dogs' ancestors already possessed cooperative skills and were then selected to be good cooperative partners specifically to humans (Bräuer, 2015; Bräuer et al., 2020; Hare & Tomasello, 2005).

Thus, dogs' motivation to work with humans, their increased submissive inclinations, and their readiness to look into the human face have probably developed during domestication (Range et al., 2019). These skills minimize conflicts over resources and leads to successful cooperation between the humans and dogs.

1.4. This thesis

The aim of this habilitation thesis is to characterize the dog-human relationship with diverse perspectives on dog cognition and the dog-human bond. In the following, I give a short overview about the eleven papers of the theses. I will outline the different approaches I used and present the most important findings and conclusion for each paper.

I start with a general paper about the field of Comparative Psychology (Bräuer et al., 2020). Here we describe the comparative approach and discuss the challenges in the field. In particular, we argue that the term "cognition" has often been applied from an anthropocentric rather than a biocentric viewpoint. As a result, researchers tend to overrate cognitive skills that are human-like and assume that certain skills cluster together in other animals as they do in our own species. We emphasize that specific physical and social environments create selection pressures that lead to the evolution of certain cognitive adaptations. In accordance with the biocentric approach, we advocate a broader empirical perspective and argue that, to better understand animal minds, comparative researchers should focus on questions and experiments that are ecologically valid (Bräuer et al., 2020).

In this paper, we use dogs as an example of a species that shows outstanding cognitive skills in the domain of communication (see chapter 1.3.1) but performs poorly in other domains, such as physical cognition. Together with many other findings, this suggests that cognitive skills can evolve in a domain-specific manner, often independently from each other (Bräuer et al., 2020; Macphail, 1982). We also emphasize that the modality in which a task is presented is crucial for detecting the cognitive potentials of a given species. Although some skills might be modality-independent to some extent (at least for humans, i.e. Young, Frühholz, & Schweinberger, 2020), others are clearly not. For example, most data on dogs' understanding of their social and physical environment is based on performance in the visual or auditory modality (Bräuer, Keckeisen, et al., 2013; Kaminski et al., 2004; Kundey et al., 2010). But in contrast to humans who can easily manage their daily life with an impaired sense of smell (Croy, Negoias, Novakova, Landis, & Hummel, 2012), for dogs, olfaction is the most relevant sense for exploring their environment (Gazit & Terkel, 2003; Horowitz, Hecht, & Dedrick, 2013; Jezierski, Ensminger, & Papet, 2016). We therefore call for dog studies that are based on olfaction, not on vision or hearing (i.e. Bräuer & Belger, 2018).
Bräuer, (2014) is a book chapter that gives an overview of what dogs understand about others, and in particular about humans. I summarize to what extent dogs show theory-of-mind-like skills such as perspective taking, intention reading and the attribution of mental states to others. I conclude that dogs react appropriately in many social situations, using a four-part 'toolkit'. First, they are extremely attentive and interested in what humans are doing. Second, they have excellent learning abilities: they are very flexible and quick to make associations and to generalize from known to similar situations in their human environment. Third, they are able to read subtle cues of human behavior. Finally, they have extensive experience with different communicative situations. What is often considered as 'understanding' of the owner can be developed without much insightful recognition of others' subjective mind states (i.e. Topál, Erdõhegyi, Mányik, & Miklósi, 2006; Udell, Dorey, & Wynne, 2011; Whiten, 1997). Thus, dogs solve many social problems successfully but probably often use different strategies than humans do.

The following papers address domains in which dogs might show unique cognitive skills, such as communication, perspective taking and cooperation (see also chapter 1.3).

Henschel et al. (2020) is about communication between dogs and their owners. We employed a task in which dogs could inform their naïve owners about their hidden toy. The position of the hiding places varied in two conditions, requiring either high or low precision in indicating the target location. We found that the spatial set-up affected success and choice of showing strategies. However, dogs did not adjust their showing effort according to different spatial set-ups. Instead, owners influenced the showing behavior of their dogs. Owner prompting generally increased the effort of their dog's showing behavior. Moreover, owners also influenced their dog's showing accuracy (and thereby success). This influence, however, tended to be obstructive. Thus, our findings replicate previous findings that dogs without special training are able to successfully communicate with a human about a hidden object (Cavalli, Carballo, Dzik, & Bentosela, 2020; Gaunet & Deputte, 2011; Heberlein et al., 2016; Kaminski et al., 2011; Miklósi et al., 2000; Piotti & Kaminski, 2016; see chapter 1.3.1) and that showing behavior in dogs is a means to successfully communicate the location of a hidden object. We could also show how much the owners influence the dogs' showing accuracy in the task by analyzing how encouragement increased mistakes in dogs' showing accuracy. These results could also have impacts on the training of dogs and handlers in fields where dogs are working professionals. In general, these findings support the idea that dog-human communication has evolved during domestication (see chapter 1.3.1).

In the next study, Bräuer, Keckeisen, et al. (2013), we also used a common situation between dog and owner: this time the human forbade the dog to eat a piece of food. Here we examined perspective taking. In particular, we investigated whether dogs know what a human can see and hear, even when dogs themselves are unable to see the human. Dogs faced a task in which the forbidden food was placed in a tunnel that they could retrieve by using their paw. Whereas the dogs could not see the experimenter during their food retrieval attempts, the experimenter could potentially see the dog's paw. In the first experiment, dogs could choose between an opaque and a transparent side of the tunnel, and in the second experiment, they could choose between a silent and a noisy approach to the tunnel. The results showed that dogs preferred a silent approach to forbidden food but that they did not hide their approach when they could not see a human present. We concluded that dogs probably rely on what they themselves can perceive when they assess what the human can see and hear (but see Kaminski et al., 2013). Thus, our findings add to the growing literature about the perspective taking abilities of dogs (see chapter 1.3.2).

Another skill that might be unique for dogs is their ability and motivation to cooperate with humans (see chapter 1.3.3). As stated above, I use the Melis and Semmann (2010) definition of cooperation, i.e. a behavior that is beneficial to another individual or to both individuals involved in a task (Melis & Semmann, 2010). In the review Bräuer (2015), I discuss one kind of cooperation of domestic dogs (prosocial behavior) in comparison to other species. I summarize the findings under the headline "I do not understand, but I care: the prosocial dog". Thus, I address the cognitive and motivational skills required for the dog actor in order to support the recipient. I conclude that dogs display a number of prosocial behaviors when they are able to infer the goal of the human and when they understand how to fulfill it (see chapter 1.3.3). In Bräuer, Schönefeld, et al. (2013) we used a setup in which we tried to make the human goal as obvious as possible and, consequently, dogs helped a desperate human by opening a door.

The studies Bräuer, Bös, et al. (2013) and Bräuer et al. (2020) deal with cooperation within dogs and within wolves. We used a problem-solving paradigm that involved aspects of a hunting-like situation. Pairs of subjects could approach a food reward behind a fence with two openings in it. A sliding door operated by the experimenter could block one opening but not both simultaneously. Subjects needed to coordinate their actions, so that each was in front of a different opening, if one of them was to cross through and get food. This paradigm is not only a cooperative situation, but also a social dilemma in which an individual benefits from being selfish, unless the partner also chooses the selfish alternative, in which case the whole dyad loses. We found that most dyads solved the problem with significant variation in their performance but no differences between species. Subjects coordinated better when they shared the reward. We did not observe the subjects monitoring one another, suggesting that their solutions were achieved by each individual attempting to maximize for itself. We concluded that the cooperative behavior of dogs and wolves depends on many factors, including rank, type of task, and tolerance within the dyad. Our results also suggest that the abilities needed to coordinate their actions were already present in the dog-wolf ancestor. Thus, as described in chapter 1.3.3, dogs and wolves may show similar cooperative skills with their conspecifics but dogs might cooperate better with humans, as they have been selected to cooperate specifically with humans during the domestication process (Bräuer, 2015; Bräuer, Schönefeld, et al., 2013; Range et al., 2019).

Another often overlooked domain in which dogs show outstanding skills is their excellent sense of smell. Although there are some studies about dogs' general olfactory skills, it remains mainly unclear how odors are processed. In other words, we know much about cognitive skills and olfaction in dogs, but there is a lack of knowledge about how the two are linked or how olfaction influences cognitive processes in dogs. Their olfactory acuity, that is, their ability to sense chemicals by smell at low concentrations, is excellent (Köhler, 2004; Miklósi, 2007; Walker et al., 2006; but see also Horowitz et al., 2013). They can also learn to recognize various odors (Hall, Glenn, Smith, & Wynne, 2015; Williams & Johnston, 2002). In detection tasks, they indicate the presence of specific trained odors. Dogs can be trained to discriminate between and indicate the presence of a great variety of odors (see chapter 1.2). In addition, dogs are also able to match odors (Marchal, Bregeras, Puaux, Gervais, & Ferry, 2016), that is, they can confirm or deny that two odors come from the same source (Brisbin & Austad, 1991; Schoon, 1996; Vonk & Leete, 2017). They are effective in following tracks to find a target (i.e. Hepper & Wells, 2005; Woidtke, Dreßler, & Hädrich-Babian, 2017). Bräuer & Belger (2018) investigated how dogs represent objects via odors, that is, whether they have an expectation of something specific when smelling an odor trail. Dogs were presented with a violation-of-expectation paradigm in which they could track the odor trail of one target (Target A), but at the end of the trail, they found another target (Target B). We explored (a) what dogs expect when they smell the trail of an object, (b) how they search for an object, and (c) how their educational background influences their ability to find a hidden object, by comparing family dogs and working dogs that had passed exams for police or rescue dogs. We found that all subjects showed flexible searching behaviors, with the working dogs being more effective but the family dogs learning to be effective over trials. In the first trial, dogs showed measurable signs of "surprise" (i.e., further searching for Target A) when they found Target B, which did not correspond to the odor of Target A from the trail. We conclude that dogs represent what they smell and search flexibly, independent of their educational background. Thus, not only is their sense of smell itself quite outstanding, similar to other microsmatic animals, but so also the related cognitive skills.

Finally, I also investigated cognitive skills of dogs in domains in which they do not show outstanding skills due to their domestication, but perform similarly to other social mammals and often worse than, for example, great apes, our closed relatives. In Belger & Bräuer (2018) we investigated metacognition in dogs. In particular, we investigated whether dogs were sensitive to the information that they themselves had or had not acquired. We conducted three consecutive experiments in which dogs had to find a reward hidden behind one of two V-shaped fences with a gap at the point of the V. This setup allowed us to distinguish between selecting one of the fences by walking around it and seeking additional information by checking through the gap in the fence. We varied whether dogs had visual access to the baiting procedure or not. In addition, we manipulated the type and quality of reward as well as the time delay between baiting and analyzing if the dogs' searching behavior was affected. We found that dogs checked more often through the corner of the V-shaped fence when they had not seen where the reward was hidden. Interestingly, dogs rewarded with toys selected the correct fence more often than dogs rewarded with food. Even though the dogs' performance was not affected by the food quality condition, dogs were significantly faster at fetching a high quality food reward as opposed to a low-quality food reward. When testing whether forgetting and checking would increase as a function of delay, we found that although dogs slightly decreased their success in finding the food when time delays were longer, they were not more likely to check before choosing. We show that dogs seek additional information in uncertain situations, but their behavior in uncertain situations is less flexible compared to great apes or human children (Call, 2010; Call & Carpenter, 2001).

In Silva et al. (2020), the last study presented in this thesis, we investigated behavioral matching – also called behavioral mimicry (Duranton & Gaunet, 2015). During social interactions, humans reflexively mimic others to communicate affinity (Bavelas, Black, Lemery, & Mullett, 1986) and to create rapport, leading to increased feelings of affiliation (Lakin, Jefferis, Cheng, & Chartrand, 2003), empathy (De Coster, Verschuere, Goubert, Tsakiris, & Brass, 2013), and trust (Stel, van den Bos, Sim, & Rispens, 2011) in the mimicked. We investigated in two experiments whether dogs develop an increased affiliation towards a human who mimics them. In particular, we tested whether dogs prefer the one of two humans who display matching behavior (walking). Dogs showed no increased preference for the human experimenter who matched the dogs' walk. This can be due to methodical problems. For example, it is conceivable that the situation with three individuals (i.e. the subject and two humans) is too complex for dogs (Nitzschner, Melis, Kaminski, & Tomasello, 2012; see also Bräuer & Amici, 2018), or the body movements of humans and dogs are too different for dogs to match them. But it is also possible that dogs do not have increased feelings of affiliation, empathy or trust when they are mimicked by humans. In that case, either behavioral matching is not in their repertoire although it is thought to be adaptive (Dijksterhuis & Bargh, 2001), or dogs only show behavioral matching with conspecifics.

2. Scientific papers

2.1 Bräuer, J., Hanus, D., Pika, S. Gray, R., Uomini, N. (2020).
Old and new approaches to animal cognition: There is not "one cognition".
Journal of Intelligence, 8(3), 28.

2.2 Bräuer, J. (2014).
What dogs understand about others. In: J. Kaminski & S. Mashall Pescini (eds)
The Social Dog: Behavior and Cognition, Elsevier publishers.

2.3 Henschel, M., Winters, J., Müller, T.F. & Bräuer, J. (2020).
Effect of shared information and owner behavior on showing in dogs *(Canis familiaris).*
Animal Cognition, 23(5), 1019–1034. (Master thesis under my supervision.)

2.4 Bräuer, J., Schaub, M., Pitsch, A., Kaminski, J., Call, J., & Tomasello, M. (2013).
Domestic dogs conceal auditory but not visual information from others.
Animal Cognition, 16(3), 351–359.

2.5 Bräuer, J. (2015).
I do not understand but I care: the prosocial dog. *Interaction Studies, 16*(3), 254–263.

2.6 Bräuer, J., Schönefeld, K., & Call, J. (2013).
When do dogs help humans? *Applied Animal Behaviour Science, 148,* 138–149.

2.7 Bräuer, J., Bös, M., Call, J., & Tomasello, M. (2013).
Domestic dogs *(Canis familiaris)* coordinate their actions in a problem–solving task.
Animal Cognition, 16(2), 273–285.

2.8 Bräuer, J., Stenglein, K. & Amici, F. (2019).
Dogs *(Canis familiaris)* and wolves *(Canis lupus)* coordinate with conspecifics in a social dilemma. *Journal of Comparative Psychology, 134*(2), 211–221.

2.9 Bräuer, J., & Belger, J. (2018).
A ball is not a Kong: Odor representation and search behavior in domestic dogs *(Canis familiaris)* of different education. *Journal of Comparative Psychology, 132*(2), 189-199.

2.10 Belger, J. & Bräuer (2018).
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Journal of Learning & Behaviour 46(4), 398–413. (Master thesis under my supervision.)

2.11 Silva, K., Bräuer, J., de Sousa, L. et al. (2020).
An attempt to test whether dogs *(Canis familiaris)* show-increased preference towards humans who match their behavior. *Journal of Ethology, 38,* 223–232.
(Karine Silva and me contributed equally to this work.)

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Review

Old and New Approaches to Animal Cognition: There Is Not "One Cognition"

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Abstract: Using the comparative approach, researchers draw inferences about the evolution of cognition. Psychologists have postulated several hypotheses to explain why certain species are cognitively more flexible than others, and these hypotheses assume that certain cognitive skills are linked together to create a generally "smart" species. However, empirical findings suggest that several animal species are highly specialized, showing exceptional skills in single cognitive domains while performing poorly in others. Although some cognitive skills may indeed overlap, we cannot a priori assume that they do across species. We argue that the term "cognition" has often been used by applying an anthropocentric viewpoint rather than a biocentric one. As a result, researchers tend to overrate cognitive skills that are human-like and assume that certain skills cluster together in other animals as they do in our own species. In this paper, we emphasize that specific physical and social environments create selection pressures that lead to the evolution of certain cognitive adaptations. Skills such as following the pointing gesture, tool-use, perspective-taking, or the ability to cooperate evolve *independently* from each other as a concrete result of specific selection pressures, and thus have appeared in distantly related species. Thus, there is not "one cognition". Our argument is founded upon traditional Darwinian thinking, which—although always at the forefront of biology—has sometimes been neglected in animal cognition research. In accordance with the biocentric approach, we advocate a broader empirical perspective as we are convinced that to better understand animal minds, comparative researchers should focus much more on questions and experiments that are ecologically valid. We should investigate nonhuman cognition for its own sake, not only in comparison to the human model.

Keywords: animal cognition; comparative psychology; comparative cognition; animal psychology; animal minds; cognitive evolution

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1. Current Hypotheses on Animal Cognition

Some of the most enduring questions in contemporary behavioral science concern which cognitive skills humans share with other animal species and which are uniquely human (Premack and Woodruff 1978; Byrne 1996; Tomasello 2019). One prevalent approach to this question is the comparative approach, which pinpoints similarities and differences between human and nonhuman animals to then draw informed inferences about the evolution of human behavior and cognition (Heyes and Huber 2000; Tennie et al. 2009; Borrego 2017). The term "cognition" (see Box 1) refers to "adaptive information processing in the broadest sense, from gathering information through the senses to making decisions and performing functionally appropriate actions, regardless of the complexity of any internal representational processes that behavior might imply" (Shettleworth 2000, p. 43). According to this definition, animals receive inputs to their brain through, e.g., vision, hearing, touch, smell, taste, electric fields, air currents, or magnetic fields. The brain processes these inputs and controls behaviors. Behavior is the result of an animal's decision to act on the inputs received. This definition of cognition encompasses all possible inputs and actions that are the result of mental processes. In this paper, we rely on this definition without distinguishing between more or less complex or sophisticated forms of cognition, as that would involve a judgment of what qualifies as "sophisticated", which is what we want to avoid here, as we argue below. We are aware that animals may often use simple mechanisms to solve their social and physical problems, reserving the more complex mechanisms for situations in which the simpler mechanisms do not work. The important point for us is that individuals show flexible behavior and do not rely on innate or learned strategies only. In this paper, we show how this broad definition of cognition is at odds with narrow views that are still prevalent in viewing cognition as "one cognition", in contrast to the biocentric perspective that focuses on each species in its own evolutionary history, which we support here.

Box 1. Definitions used in this article.

Comparative Psychology: Investigation of similarities and differences in multiple animal species—including humans—using techniques that encompass everything from observational studies in nature to neurophysiological research in the laboratory (Call et al. 2017; Tomasello and Herrmann 2010).

Cognition: Adaptive information processing in the broadest sense, from gathering information through the senses to making decisions and performing functionally appropriate actions, regardless of the complexity of any internal representational processes that behavior might imply (Shettleworth 2000).

Physical Cognition: Knowledge of the physical world (Tomasello and Call 1997).

Social Cognition: Knowledge of the social world (Tomasello and Call 1997).

Animal Cognition: Describes the mental capacities of nonhuman animals and the study of those capacities. The field developed from comparative psychology, including the study of animal conditioning and learning (Shettleworth 2000.)

We now know that cognition comes in many forms across a huge diversity of nonhuman animal species (i.e., Shettleworth 1998; McMillan et al. 2015; Vonk 2016; Allen 2017; Call et al. 2017). The first studies on the complexity of animal minds were carried out by psychologists and traditionally centered on the phenomenon of learning (Kamil 1987; Hanus 2016; Maestripieri 2003), for instance, in a few model species such as rats and pigeons (Beach 1995; Hodos and Campbell 1969; Papini 2002). However, they were ignoring the biological context of behaviors, i.e., their potential adaptive implications (i.e., Kamil 1987). In a pioneering article entitled "A synthetic approach to the study of animal cognition", Kamil (1987) argued for a broader approach to understanding animal minds and stressed two main points: (1) that the range of investigated skills needs to be expanded—i.e., to study phenomena besides learning, and (2) that researchers should consider ecological factors to situate their findings within a comparative evolutionary framework (Kamil 1987; see also Shettleworth 1983; Bates and Byrne 2007; Bshary et al. 2011).

Since the publication of that article, researchers in the fields of comparative cognition, animal psychology, cognitive archaeology, and cognitive biology (Shettleworth 2009; Fitch et al. 2010) have made considerable advances in tackling different cognitive and behavioral elements that form the layered system of cognition. Consequently, the range of skills and species studied has now significantly increased. In particular, in the last 20 years, there has been a growing interest in these fields (see Shettleworth 2009 for an overview), resulting in increasing citation rates from about 400 citations per year in 2000 to over 4000 citations in 2019 (Table 1). The research in these fields focused on two major challenges animals have to deal with: foraging and maintaining social relationships (Tomasello and Call 1997; Seyfarth and Cheney 2003; Seed et al. 2009). To date, the majority of the studies have examined distinct aspects of physical cognitive skills such as tool-use, memory, future planning, and numerosity, as well as social cognitive skills such as communication, cooperation, and social learning (Call et al. 2017; Shettleworth 1998; Shettleworth 2010; De Waal and Tyack 2009; Reznikova 2007; Wasserman and Zentall 2006; Zentall and Wasserman 2012).

Table 1. Citations of animal cognition papers from Web of Science, all databases 1894–2020 (accessed 25 April 2020), for the following search terms in the "topics" field: "animal cognition", "animal psychology", "cognitive ethology", "comparative cognition", "comparative psychology".

Topic Search Term	Number of Publications	Total Citations	Total Excluding Self-Citations	Citations Per Year in 2000	Citations Per Year in 2019
animal cognition	1202	18,550	17,760		
animal psychology	435	3329	3295		
cognitive ethology	216	3242	3051		
comparative cognition	642	8379	7822		
comparative psychology	1376	13,496	12,587		
Any of the above	**3657**	**43,590**	**39,619**	**396**	**4394**

Kamil's (1987) first suggestion was heeded. However, Kamil's (1987) second suggestion, to adopt a biocentric view of cognition by considering ecological factors, which is quite natural for biologists, has been at times neglected by psychologists (Sewall 2015; Macphail 1982; Eaton et al. 2018; Vasilieva 2019). We see two main problems that hinder current research in comparative psychology. Firstly, an anthropocentric approach dominates research (Shettleworth 2010). Secondly and relatedly, cognition is viewed as a cluster of skills that evolve together, as in humans. We see that these positions are still prevalent in comparative psychology (Vasilieva 2019).

In particular, psychologists have postulated several prominent hypotheses to explain why certain species are considered "intelligent". These hypotheses assume that cognitive skills are linked together to create a broad (or universal) instantiation of intelligence, often termed cognitive flexibility (for an overview, see Allen 2017). For instance, the *Social Intelligence Hypothesis*—also termed the Machiavellian Intelligence Hypothesis or Social Brain Hypothesis (Dunbar and Shultz 2007; Humphrey 1976; Jolly 1966; Byrne and Whiten 1988)—seeks to explain the origins of primate intelligence in their sociality. It predicts that natural selection favored those individuals living in complex social environments, such as fission–fusion societies, for their ability to deal with the frequent unpredictable situations that occur in social interactions in such societies. Thus, intelligence is triggered by the demands and complexity of sociality. In a similar vein, the *Cognitive Buffer Hypothesis* predicts that large brains facilitate the construction of behavioral responses to unusual, novel, or complex socioecological challenges. This buffer effect should increase survival rates and favor a longer reproductive life, thereby compensating for the costs of delayed reproduction (Sol 2009). The *Domestication Hypothesis* (Hare and Tomasello 2005; Hare et al. 2012) proposes that selection for reduced aggression in some species, such as in domesticated species like dogs, but also in wild bonobos (*Pan paniscus*), caused a set of cognitive changes, including increases in levels of social tolerance, sensitivity to social cues, cooperation, risk aversion, occurrence of juvenile behaviors, and reduction of spatial memory. Similar to the Social Intelligence Hypothesis, the Domestication Hypothesis argues that a whole suite of cognitive skills was triggered by a single factor. The *Cooperative Breeding Hypothesis* (Burkart et al. 2016; Burkart and Van Schaik 2010; Burkart et al. 2009) considers the practice of cooperative breeding to have caused a "cascade" of effects on cognition such as changes in general intelligence, language, prosociality and social tolerance, teaching, and tool-making skill. It proposes that human cognitive abilities were amplified by our prosocial tendencies, again placing sociality at the center of a suite of changes. The *Technical* (or *Physical*) *Intelligence Hypothesis* proposes that great apes' complex food manipulations using tools caused the emergence of an ability for "flexible plan-building", which involves a representational ability that could then be applied to living entities like conspecifics (Byrne 1997). This ability allowed great ape ancestors to view other individuals as intentional agents, and thus to engage in social manipulations involving complex planning. Hence, the Technical Intelligence Hypothesis also predicts that tool-use and sociality are linked by a shared ability for flexible action planning.

This brief survey of selected major hypotheses exemplifies the problematic assumption that "intelligence" results from a cluster of cognitive skills that are linked together and are elicited by *single* evolutionary conditions and factors that create a set of selection pressures. All these hypotheses seek to explain why cognitive skills have evolved in particular species, but not in others—there is evidence for all of the hypotheses presented above, but they do not explain the whole picture. The data supporting these hypotheses have been discussed elsewhere (i.e., Burkart et al. 2016). However, cognitive arrays are the result of species-typical adaptions to their *whole* ecological and social environments (Burkart et al. 2016).

Hence, the aim of the current paper is to counteract an overly simplistic reading of these hypotheses by emphasizing the cases that contradict them, showing that cognitive skills are often not linked together.

The related problem which arises from the "one cognition" assumption is that, implicitly or explicitly, the presented hypotheses consider human cognition as the maximum and standard capacity (Vasilieva 2019). This idea is exemplified in cognitive niche construction theory, which considers human cognition to have evolved into the most flexible and adaptable form of intelligence due to a runaway feedback process of cumulative culture and developmental plasticity (Sterelny 2003; Laland et al. 2000). Cognitive abilities of target species are subsequently compared and measured according to whether and how much they match the suite of human abilities. Historically, comparison against human standards was one of the original roles of animal cognition research derived from comparative psychology (Beran et al. 2014; Shettleworth 1998; Kamil 1987; Box 1). As interest in other minds shifted from humans to nonhuman species, methods of human psychology were often transferred to other animals. However, this approach can only produce a restrictive, anthropocentric view of cognitive evolution that ignores the incredible diversity of cognitive skills present in the world (Bates and Byrne 2007). On the contrary, considering each species in its own right—in accordance with traditional Darwinian thinking (Darwin 1859)—allows us to reveal the evolutionary, developmental, and environmental conditions that foster the growth of certain unique abilities in the young of a species, or the convergence of skills shared among species (Griffiths and Stotz 2000; Shettleworth 2009; Shettleworth 2010). The core of this biocentric view is expressed in Darwin's metaphor: "Nature [selects] only for that of the being which she tends. Every selected character is fully exercised by her, and the being is placed under well-suited conditions of life." (Darwin 1859, p. 83).

We believe the criticism raised by Shettleworth in 2010 is still valid today: "Although the extent of human–animal cognitive similarity is undoubtedly a key issue for comparative psychology, it sometimes seems the agenda is to support anthropomorphic interpretations" (Shettleworth 2010, p. 2). One example is the investigation of the understanding of the human pointing gesture. There are a plethora of comparative studies in which animals are required to use human gestures—mainly the pointing gesture—to locate hidden food (reviewed by Krause et al. 2018; i.e., Bräuer et al. 2006). From a biocentric point of view, it does not make much sense to ask whether, for example, a nonhuman ape follows a human gesture as this task is not ecologically relevant to the ape. Firstly, humans are not relevant; secondly, although apes produce pointing gestures to communicate with humans in captivity (Leavens et al. 1996; Halina et al. 2018), they rarely inform others about external events in the wild (Burrows et al. 2013). Thirdly, due to their competitive social systems, nonhuman apes would not be expected to inform others about the location of hidden food (Sterck et al. 1997; Wittig and Boesch 2003; Bräuer et al. 2006). Not surprisingly, for biologists, it turned out that apes and most of the animal species tested did not reliably follow the human pointing gesture to locate hidden food unless they were enculturated (i.e., had a lot of intense experience with humans) or belonged to a species that was domesticated. It is interesting that domesticated animals follow the pointing gesture, but it is not surprising that apes have problems doing so, given their social, ecological, and evolutionary backgrounds. Similarly, the studies of language-trained apes (reviewed in

Gillespie-Lynch et al. 2014) give us some insight into what these animals are capable of with a large amount of training, although during evolution, there was no selection pressure to communicate with humans. Thus, these studies do not tell us much about apes, but rather about humans' specially evolved skills such as language (Morgan et al. 2015; Uomini and Meyer 2013; Uomini 2009; Uomini 2014; Uomini 2017; Uomini and Ruck 2018). Instead, these studies can tell us what these species are able to learn about situations they do not encounter naturally. For example, if some chimpanzee individuals can learn such "unnatural" skills as following the human pointing gesture or using a lexigram language, this shows us chimpanzees' cognitive flexibility and can help us to understand the factors leading to innovation and their ability to learn and generalize. In contrast, the aim of a less anthropocentric approach should be to investigate their natural forms of communication and not to force them to use human-like communication.

In this paper, we discuss two related problems, namely, the assumption that cognition evolves as a cluster of skills as in humans, and the anthropocentric approach, following the criticisms raised by Shettleworth (1998, 2009, 2010). However, despite the subsequent progress noted by Shettleworth (2009), we still consider it necessary to advocate for a broader perspective on cognitive evolution. To be clear, we do not argue against comparative psychology as a valid discipline to gain insights into animal cognition; rather, we argue against *how* comparisons between humans and other animals are carried out by favoring the anthropocentric issues mentioned above. If we want to account for the fascinating variety of animal minds, comparative scientists should focus on skills that are ecologically relevant for a given species (Section 2), as well as skills in which humans are outperformed by other animals (Section 3). Moreover, the experimental operationalization of a research question should be ecologically valid, i.e., using naturalistic situations with relevant test settings that match naturally occurring contexts and—most importantly—the modality must be relevant for the tested species (Section 4). By eschewing the traditional anthropocentric approach and turning our attention to skills that humans either do not excel in or do not possess, we are better positioned to advance the science of animal cognition (Cantlon and Hayden 2017).

2. Performing Competently–Performing Poorly: Cognitive Skills Are Not Necessarily Linked Together

To illustrate the pitfalls of the anthropocentric approach, let us briefly consider human cognition as unique (i.e., MacLean 2016; Tomasello 2019; Sterelny 2003) and as the maximum capacity (Pinker 2010; Suddendorf and Busby 2003; Jiang et al. 2018). In this case, we would assume that our closest living relatives, great apes, would show cognitive skills similar to humans, whereas less related species from other clades would underperform. However, numerous empirical findings of the past decades confirm that not only apes but also several other previously underestimated animal species demonstrate unexpected cognitive skills. Several bird species, for instance, show skills comparable to nonhuman primates in tasks concerning object permanence, delay of gratification, causal reasoning, theory of mind, and mental time travel (see Güntürkün and Bugnyar 2016 and McMillan et al. 2015 for reviews). As an example, western scrub jays (*Aphelocoma californica*) hide food caches for future consumption, steal others' caches, and engage in tactics to minimize the chance that their own caches will be stolen (Dally et al. 2006). They also show spontaneous future planning behavior without reference to their current motivational state (Raby et al. 2007). Similarly, two more recent studies revealed that ravens (*Corvus corax*) seem to plan for the future by saving tools for future use and tokens for future bartering (Kabadayi and Osvath 2017; but see Redshaw et al. 2017 for an alternative interpretation). They also attribute visual access to unseen competitors (Bugnyar et al. 2016). Moreover, in a study on the natural communication abilities of ravens in the wild, Pika and Bugnyar (2011) showed that ravens use an extremely rare form of attention-getters, a communicative ability previously confined to primates only. Furthermore, there is evidence for flexible cognitive skills in fish (see Patton and Braithwaite 2015; Bshary and Brown 2014 for reviews). Examples include the ability to use transitive inference—i.e., to conclude that if $A > B$ and $B > C$ then $A > C$—in cichlid fish (Grosenick et al. 2007), numerical competence to track shoal size in shoaling fish (Agrillo et al. 2012), updating rules to decide whether and from whom to learn about the location of food sources in nine-spined sticklebacks (Pike and Laland 2010), and interspecific collaborative hunting in coral reef fishes (Vail et al. 2013). Additionally, in reptiles (Matsubara et al. 2017), insects (Feinerman and Korman 2017; Webb 2012) and nonprimate mammals, there are new findings of unexpected cognitive skills such as social learning and face discrimination in domestic pigs (Veit et al. 2017; Wondrak et al. 2018) or size and shape discrimination in horses (Tomonaga et al. 2015). Data from social carnivores show that they are capable of "numerically assessing" the odds during aggressive encounters and only engage in aggression when the odds are favorable or the resource value is high (McComb et al. 1994; Benson-Amram et al. 2011; see also Borrego 2017). Finally, elephants have extremely large-scale and long-lasting memories (Hart et al. 2008; Polansky et al. 2015), and elephants show olfactory discrimination at least equal to dogs (Arvidsson et al. 2012).

In addition to discoveries of surprising cognitive abilities in nonhumans, recent studies have also shown that animals that appear highly sophisticated in one cognitive domain often perform poorly in another. In the next paragraphs, we will illustrate this point by summarizing recent findings on three different, distantly related species on which we are experts (Figure 1): chimpanzees (*Pan troglodytes*), domestic dogs (*Canis familiaris*), and New Caledonian crows (*Corvus moneduloides*). Chimpanzees are one of two closest living relatives to humans, and due to this shared phylogenetic trajectory, they are expected to share many cognitive skills with humans. Dogs have a long domestication history with humans, in which they have evolved some special skills. New Caledonian crows show sophisticated tool manufacturing skills and provide an example of convergent evolution of cognitive skills (Hunt and Uomini 2016; see also below). These species are fairly well-studied, providing us with enough data to illustrate the main point of the present paper—that there is not always "one cognition".

Figure 1. Clockwise from top left: chimpanzee, domestic dog, and New Caledonian crow participating in our research. Photographs by Simone Pika, Juliane Bräuer, and Natalie Uomini, respectively.

2.1. Chimpanzee Cognition

Chimpanzees have a very rich set of cognitive skills, and concerning the physical domain, often perform similarly to human children in captive settings (see, for example, Herrmann et al. 2007; Hanus et al. 2011). These findings renewed debates and theories about how human and chimpanzee cognitions differ (i.e., Tennie et al. 2009; Herrmann et al. 2007; Tomasello et al. 2005; Premack and Woodruff 1978; Kellogg and Kellogg 1933). Recent studies have shown that chimpanzees can also solve social problems using skills, such as mind-reading, that were previously thought to be uniquely human (i.e., Krachun et al. 2009; Call and Tomasello 2008). Chimpanzees seem to operate—at least on an implicit level—with an understanding of false beliefs, as they reliably look in anticipation of an agent acting on a location where an object is falsely believed to be hidden, even though the chimpanzees know that the object is no longer there (Krupenye et al. 2017, 2016; Kaminski et al. 2008). Moreover, chimpanzees are aware of others' visual perspectives (Figure 1) to target information toward ignorant group members (Crockford et al. 2017; Crockford et al. 2012) and seem to plan for the future by building their night nests in the direction of their anticipated feeding tree the next morning (Janmaat et al. 2014). They communicate in referential ways and show similarities to human conversational turn-taking (Pika and Mitani 2006; Pika et al. 2018). In other social domains, chimpanzees also show remarkable behaviors comparable to humans; for example, they incur costs to watch the punishment of antisocial others (Mendes et al. 2018).

Thus, the findings on chimpanzee cognition strongly support the Social Intelligence Hypothesis as this species lives in fission–fusion societies and faces selection pressure for general cognitive flexibility to deal with frequent unpredictable situations. However, although they show great flexibility in many distinct tasks, chimpanzees do not outperform other species from less complex societies in *all* cognitive domains. For instance, chimpanzees are only able to use pointing cues to locate hidden food in competitive, rather than cooperative, experimental tasks (Bräuer et al. 2006; Herrmann and Tomasello 2006; Hare and Tomasello 2004). This limitation seems to be related to the fact that cooperative pointing does not play a dominant role in their social environment (Bräuer et al. 2006; Hare and Tomasello 2004; see above) and is instead restricted to specific contexts and social settings (e.g., Pika and Mitani 2006; Pika 2014). Another study showed that captive chimpanzees are outperformed in inhibition tasks by orangutans (*Pongo abelii)* (Vlamings et al. 2010) that live semi-solitary. This difference may be due to chimpanzees being strongly attracted by the food, as they face much stronger food competition with group mates in their natural environments than do orangutans (Vlamings et al. 2010; Pusey and Schroepfer-Walker 2013; Goodall 1986). Thus, although living in fission–fusion societies might have created selection pressures for the development of a number of cognitive skills in chimpanzees, other skills such as inhibition may have been less adaptive. Indeed, it is conceivable that the pressure to react quickly in social situations with high competition was more adaptive for chimpanzees than the development of inhibition skills. Future studies should focus more on socially and ecologically relevant needs for chimpanzees. Studies could, for example, address how the short reaction times of chimpanzees influence their behavior in rapidly-changing social interactions (Inoue and Matsuzawa 2007).

2.2. Dog Cognition

The domestic dog was domesticated about 30,000 years ago (Botigué et al. 2017; Thalmann et al. 2013) and shows outstanding skills in the social-cognitive domain (see Kaminski and Marshall-Pescini 2014; Miklosi 2007; Huber 2016 for reviews). These skills involve, in particular, the way dogs communicate with humans (Figure 1; Kaminski et al. 2004a; Kaminski et al. 2012; Kaminski et al. 2009a), their sensitivity to human attention and perspectives (Kaminski et al. 2017; Kaminski et al. 2009b; Call et al. 2003; Bräuer et al. 2013b), and their motivation to cooperate with humans (i.e., Bräuer et al. 2013a; Bräuer 2015; Piotti and Kaminski 2016; but see also Quervel-Chaumette et al. 2016; Marshall-Pescini et al. 2016). In contrast, dogs do not show exceptional physical cognitive skills but perform similarly to other nonprimate mammals and birds (Bräuer et al. 2006; Erdohegyi et al. 2007; Osthaus et al. 2005; Rooijakkers et al. 2009; Miletto Petrazzini and Wynne 2016). In some tasks, dogs are outperformed by wolves (*Canis lupus*), their closest living relatives, who are able to use causal cues to locate hidden food (Lampe et al. 2017). These findings have been explained as ancestral dogs experiencing selection pressures for cognitive flexibility only in the social domain, as they have adapted to function effectively in human society (Kaminski and Marshall-Pescini 2014). In comparison to wolves, dogs faced new challenges and thus may have acquired new social skills while losing those skills related to independent problem-solving and understanding their physical environment, skills that were critical for survival in the wild (Lampe et al. 2017). However, even within the social domain, there is evidence for wolves outperforming dogs. For instance, a number of studies showed that dogs cooperate poorly with each other (Bräuer et al. 2013c; Dale et al. 2016; Marshall-Pescini et al. 2017), suggesting that dogs were selected to cooperate *specifically with humans* (Bräuer et al. 2013a; Bräuer 2015; Range et al. 2019). In other words, the specific social environment of the domestic dog created a specific selection pressure for a specific cognitive skill such as the ability to cooperate *with humans*, but not for cooperative ability in general. This should be investigated further.

In sum, areas in which dogs show outstanding cognitive skills and outperform all other species—such as the ability to communicate with humans—are not necessarily linked together with other cognitive skills. Although dogs are more socially tolerant, more cooperative, and more sensitive to social cues than wolves, as predicted by the Domestication Hypothesis, the abovementioned findings go against predictions of the Social Intelligence Hypothesis or the Cooperative Breeding Hypothesis. Consequently, it is more likely that these abovementioned skills evolved *independently* from each other.

2.3. New Caledonian Crow Cognition

A disconnection between cognitive abilities has also been shown in a member of the corvid family. New Caledonian crows are renowned for their technological abilities (Weir et al. 2002; Taylor et al. 2007; Hunt and Gray 2004; Rutz et al. 2010; Hunt and Uomini 2016; Uomini and Hunt 2017). They not only use stick, stem, and grass tools in their natural environments (Figure 1) but also manufacture pandanus tools following templates to produce specific tool shapes that vary between populations and between individuals (Hunt and Gray 2004; Kenward et al. 2006; Taylor et al. 2012b). According to the Technical Intelligence Hypothesis (see above; Byrne 1997), one would predict that the New Caledonian crow, as a tool-making species, should possess enhanced physical cognition and should outperform closely related species in physical problem-solving tasks. However, evidence for enhanced abilities beyond their exceptional technological skills is still uncertain (see Taylor and Gray 2014 for a review). In the tool-using woodpecker finch (*Cactospiza pallida*), there was no difference in physical cognition between tool-using and non-tool-using individuals, when tested on non-tool physical tasks such as a movable perch that caused a food reward to be released or a puzzle box with a lid (Teschke et al. 2011). However, a follow-up study that tested woodpecker finches, New Caledonian crows, and related non-tool-using species from each clade found that non-tool-using small tree finches (*Camarhynchus parvulus*) performed equally to woodpecker finches. In contrast, New Caledonian crows outperformed carrion crows; the authors attribute these differing results to the more sophisticated tool skills of New Caledonian crows compared to woodpecker finches (Teschke et al. 2013). Therefore, it is possible that very elaborated tool skills and the related enhanced physical cognition can be found in New Caledonian crows. In particular, to resolve this question, observational data from wild crows are needed, because all of the data currently available on New Caledonian crows are from experiments in captive settings using artificial (human-created) tasks. In future studies, increased attention to observational data on wild crows can help to greatly improve ecological validity for this species, as called for by Kamil (1987), and as we discuss in Section 4.

Although New Caledonian crows may have a better understanding than related bird species of how to use metatools (i.e., the ability to use one tool on another tool; Taylor et al. 2007; Kenward et al. 2006;

Gruber et al. 2019), they do not outperform them in other physical cognition tasks. So far, in captive setups, all corvid species tested have been found to show equal skills in the Aesop's fable paradigm, a task designed to assess causal understanding of water displacement, in which subjects must discover how to drop stones into a water-filled container to raise the water level in order to obtain a floating reward (Logan et al. 2014), as well as in hook manufacture (Weir et al. 2002; Taylor et al. 2012b; Laumer et al. 2017), and trap-tube tasks (Taylor et al. 2009; Tebbich et al. 2007; Seed et al. 2006). In perceptual feedback studies, New Caledonian crows show the same understanding of the problem as keas (*Nestor notabilis*) and ravens, but they do not solve most string-pulling tasks as fully as keas and ravens, leading Taylor and colleagues (2010) to conclude that New Caledonian crows fail to perceive connectivity (Taylor et al. 2012a; Werdenich and Huber 2006; Taylor et al. 2010). The complex tool-using behaviors of New Caledonian crows also possibly do not enable them to make causal interventions, i.e., to learn a cause–effect relationship and then act to take advantage of that cause (Taylor et al. 2014; but see Jacobs et al. 2015 for an opposite viewpoint). Finally, these crows—although they can learn to produce collaborative behaviors to obtain food rewards in experimentally trained settings—do not understand the causality of cooperation, leading Jelbert et al. (2015) to conclude that the flexible use of physical tools does not necessarily enable animals to grasp that a conspecific can be used as a social tool (Jelbert et al. 2015). However, relatedness likely plays a role in the motivation to cooperate in this species, as New Caledonian crows are thought to spend most of their time in extended family groups (Holzhaider et al. 2011). If the crows understand that a conspecific can be used as a social tool only after direct experience with that individual, we would predict that the crows should be more likely to cooperate with kin than non-kin, particularly with kin who are already collaboration partners. To determine what factors underlie cooperative performance, future studies would need to test pairs of individuals of known relatedness, as well as to document the range of their cooperative behaviors in the wild.

Regarding other social cognitive skills, experimental results on social learning are consistent with the spontaneous behaviors documented in the wild. Logan and colleagues (2016) tested social transmission of various methods to open puzzle boxes and found that New Caledonian crows of all ages learned socially by stimulus enhancement (Logan et al. 2016). Similarly, long-term developmental observations in the wild showed that juvenile New Caledonian crows relied mostly on scaffolded individual learning—with templates as guidance to the final form of the tools—to develop their tool-making sequences; they produced the same tool types they saw being used and discarded by their parents, but they did not always produce the same variants as their parents (Holzhaider et al. 2010a; Holzhaider et al. 2010b). More developmental studies are needed to establish the variability and consistency in the social learning of New Caledonian crows (Uomini et al. 2020), but in comparison to other birds (i.e., Auersperg et al. 2014), so far they do not seem to perform especially well in social learning tasks.

In sum, the New Caledonian crow appears to be a species with excellent tool-related cognition but not outstanding social cognitive skills. However, it is not yet clear from the currently limited evidence if differences between New Caledonian crows and other species will become apparent when more nuanced tasks are used that more closely match the cognitive requirements of tool-use and tool-manufacture (Taylor and Gray 2014). At present, it appears that the selection pressures leading to the outstanding tool behaviors of New Caledonian crows did not foster the emergence of enhanced social skills (regarding cooperation and social learning), again suggesting that cognitive skills evolve in a domain-specific manner, often *independently* from each other (Macphail 1982).

3. When Animals Outperform Humans

As humans, our collective reluctance to acknowledge exceptional cognitive skills in nonhuman animals is at odds with the biological study of other species (i.e., Allen and Trestman 2017). It seems we are accustomed to accepting animal supremacy in anatomical features or physical performances: many mammalian species are bigger, stronger, or faster than humans, and we readily apply ecological explanations to determine such specific evolutionary adaptations. Interestingly, however, we do not appear willing to apply the same explanatory rigor in seeking specific selection pressures or species-typical ecological affordances when it comes to cognitive abilities. No physiologist would consider human respiration or digestion as a particularly useful reference point to describe or understand the variety and complexity of animal metabolism, but many psychologists still appear to mark human cognition as the pivotal point from which any comparison with nonhuman systems ought to start (Shettleworth 2010; Premack 2007; Vonk 2016). It is therefore not surprising that the term "cognition" (and "intelligence", respectively), even in its broadest definition, is traditionally closely connected to "human cognition" (or "human intelligence"). As a result, we tend to overrate those cognitive skills that are human-like (see also Vonk and Povinelli 2012) and—what turns out to be scientifically more fatal—we run the risk of overlooking cognitive skills that play only a minor role or no role in human psychology. Furthermore, it is no surprise that we expect (and find) more similar forms of cognition in phylogenetically closely related species (i.e., Balda et al. 1996) and assume human-like clustering of cognitive abilities in other species. To be clear, we do not argue that cognitive abilities do not cluster at all in other taxa or species, but rather we doubt the presumption that they always cluster the way they do in humans. In this section, we review the outstanding skills of animals that sometimes outperform humans. These examples illustrate our point that humans cannot be considered "superior" to other animals, but rather that each species has its own cognitive specialisms, which may be unique or exceptionally elaborated within the animal kingdom.

In the following paragraphs, we describe just a few of countless examples of animal cognition that seem astonishing in comparison with human skills, but only when human cognitive performance is considered to be the highest possible level. However, in reality, these examples simply reflect species-typical behavioral repertoires.

Adult humans have been described as exceptionally patient, especially in contrast to other primate species, which are traditionally described as more impulsive and present-oriented (Tobin et al. 1996; Roberts 2002). However, recent work has shown that the assumed phylogenetic gap between human and nonhuman inhibitory skills is strongly influenced by specific parameters of the testing situation. Rosati and colleagues (2007), for instance, demonstrated that human patience drastically decreased when the relevant currency was food instead of money—as in the vast majority of previous human experiments—but also that chimpanzees and bonobos were much more patient than any other animal species tested so far. Chimpanzees also outperformed bonobos as well as human adults in a "food-waiting-paradigm" (Rosati et al. 2007). The intra-*Pan* difference is especially interesting as it directly relates to different ecological affordances of those two closely related species. Whereas wild chimpanzees have to deal with rather unpredictable and unstable fruit and meat resources (Wrangham et al. 1998), bonobos live in rather stable forest environments with comparatively stable and predictable food patches (Boesch et al. 2002; Furuichi et al. 1998). In particular, hunting and extractive technologies (e.g., nut-cracking)—two behavioral peculiarities of chimpanzees with major nutritional benefits—are rare or nonexistent in bonobos (Surbeck and Hohmann 2008; Boesch and Boesch-Achermann 2000; Mitani and Watts 2001). Habitat variation seems, therefore, a plausible explanation for the cognitive differences found between the two *Pan* species in the social and physical domains (Rosati et al. 2007; Rosati 2017; Rosati and Hare 2011). In sum, human patience is not as exceptional as previously thought.

Humans are also thought to be the most rational of all primates. Contrary to what is predicted by traditional economic models, however, humans are far from being rational maximizers when it comes to resource distribution in a social scenario. Instead of pure self-interest, their decision-making seems to be strongly affected by fairness concerns, which lead, in certain situations, to (seemingly) less rational decisions. Using the experimental paradigm of the Ultimatum Game, robust findings from several laboratories and multiple human cultures confirm the assumption that adult humans are willing to pay a cost by rejecting offers that they consider unfair (e.g., Fehr and Gächter 2002). In contrast, confronted with an adapted ape-version of the task, chimpanzees appear more rational than humans by accepting any non-zero offer and therefore maximizing their benefits more efficiently (Jensen et al. 2007). It is crucial to note that "rational" does not necessarily translate to "adaptive" here, even though it seems prima facie disadvantageous to prefer a zero outcome over a non-zero outcome just to punish a violation of a fairness principle. What appears rational and clever in the chimpanzee case is simply the most successful strategy in a social system that does not have strong other-regarding concerns of equality or fairness. In human societies, on the other hand, it might be highly adaptive to pay short-term costs to ensure fair future interactions. Such investment might pay off in the long run, given social systems with omnipresent implicit fairness expectations and explicit fairness norms.

Other than apes, several nonmammalian species show extraordinary cognitive performances that are comparable to those of human experts or even beyond. In order to navigate and communicate, birds have evolved considerable information-processing capabilities (McMillan et al. 2015). For example, many raptor bird species (e.g., eagles, hawks) are equipped with remarkable visual perception and classification abilities. Experiments with pigeons demonstrated that they can recognize different letters of the alphabet, can classify images based on animal taxa criteria (e.g., cats vs. dogs) or physical features of inanimate objects (chairs vs. tables), and are able to distinguish between Monet and Picasso paintings after some period of training (Watanabe 2001; Watanabe et al. 1995; Emery 2006). Results from a recent study even suggest that pigeons can be trained to "detect" cancer. The task consisted of classifying histopathological images as well as mammograms as either benign or malignant. Pigeons were able to generalize from training stimuli to new exemplars, and the performance level of the birds reached that of experienced human pathologists (Levenson et al. 2015). These skills seem impressive to a human observer, even though they demonstrate nothing but ordinary pattern recognition skills—a rather specific adaptation of pigeons. Similarly, it was shown that pigeons rely on a more efficient process than humans to visually identify objects presented in various spatial orientations. This difference is presumably rooted in the differing ecological demands placed on the visual systems of flying birds compared to earth-bound humans (Hollard and Delius 1982; McMillan et al. 2015).

Pigeons also outperform humans in other tasks. For instance, Herbranson (2012) compared pigeons and humans in a probability puzzle, i.e., the Monty Hall Dilemma. Subjects were given a choice from among three doors, one of which concealed a valuable prize. After an initial selection, one of the remaining, nonwinning doors was opened, and the participant was given a chance to switch to the other unopened door. The probability of winning is higher if the participant switches. Pigeons maximized their wins by switching on nearly all trials of a Monty Hall Dilemma analog, whereas humans utilized a suboptimal strategy involving probability matching (Herbranson 2012). One possible reason why humans used probability matching is that they were searching for a strategy that would be correct 100% of the time, whether or not that level of accuracy can actually be attained. This human use of probability matching might reflect an active search that progresses even when there are no consistent patterns to be found (Gaissmaier and Schooler 2008; Herbranson 2012). This idea is supported by another study in which rats and humans were trained in rule-based and information-integration category-learning tasks with visual stimuli. The generalization performance of rats and humans was equal in rule-based categorization, but rats outperformed humans on generalization in the information-integration task. While the performance of the rats was consistent with a nondimensional, similarity-based categorization strategy, humans again showed a bias toward rule-based strategies, which in that case impeded their performance on generalization tasks (Vermaercke et al. 2014).

Humans are also outperformed in spatial memory tasks, in particular by specific bird species. The most impressive spatial memory has been demonstrated by members of food-storing bird families like parrots and corvids (see Shettleworth 1983; for overviews, see Clayton et al. 2006; Clayton and Emery 2002). Some of these bird species (e.g., Clark's nutcracker *Nucifraga columbiana* and marsh tit *Poecile palustris*) are able to remember over 100 cache sites after time delays of several months, by far exceeding the average human memory. Remarkably, not only can bird species that cache food for themselves (e.g., marsh tits) correctly remember the hiding locations they visited before, but so can species that are specialized in cache pilfering. Great tits, for example, are capable of memorizing caching locations just by "secretly" observing marsh tits caching (Urhan et al. 2017; Balda and Kamil 1992.)

What all these remarkable animal performances have in common is that they fascinate and puzzle human observers at the same time. The fascination comes from the fact that these demonstrated abilities are comparable or even superior to those of our own species within the same domains. They are puzzling because these are *cognitive* domains, and some aspects of cognition were traditionally thought to represent a unique characteristic of human minds that distinguishes us from other animals more than any other trait (Premack 2007; Uomini 2008; Shettleworth 2012; Uomini 2014; MacLean 2016; Uomini and Ruck 2018; Uomini et al. 2020). From an anthropocentric perspective, such skills would need an explanation because they challenge human superiority, but from a genuine biological perspective, such skills are simply examples of the unique traits that each species has evolved due to specific situations and needs. Just as physical traits (e.g., an elephant's trunk, life history, or a digestive system that can process poisonous leaves) are considered in their evolutionary context, cognitive traits should similarly be considered according to their species-specific context.

4. Ecology, Perception, and Crucial Limitations

In addition to the fact that research approaches in animal cognition are often anthropocentric and driven by our own cognitive skills, we see another problem with the current comparative character of the field. The usual approach is to present the same task to different species. This strategy is problematic when the experimental task is not equally relevant to each of the compared species (Boesch 2007; Tomasello and Call 2008; MacLean et al. 2012; Roth et al. 2019). One classic example is the question of whether animals, chimpanzees in particular, can take the visual perspective of others. In a number of studies in which chimpanzees had to beg for food from humans, they did not show outstanding perspective-taking skills (Povinelli and Eddy 1996; Kaminski et al. 2004b). However, begging from humans is far from being a natural situation for a chimpanzee, which led Hare and colleagues to create a competitive situation in which two chimpanzees compete over a food resource. Given such a new and ecologically relevant situation, chimpanzees suddenly knew what others can see (Hare et al. 2000; Bräuer et al. 2007) and even understood what others have seen (i.e., that seeing leads to knowing; Hare et al. 2001; Hare 2001). Kaminski and colleagues (2008) followed up the idea of a competitive and, therefore, relevant situation and tested pairs of chimpanzees in a setup in which they sat opposite to each other and competed over two pieces of food on a sliding table that was pushed back and forth. They found that chimpanzees understood what their rival knows, but not what the rival believes (Kaminski et al. 2008). Thus, experiments do not have to be "natural", but species-relevant, and subjects have to understand the test situation. Although subjects in these studies were not tested in a "natural" competitive situation in which chimpanzees physically compete over food, they showed very flexible perspective-taking skills. This finding suggests that it was crucial that chimpanzees were able *to perceive* the situation as competitive.

Certainly, one aspect of experiments that is often overlooked is how animals are able to perceive a situation. Shettleworth's definition of cognition includes perception as it refers to adaptive information processing in the broadest sense. The modality in which a task is presented is absolutely crucial for detecting the cognitive potentials of a given species. For example, until now, nearly all studies about dog cognition have taken an anthropocentric view, mainly searching for skills and modalities that are important for humans, such as perspective-taking, cooperation, social learning, and visual or auditory communication. Most data on dogs' understanding of their social and physical environment is based on performance in the visual or auditory modality (Bräuer et al. 2013b; Kaminski et al. 2004a; Kundey et al. 2010), even though olfaction is the most relevant sense that dogs use to explore their environment (Gazit and Terkel 2003; Horowitz et al. 2013). Therefore, dog cognition studies should, in fact, design tests based on olfaction, not on vision or hearing. Indeed, a recent study by Bräuer and Belger (2018) suggests that dogs have a flexible representation of what they smell. The fact that olfaction was neglected in dog cognition research until recently, when dogs were shown to excel at a task when it was reframed in the olfactory modality, illustrates how an anthropocentric approach can create the appearance of limitations in cognitive performance. On the contrary, apparent limitations can be due simply to the use of a perceptual modality that is disadvantageous to the animal being tested.

The modality also seems to be crucial in biological market tasks. In a study by Salwiczek and colleagues (2012), individuals of several fish and primate species had to make a choice between two actions in a foraging task. They could choose between two plates (differing in color and patterns to allow discrimination) with exactly the same food. However, one plate was ephemeral and the other one permanent. The food maximizing solution involved eating from the ephemeral food source first and only then from the permanent one that yielded an additional delayed reward. This task was ecologically relevant for the tested cleaner fish as it mimicked the simultaneous visit of a resident and a visitor to the cleaning station. Indeed, the cleaner fishes outperformed the tested chimpanzees, orangutans, and capuchin monkeys in that task (Salwiczek et al. 2012). However, when the task was made more perceivable for primates, primates improved their performance: when the food was colored instead of the plates, and when the food reward was hidden, capuchin monkeys readily learned to solve the task (Prétôt et al. 2016). Similarly, rats and pigeons could solve the task when there was a 20-second delay between the choice and its outcome (Zentall and Case 2018). These examples reflect the prime importance of perceptual modality on reaching conclusions about a species' cognitive abilities.

In addition to the importance of modality on how species perceive tasks, there are ecological restrictions to what a member of a certain species can learn (Campbell et al. 2008). For example, cleaner fishes can only use generalized rule learning when the rule has ecological relevance. They can learn that predators are safe havens when chased by a punishing client while nonpredatory clients are not. However, they cannot learn to approach a nonpredatory client as a safe haven (Wismer et al. 2016). Similarly, bees can associate color with food but apparently not with danger (De Ibarra et al. 2014; Craig 1994). This difference between learnability in modalities might be comparable to the way humans who get food poisoning in a restaurant will develop an aversion to the food rather than to the person they went out with.

In sum, we emphasize again the importance of ecologically relevant experiments to uncover cognitive processes in nonhuman animals. As we illustrated above, many experiments that were designed anthropocentrically found negative results, which were then prematurely generalized to the species. The solution to this problem is that the tested skills *and* the experiments themselves should be ecologically valid. Ecological validity can be achieved by taking into account the importance of perception due to the modality of task presentation and the limitations for learning. One of the hardest tasks for animal cognition researchers in the coming years will be to design experiments that can detect the upper limits of animals' abilities—a challenge that is especially difficult for us, as humans, in the case of nonhuman cognitive abilities that exceed anything we can imagine with our limited perception and cognition.

5. New Challenges in Animal Cognition

We began with a reminder of the fundamental but sometimes neglected call (Kamil 1987) for comparative research to take a biocentric view of cognition and to avoid common anthropocentric viewpoints (Allen 2017; Shettleworth 2010; Shettleworth 2012; Vonk 2016). We see three concrete weaknesses in current animal cognition research. Firstly, there is a widely shared conception that certain cognitive clusters found in humans, such as technical intelligence, are similarly organized in other animals, although there is no clear evidence for such similarities (Ducatez et al. 2015; see Section 2). Secondly, skills that are on par with those of humans have sometimes been overrated in humans and underrated in other species (i.e., Boesch et al. 2017). Therefore, species-specific cognitive skills (i.e., Kaminski and Marshall-Pescini 2014; McMillan et al. 2015) and findings of species that outperform humans on distinct tasks were sometimes overlooked or not tested, as it is difficult to find the appropriate experimental design (see Section 3). Thirdly, another element that should be strengthened is the importance of ecologically relevant experimental designs that consider perception and the limitations for learning in the tested species (Bates and Byrne 2007; De Waal 2016; see Section 4).

In addition to the concerns we have raised here, other researchers have highlighted the need to consider within-species variability (Barrett 2016), phylogenetic factors (to control for effects of shared descent; Balda et al. 1996), and social characteristics (e.g., level of competition and tolerance; Hare 2001; Fröhlich et al. 2016), as well as the application of different methodologies across species (Leavens et al. 2017). To remedy these issues, researchers interested in animal cognition should collaborate to test a wider variety of animal taxa rather than only the most common model species with presumably human-like cognitive abilities (i.e., Rowell 1999; Stanton et al. 2017). As animal cognition research is a truly interdisciplinary subject that appeals to researchers from distinct disciplines such as psychology, biology, anthropology, and neuroscience (e.g., Osiurak et al. 2020), we need to acknowledge the fact that they can and should complement each other. For example, it would be helpful for behavioral ecologists to include more cognitive research in their studies as they are experts on the ecology of a given species. On the other hand, psychologists who usually concentrate on the mechanism of a behavior could consider the ecological relevance and the phylogenetic history of their behavior of interest. Hence, observational investigations of the natural behavior of species and experimental studies should go hand in hand to enable detailed insights into the cognitive potential of a given species (Janmaat 2019).

In summary, taking together all of the old and new criticisms that we have identified for the future of animal cognition, we advocate that

1. Studies should be clear about which cognitive skill(s) they are testing and should not interpret evidence for one skill as automatically proving another, untested skill. Research should not assume that cognitive skills cluster the way they do in humans, but rather should start from the expectation of multiple cognitions until proven otherwise.
2. Studies should be based on detailed knowledge of the natural behavior and the ecological environment of the test species, so that it is possible to generate precise hypotheses about the species' performance on a specific cognitive task (Bates and Byrne 2007).
3. Experimental settings should take into account social structures, developmental constraints, and preferred modality of the species under study (Bates and Byrne 2007; Roth et al. 2019).
4. Studies with nonhuman animals should no longer target *only* typically human cognitive skills such as tool-use, self-control, or social cooperation, but should also test skills in which humans might be outperformed by other animals, such as visual and odor perception, working memory, and reaction time (i.e., De Waal 2016; Bräuer and Belger 2018; Inoue and Matsuzawa 2007).
5. A holistic approach should be implemented to better integrate laboratory and fieldwork of behavioral ecologists, including the conducting of more rigorous observations and field experiments (Janmaat 2019; Boesch 2010; Bueno-Guerra and Amici 2018).
6. An even wider variety of animal taxa should be tested—starting with species that are as yet untested and under-represented in experiments—to gain a whole picture of cognition in the Animal kingdom (Vonk 2016; Roth et al. 2019).

Once research turns to the study of each species' cognitive skills for its own sake (Allen 1998; Holekamp 2007; Borrego 2017), we will gain a more relevant perspective on animals' cognitive skills that incorporates factors such as ecology, social environment, behavior, and development (Uomini 2008; Sewall 2015; González-Forero and Gardner 2018; Uomini et al. 2020), overlain onto the recognition that unique single cognitive capacities in some species coexist with full-blown cognitive arrays in others. Hence, there is not "one cognition".

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Chapter 10

What Dogs Understand about Humans

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Many dog owners claim that their dogs can ‘understand’ them. In this chapter I try to answer the question of what dogs really understand about others. Because dogs do prefer humans over their conspecifics as social partners (Gacsi et al., 2005; Topál et al., 2005; Miklósi, 2007; Horowitz, 2011; see also Chapter 6 in this book, Prato-Previde & Valsecchi), I concentrate on the question of what they understand about their human companions. Do dogs know what humans can perceive? And if so, *how* do they assess what humans can perceive? Do they understand humans’ goals and intentions? Are they able to attribute mental states to others, such as beliefs and knowledge?

10.1 MONITORING

One precondition to understanding human behaviour, perception, and mental states is ‘monitoring’, i.e., looking at the human and being attentive to what he or she is doing (see Emery, 2000). Indeed, dogs constantly monitor humans, similar to subordinates in a social group who always pay attention to dominants (Chance, 1967; Emery, 2000). They are highly attentive to what humans are doing.

This attentiveness towards humans is already present in dog puppies. One difference in the behaviour of dog puppies in comparison to hand-reared wolf puppies is dogs’ increased tendency to gaze at the human’s face (Gacsi et al., 2005; see also Miklósi et al., 2003). Thus, even when dog puppies and wolf puppies have the same experiences (because they are raised in an identical way), dogs gaze more at humans. This suggests that the exceptional attentiveness towards humans has an innate component that was probably selected for during domestication.

Dogs not only constantly monitor humans but also are able to receive important information by watching them. They have outstanding skills in using human communicative cues, especially the pointing gesture (see Chapter 11, Topál).

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Dogs also use social referencing. Similar to children, they seek information from the owner about an object to form their own understanding and guide their actions. In particular, when presented with an ambiguous object, they react in accordance with the information delivered by the owner. If owners express their worries, dogs inhibit their movements towards the object. But if owners show a positive attitude, dogs move closer to the object and interact with it sooner (Merola et al., 2011; Merola et al., 2012).

There is also some evidence that dogs can use information when it is not directed at them. Dogs might be able to make reputation-like inference by observing third-party interactions (Kundey et al., 2011; Marshall-Pescini et al., 2011; but see Nitzschner et al., 2012). And there is very clear evidence that they evaluate humans on the basis of direct experiences, i.e., searching for contact with a 'nice' experimenter—compared to an ignoring experimenter (Nitzschner et al., 2012).

Thus, dogs are highly attentive towards humans—and seem to be able to extrapolate information about specific humans (and their environment). But do they also monitor humans' head and eye orientation and look in the same direction? Following the gaze of others is an adaptive skill that enables individuals to obtain useful information about the location of food and also about dangers and social interactions. It is also considered to be an important step towards an understanding of mental states such as attention and intention (Baron-Cohen & Cross, 1995; Tomasello et al., 2005; Range & Virányi, 2011).

Agnetta et al. (2000) first investigated whether dogs follow human gaze by adopting a procedure that was first used with human infants (Butterworth & Jarrett, 1991). The subject sat in front of the experimenter. The experimenter first looked at the subject and gained its attention. Then she suddenly turned her head straight up or to the left/right of the subject and looked into free space for about 5 seconds. In control conditions, the experimenter looked straight at the subject for 5 seconds.

Dogs did not follow the human gaze in that setup. That is surprising, as they have been shown to be able to use human gaze in an object choice task to locate hidden food (Miklósi et al., 1998; Agnetta et al., 2000; Soproni et al., 2001; but see also Hare et al., 2002, and Bräuer et al., 2006). In the object choice task, a piece of food is hidden in one of two containers, but the dog is unable to see in which one. The experimenter then gives a cue to the correct location by gazing at it. The question here is which container the dog will then approach.

In most studies using the object choice task, dogs followed the human gaze and found the correct cup, but they did not follow human gaze into free space in the study of Agnetta et al. (2000). The authors speculated whether dogs follow human gaze only in a foraging situation—when food is involved. Strikingly, wolves, dogs' closest relatives, do follow human gaze into free space in a similar situation (Range & Virányi, 2011).

Teglas et al. (2012) recently addressed these contrasting results on dogs' gaze-following skills by using an eye tracker. Dogs were presented with a series of movies in which a human turned her head and gazed towards one of two identical containers—either in an ostensive or a non-ostensive way. In the ostensive condition, the human looked straight at the dog and addressed the subject in a high-pitched voice before she gave the cue, whereas in the non-ostensive condition, she did not look at the dog and addressed it using a low-pitched voice. Dogs' eye-gaze patterns were recorded with an eye tracker.

Dogs looked longer towards the gaze-congruent area (i.e., the area around the cup the human was gazing at) in the ostensive condition compared to the non-ostensive condition. However, there was no significant difference in first look towards the gaze-congruent area. The authors conclude that dogs' following of human gaze is context-dependent—i.e., it occurs only when the human head turning is proceeded by ostensive cues (see also Chapter 11, Topál).

Thus, there are potentially two different explanations as to why dogs sometimes use human gaze in an object choice task (Miklósi et al., 1998; Agnetta et al., 2000; Soproni et al., 2001) and sometimes do not (Hare et al., 2002; Bräuer et al., 2006) and why they do not follow human gaze into free space (Agnetta et al., 2000).

First, it may be due to the different ways in which dogs were made attentive before the human turned her head, in the different studies. This is difficult to evaluate based on the reported methods. Usually, the human experimenter simply establishes eye contact with the dog prior to delivering the cue; however some authors also state that they call the dog by name if it is not attentive (i.e., Soproni et al., 2001). But without a detailed comparison between methods, it is impossible to draw a conclusion about how 'ostensively' humans behaved to gain the dogs' attention (i.e., whether or not they called with a high-pitched voice) and if this reliably affected results in the expected direction.

A second potential explanation for the contrasting results is the different measures that Teglas et al. (2012) used. Whereas in an object choice task, it is measured which container subjects approach, Teglas et al. (2012) measured the first look of subjects and the duration of the look towards the target area. They found that dogs looked longer towards the correct cup, but they did not find an effect for the first look.

Thus, one question is how dogs make their choice to select the container in an object choice task. Do they go to the cup they first looked at, or do they approach the container where they looked longer? Here, the duration of the gaze-cue in the object choice task might become crucial for what container dogs select. For example, in the study of Bräuer et al. (2006), dogs used continuous looking more effectively than a looking cue that lasted 4 seconds. Further studies have to investigate systematically whether and how ostensive attention-getters or duration of the gaze cues account for the mixed results in dogs' gaze-following abilities.

10.2 PERSPECTIVE TAKING

But for the main question addressed in this chapter—i.e., what do dogs understand about humans?—it is less important under what circumstances dogs follow human gaze but more crucial what they *understand* about the human gaze. In other words, do they understand what humans can see? A first step to address this question is to consider whether they are sensitive to human attention. In three different experimental approaches, it was found that dogs behave differently depending on the human's attentional stance.

In the first approach that was borrowed from studies with primates (Povinelli & Eddy, 1996; Kaminski et al., 2004), dogs were tested in a situation in which they could beg for food. Subjects could choose between two humans who were eating based on either the visibility of the humans' eyes or the direction of their face. Dogs begged more from the attentive than from the inattentive human (Gacsi et al., 2004; Virányi et al., 2004; Udell et al., 2011; see also Udell & Wynne, 2011, and Virányi & Range, 2011). Similarly, dogs take into account the attentional state of an experimenter when they beg for help because they cannot solve a problem (Marshall-Pescini et al., 2013).

In the second experimental approach, owners gave a command to their dogs to lie down. Either the owner was facing the dog, a human partner, or neither or he was visually separated from the dog. Subjects were more ready to follow the command if the owner attended them during the instruction delivery (Virányi et al., 2004).

In the third approach, the dogs also had to follow a command. In this case, the experimenter forbade dogs to eat a piece of food on the floor. The human either looked at the dog or was distracted, having eyes closed or back turned. Dogs obeyed the command better when the human was attentive compared to all other conditions (Call et al., 2003; Schwab & Huber, 2006).

Thus, in all three approaches, dogs were sensitive to the human attention and behaved accordingly. One explanation for this sensitivity is that they simply reacted to certain stimuli such as the open eyes when assessing whether the human was attentive. In other words, dogs might have learned that they have to obey only when they can see the open eyes of the human and that begging is successful only when the eyes are visible—without truly understanding what humans can see.

To start to address this problem, in a study by Bräuer et al. (2004), the authors placed forbidden food behind three different kinds of barriers. One barrier was small, one was big, and the third one was big but had a Plexiglas window in the middle through which the food could be seen. The authors found that dogs were sensitive to whether or not the presented barrier was effective or ineffective at obstructing a human's vision. Dogs ate more forbidden food when the barrier was large compared to when it was small or when it had a window (in the latter two cases, the human could see either the approach or the taking of the forbidden food). However, these results also can be explained by dogs relying on stimuli, instead of an understanding of the human's visual access to the food. For example, dogs could have tried to avoid seeing the human during the approach (small barrier) and during taking of the food (big barrier with the window)—and that is why they ate the forbidden food preferentially when the barrier was big and opaque.

Therefore, Kaminski et al. (2009a) used a different approach in which dogs could not simply rely on different stimuli in order to solve the problem. They investigated whether dogs could take the visual perspective of a human when that differed from their own perspective. In that study, dogs were encouraged to cooperate with the human experimenter. Each of two toys was placed on the dog's side of two small barriers so that the dog could see both of them. One barrier was opaque, and the other one was transparent.

There were three conditions. In the experimental condition, a human sat on the opposite side of the barriers, such that she could see only the toy behind the transparent barrier. The experimenter then told the dog to 'Bring it here!' but without designating either toy in any way. In the Back Turned control, the experimenter also sat on the opposite side but with her back turned so that she could see neither toy; and in the Same Side control, she sat on the same side as the dog such that she could see both toys. Dogs preferred to approach the toy behind the transparent barrier in the experimental as compared to the back turned and the same side conditions.

Thus, if the human could see only one of the toys, dogs brought back precisely the one that the human could see. They did so although they themselves could see both toys. The authors concluded that dogs are really sensitive to humans' visual access, even if it differs from their own perspective (Kaminski et al., 2009a).

This conclusion is supported by another study by Kaminski et al. (2013). In this case, researchers used another approach in which dogs could not react to certain cues because contextual information and social cues were in conflict. As in other studies (see preceding descriptions), the experimenter forbade food to the tested dogs. However, in this version of the task, how the room was illuminated varied. Either the human, the food, or both were dark, or everything was illuminated. Dogs stole significantly more food when it was dark compared to when it was light. That is not surprising, as in the dark, social cues are absent. Thus, dogs could simply have stolen the food because they did not see the human and her eyes.

However, the dogs' choice to steal forbidden food and how they behaved depended on what was illuminated. Illumination around the food, but not the human, affected the dogs' behaviour. They hesitated longer to steal the food when it was illuminated compared to the condition in which only the human was illuminated. Thus, dogs did not simply take the sight of the human as a signal to avoid the food.

One could argue that dogs simply hesitate to approach forbidden food that is illuminated if the rest of the room is dark. But the authors excluded that possibility because they showed in another experiment that dogs do not hesitate to approach illuminated forbidden food when they are in private. It is therefore possible that dogs really understand that when the food is illuminated, the human can see them approaching and stealing the food.

Taken together, all these studies offer very strong evidence that dogs know what humans can see in the sense that they understand when the humans' line of sight is currently blocked or when they are not in a position to see things. Dogs have shown this understanding in different situations—when they should obey, when they beg, and when they fetch toys. That implies that their perspective-taking skills are very flexible. This is similar to chimpanzees that are also able to assess what others can see in various situations (Hare et al., 2000; Kaminski et al., 2004; Liebal et al., 2004; Bräuer et al., 2007).

However, in contrast to our closest living relatives, dogs rely on what they themselves can perceive when they assess what the human can see (Melis et al., 2006; Bräuer et al., 2013). In a study by Bräuer et al. (2013), dogs were confronted with the following task (see Figure 10-1). Forbidden food was placed in a tunnel so that they could retrieve it by using their paw. At the beginning of each trial, dogs were placed opposite the experimenter so that they could see both the experimenter and the tunnel. However, when they tried to retrieve the food from one side of the tunnel, they were unable to see the experimenter, but the experimenter could potentially see the dog's paw. Dogs could choose between an opaque and a transparent side of the tunnel, but they did not show a preference for the opaque one. Thus, they did not hide their approach when they could not see a human present. This indicates that here they use an egocentric strategy to assess what humans perceive. In other words, in that setup, dogs seem to conclude: 'If I do not see her, then she does not see me'. This is a very successful strategy—in most but not in all cases. To date, only chimpanzees have shown they can solve this problem. They do understand 'Although I cannot see the human, she can see my hand grabbing the forbidden food' (Melis et al., 2006).

Dogs are sensitive to what humans can see, but what about other modalities? Do dogs know what humans can hear? Kundey et al. (2010) first raised this question using a design that was also borrowed from studies with primates (Melis et al., 2006; Santos et al., 2006). In a pretest, dogs experienced that the human experimenter would forbid them to eat food. In the subsequent test, subjects had the opportunity to take food from one of two containers. The human experimenter now either looked straight ahead (hence she could see the containers) or placed her head between her knees facing the ground, not looking at the containers. The containers only differed in one way: one was silent both when food was being inserted and when it was removed, whereas the other was noisy. In both cups, small bells were attached across the opening with a translucent cord, but in the silent cup, the ringers of the bells had been removed. Dogs preferred the silent container when the human experimenter was not looking. This suggests that they did

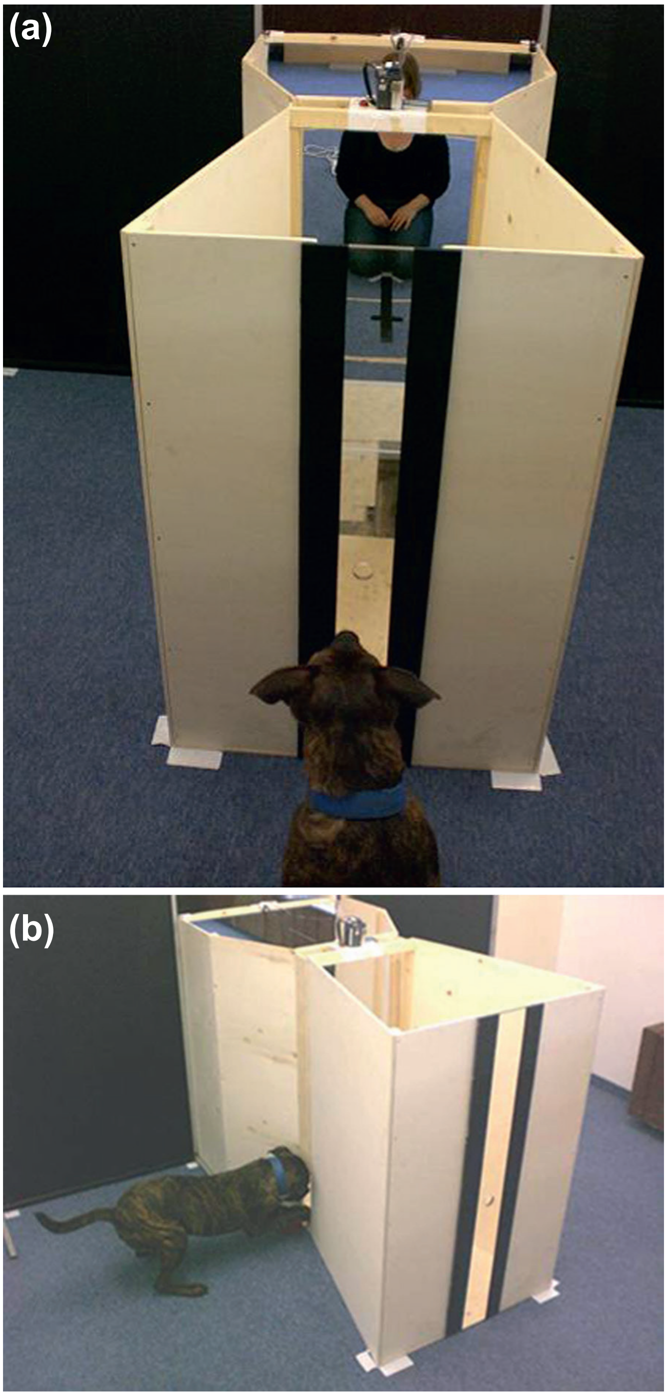

FIGURE 10-1 Experimental setup of the study of Bräuer et al. (2013): (a) apparatus from the view of the dog; (b) dog's approach to the tunnel. *(With kind permission from Springer Science and Business Media.)*

not simply have a preference for silence when they approached a potentially forbidden food, but they preferred silence if it was relevant to obtaining food unobserved by a human gatekeeper.

Raising a similar question, Bräuer et al. (2013) found that dogs preferred a silent approach to forbidden food. They used the paradigm described in the preceding paragraphs in which forbidden food was placed in a tunnel so that dogs could retrieve it by using their paw. This time both sides of the tunnel were transparent, and there was a carpet inside and around each side of the tunnel. One carpet was made of crinkly plastic foil and therefore produced a noise when the dog approached that side, while the other carpet was silent.

As in the study by Kundey et al. (2010), the experimenter did not look at the forbidden food and oriented her face downwards. Bräuer et al. (2013) found that dogs preferred the silent tunnel approach to the forbidden food. They did so although they could not see the human while they took the forbidden food; thus, they obviously had no problem remembering that the human was there.

But dogs preferred the silent approach only when this was really necessary, i.e., when the human stayed in the room and when the food was really forbidden. In the two control conditions in which the experimenter either left the room or verbally motivated the dog to take the food, dogs had no preference for the silent approach.

In conclusion, dogs are sensitive to what humans can hear. It is not simply a predisposition to be silent in critical situations which may be derived from their being carnivores (note that, for example, dogs' closest living relatives, wolves, try not to be detected when stalking prey; Peterson & Ciucci, 2003), because dogs do not always choose to approach silently; rather, they do so only when humans are present and *could* detect their forbidden approach. Overall, these studies suggest that dogs do not simply use strategies such as approaching forbidden food silently, but that their sensitivity to what humans can hear is flexible (Kundey et al., 2010; Bräuer et al., 2013).

It is, however, striking that dogs avoid the noisy tunnel but not the visible tunnel to approach forbidden food. In both cases, they could not see the human. This can be explained by the intrinsic differences between the way visual and auditory information is propagated. Whereas two subjects can have a completely different view (for example, when they stand opposite each other), both subjects will hear the same sound when they are in one room. The crucial point here is that while the dog is approaching the noisy tunnel, she/he can hear the noise herself/himself. In that moment, she can hear what the human can (and should not!) hear. In other words, also in this situation she/he can use the egocentric strategy 'When I hear the noise, then the other hears it too'(Bräuer et al., 2013).

Thus, dogs are very sensitive to humans' perception, but they most likely rely on what they themselves can perceive when they assess what the human can see and hear.

10.3 SEEING LEADS TO KNOWING

Dogs have developed skills to assess what humans can see, but do they also understand what humans register from their environment? In other words, do dogs understand what humans *have seen*—and more importantly—that seeing leads to knowing? To investigate this issue, two paradigms were used with dogs that were originally developed in studies with apes: the 'Ignorant helper' paradigm and the 'Guesser-Knower' paradigm.

Virányi et al. (2006) used the 'Ignorant helper' paradigm invented by Gomez (1996; see also Whiten, 2000) to investigate whether dogs are able to recognise a human's state of knowledge and ignorance depending on what she/he has seen. Two objects were hidden in a room: the dog's favorite toy and a stick, necessary to retrieve the out-of-reach toy. The helper was absent or present while the two objects were hidden. After the hiding process, the helper either knew the places of (i) both the toy and the stick, (ii) only the toy, (iii) only the stick, or (iv) neither of them. Dogs observed the whole hiding process in all conditions, but they could not reach the objects.

As other studies have shown, dogs are able to indicate the location of hidden objects without training (Miklósi et al., 2000; Kaminski et al., 2011a). The question here was what hiding place the dog would show to the helper. Dogs rarely indicated where the stick was hidden, suggesting that they did not understand that the helper needed the stick in order to retrieve the toy (Virányi et al., 2006). But dogs showed the place of the toy more often if the helper had been absent during the toy-hiding process compared to when she was present. Does that mean that dogs informed the helper about the toy because they understood that the helper had not seen where it was hidden? The helper was the owner, and her knowledge was established by her being present during the hiding of the toy the entire time or her being absent and re-entering after the objects had been placed. In all conditions, the stick was placed first and the toy was placed second. That means that in the conditions in which the helper was ignorant about the place of the toy, she re-entered immediately before the dogs started to indicate the objects (Virányi et al., 2006). Thus, dogs' increased showing behaviour in these conditions may reflect their different levels of arousal because owners reappeared rather than being evidence for understanding of past visual access (Kaminski et al., 2009a).

Topál et al. (2006) used a similar design with Philip, a highly trained assistance dog. The objects were a ball and a key. The ball was placed in one of three boxes. The helper—which was again the owner—needed the key in order to open the boxes. The question was whether Philip would indicate the place of the key only in cases when the helper was absent while the key was hidden. Indeed, he was able to adjust his communicative behaviour adequately to the different conditions; i.e., he informed the helper in 6/8 trials when he did not know where the key was hidden.

The authors state that the exact mechanism underlying this performance is not clear. One explanation is rapid discrimination learning, as Philip has sophisticated abilities for reading subtle cues of human behaviour and extensive experience with different communicative situations, in particular with his owner. This seems to be more likely than the explanation that Philip was able to recognise the relationship between the information observed by the helper and his knowledge (Topál et al., 2006).

However, Cooper et al. (2003) also reported some evidence that dogs know what humans have seen. They used the famous Guesser–Knower paradigm invented by Povinelli et al. (1990). Here, subjects can see that one of three places is baited with food, but they do not see which location. There are two informants. One informant (the knower) is present at the moment of the baiting and has full visual access to it. The second informant (the guesser) is absent during the baiting process. The question is whether subjects follow the information of the guesser or of the knower. Do they understand that only the knower is aware of the correct location of the food, as she/he has seen where it was hidden?

After the baiting, both the knower and the guesser point to different locations; the guesser always points to a wrong place. Cooper et al. (2003) reported that in the first trial 14/15 dogs (93%) chose the location pointed to by the knower (Cooper et al., 2003; Roberts & Macpherson, 2011) and ignored the pointing cue of the guesser. However, as Udell and Wynne (2011) point out, the experiment referred to in Cooper et al. (2003) has never been properly published. As the exact methods are not presented, it is impossible to assess whether alternative explanations such as experience with the experimenters or simpler behavioural cues were ruled out in that experiment (Udell & Wynne, 2011). It is striking that dogs in the study by Cooper et al. (2003) ignored the pointing gesture of a human (the guesser), since according to recent studies, they do so only in a few situations—for example, when they have seen that the target location is empty (Scheider et al., 2012) or after many trials (Petter et al., 2009; see following text).

Importantly, in the study reported by Cooper et al. (2003), the effect that dogs preferred to follow the pointing gesture of the knower was present only in the first trial. In their overall performance, dogs did not choose the knower. This drop in accuracy could be attributed to dogs' confused memories of the roles of the knower and guesser in the current trial with memories of the roles they had played on previous trials (Roberts & Macpherson, 2011). Thus, if there was an effect, it was not very strong.

Moreover, Kaminski et al. (2009a), using a novel paradigm, found no evidence that dogs understand what a human experimenter has seen in the past. In their setup, two toys were placed on the dog's side of two small barriers (see previous description), but in this experiment both barriers were opaque. The dog could witness the placing of both toys. The human experimenter sat on the opposite side of the barriers, but she witnessed only where one toy was placed because she was out of the room for the placing of the second toy.

After that, the experimenter asked the dog to fetch the toy. From the experimenter's viewpoint, neither toy was visible because the barriers were opaque—but she knew of the existence of one toy since she had seen it being placed behind one of the barriers. The question was whether dogs could also appreciate the researcher's experience with only one of the two toys. But dogs did not prefer to fetch the 'experimenter' toy. In other words, subjects did not differentiate between the two toys on the basis of whether the human had previously seen them and therefore knew about them. These results show that dogs in this study were unable to take into account what a human had seen in the immediate past.

Taken together, there is only weak evidence that dogs understand that what humans have seen leads to them knowing about it. This evidence comes from studies using the 'Ignorant helper' and the 'Guesser–Knower' paradigm. Note that these paradigms have also produced mixed results in great apes (Povinelli, 1994), and alternative explanations such as learning could not be excluded (Gomez, 1996; Topál et al., 2006). In contrast, there is clear evidence in competitive situations that chimpanzees are able to determine what a competitor has seen (Hare et al., 2001) and that seeing leads to knowing (Kaminski et al., 2008). The study by Kaminski et al. (2009a), described previously, used a cooperative setup with dogs in which dogs were asked to perform an action from their everyday lives without any prior training. The negative results in the study are particularly strong evidence that dogs are unable to understand what humans have seen in the past because the exact same paradigm was used to show that dogs do understand the human perspective in the present (see previous description).

10.4 INTENTIONS

Another question that arises if we want to know what dogs know about others is whether they understand humans' goals and intentions. It is highly adaptive not only to react to what humans are doing but also to anticipate what they will do. The question here is whether dogs understand human behaviour simply as bodily motion and use behavioural rules to predict future behaviour or whether they understand it as intentional goal-directed actions. In the latter case, dogs should discern directly what a human is trying (but failing) to do, what state of the environment she/he is trying to bring about, and what her/his goal is (see Tomasello et al., 2005; Call & Tomasello, 2008).

However, it is not easy to investigate whether dogs understand human intentions, as they constantly monitor humans, are able to read subtle cues of human behaviour, and have very good learning abilities. Thus, it is extremely difficult to prove that they have not simply learned that one action is usually followed by another event. One possible scenario, to make this point clearer, is the owner who grabs the leash, followed by the dog immediately running to the door. The dog seems to expect a walk. Does the dog understand that the owner has the intention to go for a walk, or has it just learned that if the leash is touched, a walk is likely?

Despite the difficulties in teasing these alternative explanations apart, there are some interesting findings relating to dogs' understanding of human intentions. These recent studies do not examine the ability to understand goals and intentions directly, but rather they investigate imitation, communication, deception, and the occurrence of helping behaviour. But in order to solve these problems, the ability to understand humans' goals and intentions would be helpful or even necessary for the dogs.

Range et al. (2007) found that dogs copy others' actions more often when those actions are the efficient solution to a problem rather than when they are not. In their study, they used a problem (i.e., operating a rod) that dogs could solve by using either their mouth or their paw. In a baseline condition, it was shown that dogs prefer to use their mouth for that action.

Dogs then saw a demonstrator dog that always used the less preferred action (the paw) to solve the problem. In one condition, this was the rational thing to do because the demonstrator dog carried a ball in her mouth, making it impossible for her to use her mouth for the action. But in the other condition, there was no obvious reason for the demonstrator dog's preference for paw usage. Range et al. (2007) found that the observer dogs preferred to use the mouth when they had observed the demonstrator using the paw whilst their own mouth was occupied by the ball, but they preferred to use the paw when they had observed the demonstrator using the paw with her mouth free. This indicates not only that dogs attend to others' goal-directed actions during demonstrations, but also that they copy others' choice of means to perform that action.

Kaminski et al. (2011b) replicated that study and added a further control condition. They did not find that dogs imitate rationally. They suggest that dogs in the study by Range et al. (2007) did not selectively attend to the irrational nature of the action but were simply distracted by the ball (Kaminski et al., 2011b).

Also in a second experiment, Kaminski et al. (2011b) found no evidence that dogs understand others' goals and attend to the means that others use to fulfill their goal. Here, an experimenter gave an unusual cue about the location of a hidden food in an object choice design. She moved her leg towards the target location. In one context, the human's hands were occupied because she was holding a heavy book, so using the leg was a rational means to communicate. In the other context, the human's hands were not occupied, making it irrational for the experimenter to use her leg. Thus, in the latter context, extension of the leg could be interpreted as a random action, not meant to communicate anything.

Dogs did not distinguish between these two conditions; they used the leg movement as a cue to find the hidden food irrespective of whether it was the rational or an irrational means to communicate. They were unable to infer that the human's goal in such situations would be using her hand to communicate—if it were free. Thus, dogs did not take into account the situational constraints faced by a human experimenter in that communicative situation.

In contrast, Kaminski et al. (2012) found that dogs distinguished random from intended movements in a communicative setting (see also Soproni et al., 2001). The main question here was whether dogs can understand the *communicative* intentions of the human, i.e., that they infer that the human wants to communicate something to them. This ability to recognise the communicative intent turns otherwise meaningless behaviours such as the human pointing gesture into meaningful communicative acts.

Kaminski et al. (2012) also used an object choice task. The human experimenter either communicated about the location of the hidden food with a communicative intent or she produced similar but non-communicative movements in the same direction (see Figure 10-2). For example, she either pointed at the correct cup and alternated her gaze between subject and cup; or she stretched out her arm and index finger cross-lateral from her body such that it mirrored the pointing cue while pretending to check the time on her watch and alternated her gaze between a clock on the wall and the correct cup. Dogs followed the intentional pointing cue more often than the non-intentional one.

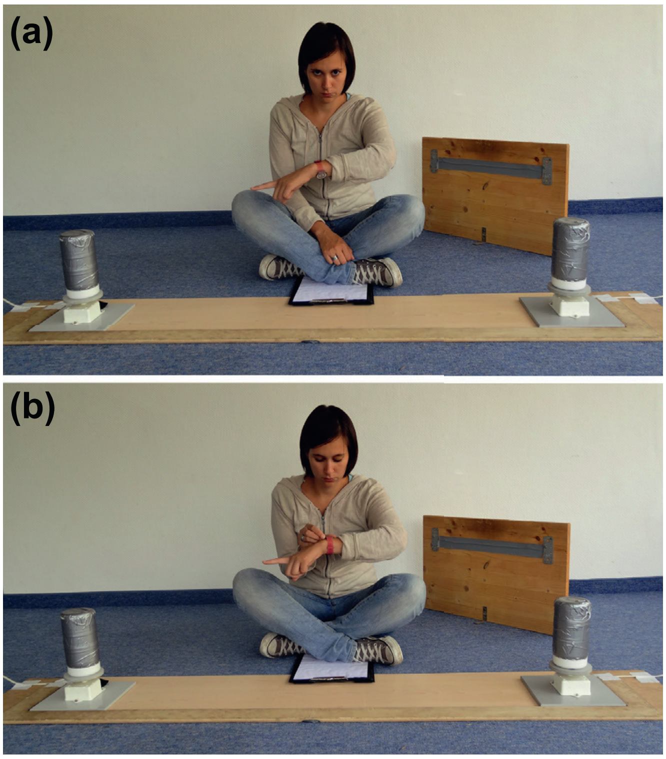

FIGURE 10-2 Conditions (a) ‘Intentional Point’ and (b) ‘Non-Intentional Point’ in the study of Kaminski et al. (2012). See color plate section.

Why did dogs preferentially follow the intentional cue in that study but not in the study by Kaminski et al. (2011b)? Note that here (but not in the study by Kaminski et al., 2011b), the communicative intent was established through eye contact. Indeed, one question addressed in the study by Kaminski et al. (2012) was what specific cues dogs use to determine when human communication is intended for them. They found that eye contact is the most important cue. It is possible that, for dogs, human eyes simply function as a kind of automatic trigger that raises the level of arousal and therefore the attention to the human—which then leads to greater accuracy in gesture following in situations with eye contact.

But it is also possible that dogs make a more discerning use of eye contact to read human communicative intentions. Indeed, dogs are very skillful in determining whether communication is intended for them—and they use exactly the same cues human infants use to identify communicative intent (Csibra, 2003; Behne et al., 2005).

Also, in another study, it was shown that dogs understood that a human was trying to communicate something to them (Kaminski et al., 2009b). Here, specially trained dogs were confronted with a new task. These dogs were trained to identify objects by their names and fetch them on command. In the new task, owners held up a replica of the object and said: ‘Bring it here!’ Dogs successfully used iconic replicas to fetch the desired object. These findings also suggest that dogs comprehended the communicative intention of the human. Holding up a replica is in itself a meaningless behaviour, but dogs understood that the human was trying to communicate to them that they should fetch the matching object. Thus, dogs have a flexible understanding of humans’ communicative intentions (Kaminski et al., 2009b; see also Pettersson et al., 2011).

A different approach to investigate whether dogs understand humans’ intentions was taken by Petter et al. (2009), who used a paradigm developed by Woodruff and Premack (1979) with chimpanzees. The question was whether dogs can detect human deception. They used an object choice task. Dogs could choose between two containers, one of which contained a food reward. Two different experimenters pointed at the containers. On half of the trials, a cooperative human tester pointed to the baited container, and on the other half of the trials, a deceptive human tester pointed to the empty container. Dogs were clearly sensitive to the deception; they either approached the alternate bucket from the one cued by the deceiver or refused to make a choice.

However, the dogs behaved in the same way when the cues were inanimate. When black and white boxes stood close to the containers representing the ‘cooperator’ and ‘deceiver’, dogs also learned to approach the ‘cooperator’ box more often than the ‘deceiver’ box. Dogs were equally good at discriminating between the cooperator and deceiver and at obtaining the reward whether the cues were delivered by humans or were represented by inanimate objects. The authors concluded that dogs do not understand the intentions of humans in that situation and simply learn the association between cues and their outcomes (Petter et al., 2009).

As dogs are selected to cooperate with humans, they might display their intention-reading abilities only in cooperative rather than deceptive situations. Dogs have been used for rescue, search, service, and guide purposes (Serpell, 1995; Svartberg & Forkman, 2002). But the question is whether dogs that help humans actually understand humans' goals and intentions or whether they only perform innate or trained behaviour.

Providing others with usful information is considered to be one kind of helping behaviour (Warneken & Tomasello, 2009). Kaminski et al. (2011a) investigated whether dogs would help a naïve human to find a hidden object. The object was hidden by a helper in one of four locations in a room. The dog witnessed the hiding process, but the human was absent and therefore unaware of the location of the object. Conditions varied presenting an object that was valuable either to the dog, the human, both, or neither. As in previous studies, dogs showed naïve humans the location of the hidden objects that were interesting for themselves (Miklósi et al., 2000; Virányi et al., 2006). However, dogs also sometimes indicated the location of objects in which they were not interested (i.e., a hole puncher, a vase). Moreover, when only the human was interested in the object, dogs often performed an informative showing behaviour, but indicating the *wrong* location of the object. They seemed to be motivated to help or at least willing to please the human, perhaps prompted by the human's utterances and search behaviour. But they were unable to infer the human goal in that situation.

In a second experiment, Kaminski et al. (2011a) investigated whether dogs could understand when the human needed helpful information to find a particular object—out of two—that she/he needed. Dogs were always presented with two objects. But only one of the objects was relevant for the owner because it was needed for a certain activity such as cutting or stapling paper. Then both the relevant and the irrelevant objects were hidden. Dogs did not differentiate between the object that the owner needed and the non-target object. They did not prefer to indicate the relevant one, probably because they did not understand what the human was looking for.

That is why Bräuer et al. (2013) raised the question whether dogs would help a human if the human's goal was made as obvious as possible. They used a setup in which a human tried to enter a target room in order to get a key. The tested dog could open the door to the target room by pushing a button. If the dogs were able to understand the human's goal and were motivated to help, they should open the door when the human tried to enter the target room. The help conditions in which the human expressed that she wanted to enter the target room were compared to a control condition in which the human did not try to enter the room.

Bräuer et al. (2013) found that dogs helped a human to open a door to a target room if the human explicitly communicated her goal to the dog. The results suggest that dogs are willing to help if they are able to recognise the human's goal. But the only effective way for a human to obtain help was to communicate her goal clearly by trying to open the door and giving ostensive cues to the dog in a natural way. How exactly the dogs perceived the human goal here is unclear. It is possible that they were instrumentally guided to the goal rather than really understanding what the human wanted by trying to open the door.

In conclusion, dogs have great difficulties in understanding humans' goals and intentions. It is unlikely that they interpret others' behaviour as goal-directed when they imitate and when they are deceived (Petter et al., 2009; Kaminski et al., 2011b; but see Range et al., 2007). The only clear evidence about recognition of intentions comes from communicative situations. Dogs understand humans' communicative intentions in a very flexible way (Kaminski et al., 2009b; Pettersson et al., 2011; Kaminski et al., 2012; Scheider et al., 2012). They are also able to recognise the goal of a human in a helping situation when it is expressed clearly by communicating with the dogs (Bräuer et al., 2013). In both cases, it is possible that dogs react to several ostensive cues. But no matter whether they are guided by these cues or have a more discerning understanding of humans' intentions, it enables them to react appropriately in most of these situations.

10.5 THEORY OF MIND IN DOMESTIC DOGS?

Some authors have suggested that due to the close evolutionary association between humans and dogs, the latter are likely candidates for finding evidence of theory of mind in a non-human animal (Topál et al., 2006; Virányi et al., 2006; Petter et al., 2009). Do dogs have a theory of mind? Are they able to attribute mental states—beliefs, intents, desires, pretending, knowledge to themselves and humans? The short answer is no. To date, there is no evidence that dogs understand that humans have beliefs, desires, and intentions that are different from their own.

But is it useful to raise the question whether dogs possess a full-fledged theory of mind like we do. Not only is it difficult to test, as many theory of mind experiments for non-verbal animals suffer from the drawback that there exist a number of other abilities that might account for the observed behaviour (Horowitz, 2011; Udell & Wynne, 2011; see also preceding description), but also for other species, namely chimpanzees, there is no clear answer to the question whether or not they have a theory of mind (Tomasello et al., 2003a, b; Call & Tomasello, 2008). Call, Tomasello, and colleagues have therefore argued that it makes no sense to answer this question with a 'yes' or 'no', but rather it makes more sense to ask which psychological states animals understand and to what extent. They also emphasise that there are many different ways in which an organism might understand the psychological functioning of others (Call & Tomasello, 2008; see also following text).

A comparison with other species can be helpful in order to find out what skills (if any) are possessed uniquely by dogs. Some skills discussed in the current chapter dogs do share with other social mammals and birds. However, in this book, we are especially interested in those skills that can be attributed to the selection pressures dogs were faced with during domestication as an adaptation to the human environment. Thus, the question is to what extent dogs' 'understanding of humans' has developed during domestication.

In their constant monitoring of humans, dogs clearly differ from other species, in particular from their closest living relatives—from wolves (Gacsi et al., 2005; see also Miklósi et al., 2003). It is surprising that they do not follow gaze into free space, a skill that is found in many primates and other mammals, birds, and even reptiles (Tomasello et al., 2001; Bugnyar et al., 2004; Bräuer et al., 2005; Kaminski et al., 2005; Wilkinson et al., 2010; see Shepherd, 2010, for a review). But if explanation by Teglas et al. (2012) is valid and dogs selectively follow human gaze when it is preceded by ostensive cues, then the fact that they do not follow gaze in some situations may be a result of their domestication history, as they were selected to be sensitive to human ostensive cues (see also Chapter 11, Topál).

Regarding visual perspective-taking, there is strong evidence that great apes, but also corvids and potentially goats, know what their conspecifics can see (Hare et al., 2000; Emery & Clayton, 2001; Dally et al., 2004; Kaminski et al., 2006; Bräuer et al., 2007). This is not surprising, as this skill is highly adaptive, both in communicative but also in competitive situations. Moreover, wolves are also sensitive to humans' attentional states under certain conditions (Udell et al., 2011; Udell & Wynne, 2011). It is possible that dogs' perspective-taking abilities reflect general mammalian skills rather than a special adaptation to the human environment. However, their sensitivity to the human eye—for example, their ability to distinguish between open and closed eyes—might be a unique adaptation to the human environment (Call et al., 2003).

Dogs do not know what humans have seen in the past and that seeing leads to knowing. But this seems to be a demanding task as, beside chimpanzees (Hare et al., 2001; Kaminski et al., 2008), there is only evidence for two corvid species that might understand that seeing leads to knowing when caching (Bugnyar & Heinrich, 2006; Dally et al., 2006).

Also regarding the understanding of others' intentions, dogs are outperformed only by great apes in the animal kingdom. This might be due to the fact that it is difficult for non-human animals to infer others' goals, or that up to now only primates have been tested in this task. Chimpanzees distinguish between an experimenter who is unwilling or unable to give them food (Call et al., 2004). They imitate selectively (Buttelmann et al., 2007) and understand others' goals in various helping situations (Warneken et al., 2007; Warneken & Tomasello, 2006, 2009). But in contrast to dogs, they do not understand humans' communicative intentions (Bräuer et al., 2006; Kaminski, 2011). The latter is most likely one of dogs' special adaptations to the human environment.

10.6 MIND READING OR BEHAVIOUR READING?

There is no evidence that dogs understand humans' knowledge about past events and beliefs, and they have problems understanding humans' intentions. But in many cases they are very skillful at solving social problems, leading many dog owners to conclude that 'my dog understands me'.

Indeed, dogs react appropriately in many social situations. The following 'toolkit' may help dogs to do so. First, they are extremely attentive and interested in what humans are doing. Second, they have excellent learning abilities: they are very flexible and quick to make associations and to generalise from known to similar situations in their human environment. Third, they are able to read subtle cues of human behaviour; and fourth, they have extensive experience with different communicative situations. Thus, such 'understanding' of the owner can be developed without any insightful recognition of others' subjective mind states (Whiten, 1997; Topál et al., 2006).

As Udell and Wynne (2011) have nicely stated, dogs are not readers of our minds; instead, they are exquisite readers of our behaviour. They solve these social problems successfully but probably use different strategies than we do. For example, dogs are very skilled in assessing humans' perspectives. But instead of really taking the other's visual perspective into account—i.e., imagining what she/he can see from her/his point of view—they might use some valid rules or assess what others can see on the basis of what they themselves can see. In the presence of humans, they avoid forbidden food when no opaque barrier is blocking it (Bräuer et al., 2004) and when it is illuminated (Kaminiski et al., 2013). In other situations, they seem to use the egocentric rule 'if I can see her/him, then she/he can see me'. Note that this rule is extremely successful unless they have to put their paw in a tunnel which the human has visual access to whilst they cannot see the human (Bräuer et al., 2013). Moreover, this rule is also valid to assess what humans can hear (Kundey et al., 2010; Bräuer et al., 2013).

Similarly, dogs solve the problem of reading human intentions under certain circumstances. Most likely they use the strategy to generalise past experiences in order to predict future human behaviour. They probably recognise that a particular sequence of events and/or actions precedes certain behaviour responses in humans. Dogs might have learned that if the human is turning her/his head in all directions and asking 'Where is it?' that she/he is looking for something (Kaminski et al., 2011a). But that is not enough to infer *what* she/he is looking for. Likewise, if she/he is moving towards a door accompanied by ostensive cues, dogs might have learned that she wants to open that door (Bräuer et al., 2013).

That also means that dogs might fail to predict humans' behaviour in completely novel situations, since in this case, interpreting another's behaviour as goal-directed and attending to the means by which others perform certain actions becomes necessary (Schwier et al., 2006). But in most situations, it is sufficient for dogs to simply monitor humans and 'predict' their behaviour on the basis of their past experience (Kaminski et al., 2011b).

Dogs' special talents lie in the understanding of humans' communicative intent. They not only know when communication is intended for them (Pettersson et al., 2011; Kaminski et al., 2012; see also Chapter 11, Topál), but they also understand the communicative intent in a new context (Kaminski et al., 2009b). It is possible that here they simply use a combination of different cues that they have learned during their extensive experience with communicative situations with humans. However, it is also possible that they have a deeper understanding of humans' communicative intents that has evolved as a special adaptation to the human environment.

In conclusion, although there is no evidence that domestic dogs possess a humanlike theory of mind, they 'understand' a lot about humans in their own way. They are very successful in solving social problems in their human environment, as they constantly monitor humans, learn valid associations, make adequate generalisations, and use egocentric strategies.

Future Directions

We are left with these open questions:

- Under what circumstances do dogs follow human gaze?
- How exactly do dogs 'read' humans' intentions?
- Do dogs really understand humans' communicative intents?
- What experiences do dogs need to develop an ability to predict human behaviour?

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ORIGINAL PAPER

Effect of shared information and owner behavior on showing in dogs (*Canis familiaris*)

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Abstract

Dogs' production of referential communicative signals, i.e., *showing*, has gained increasing scientific interest over the last years. In this paper, we investigate whether shared information about the present and the past affects success and form of dog–human interactions. Second, in the context of showing, owners have always been treated as passive receivers of the dog's signals. Therefore, we examined whether the owner's behavior can influence the success and form of their dog's showing behavior. To address these questions, we employed a hidden-object task with knowledgeable dogs and naïve owners. Shared information about the present was varied via the spatial set-up, i.e., position of hiding places, within dog–owner pairs, with two conditions requiring either high or low precision in indicating the target location. Order of conditions varied between pairs, representing differences in shared knowledge about the past (communication history). Results do not support an effect of communication history on either success or showing effort. In contrast, the spatial set-up was found to affect success and choice of showing strategies. However, dogs did not adjust their showing effort according to different spatial set-ups. Our results suggest that the latter could be due to the owner's influence. Owner behavior generally increased the effort of their dog's showing behavior which was stronger in the set-up requiring low showing precision. Moreover, our results suggest that owners could influence their dog's showing accuracy (and thereby success) which, however, tended to be obstructive.

Keywords Dog–human interaction · Dogs · Communication · Showing · Shared information

Introduction

Communication, most simply defined, is the transfer of information from one entity to another, most commonly described in terms of the sender–receiver model (Shannon and Weaver 1949). A mutual understanding about signs and rules of how to use them is essential to achieve success in this process (e.g., Stevens 1950). Based on this, developing successful communication across species borders can be viewed as a particularly difficult endeavor, since the agreement upon signs and rules has to be brought in line with already existing but potentially very different communication systems between these two species to avoid misunderstandings (e.g., the common misinterpretation of the chimpanzee fear grin as happy smile; e.g., Aldrich 2015; 2018; Keeley 2004). A number of theoretical accounts describe communication systems that allow for new signals to develop between species, including ontogenetic ritualization (e.g., Tomasello and Call 1997; Tomasello et al. 1994), co-construction of meaning (e.g., Bard et al. 2019) and invented signals (e.g., Fröhlich and van Schaik 2020), but arguably doing so is considerably more difficult than intraspecific communication. Even so, we can observe one powerful example of interspecies communication almost daily: communication between dogs and humans.

The essence of the *domestication hypothesis* is that, through the evolutionary pressures of their long coexistence,

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dogs have become particularly skilful in communicating with humans. This is supported by a growing body of research (Hare et al. 2002; Marshall-Pescini and Kaminski 2014; Miklósi et al. 2003; Piotti and Kaminski 2016; Topál et al. 1998; but see also Udell et al. 2010) and includes dogs' outstanding sensitivity to communicative behaviors on the part of humans, such as pointing or eye gaze (Hare et al. 2002; Hare and Tomasello 2005; Kaminski et al. 2012; Miklósi and Soproni 2006). Dogs' sensitivity to human-given cues is so pronounced that they sometimes respond even when there is no communicative intent from the human. For instance, Lit et al. (2011) demonstrated that scent detection dogs are more likely deceived by their human handlers' beliefs about scent locations than decoy smells (food and toys). Although Udell et al. (2010) outline valid points supporting ontogenetic learning, especially during sensitive developmental phases, as source of this heightened sensitivity of dogs towards human communicative cues, currently more experimental evidence exists in favor of the domestication hypothesis than against it. Therefore, we chose this hypothesis as the basis of our current study. Nonetheless, it is important to emphasize that this does not exclude the principal possibility of ontogenetic learning playing a role in human–dog communication (see also Sect. "Discussion").

Showing

But dogs are also able to successfully send out communicative signals towards humans themselves. One specific behavior, which has received considerable attention, is known as showing (Gaunet 2008, 2010; Gaunet and Deputte 2011; Gaunet and El Massioui 2014; Heberlein et al. 2016, 2017; Kaminski et al. 2011; Marshall-Pescini et al. 2009; Miklósi et al. 2005; Passalacqua et al. 2011; Piotti and Kaminski 2016; Savalli et al. 2014; Virányi et al. 2006). Miklósi et al. (2000) were the first to specifically investigate showing behavior in dogs. They defined showing as "a communicative action consisting of both a *directional component* related to an external target and an *attention-getting component*, that directs the attention of the perceiver to the informer or sender" (Miklósi et al. 2000, p. 159, emphases added). Miklósi et al. let dogs witness how a piece of food or a toy was hidden out of their reach. Afterwards, their naïve owner entered the room, instructed to find the hidden object with the help of their dog. To control for mere motivational or audience effects, two other conditions were implemented in which either only dog and hidden object or only dog and owner were in the room. In all conditions, the authors coded the occurrence of a number of dog behaviors, most importantly vocalizations and gazing at the hiding place and the owner, which were also subjected to a sequential analysis (*gaze alternation*). Miklósi et al. could show that, without previous training, dogs used gaze alternation as well as vocalizations, seemingly to signal the location of the hidden object to their owners.

The interest in showing behavior is mainly based on the suggestion that for species without hands, gaze alternation, i.e., repeated moving of gaze direction between target and receiver (Gómez 1990), which often accompanies pointing in humans (e.g., Bruinsma et al. 2004), could be functionally analogous to pointing and, therefore, intentional and referential (Harding and Golinkoff 1979; Leavens and Hopkins 1998; Leavens et al. 2005). In Miklósi et al.'s (2000) study, showing behavior only occurred in the presence of both owner and food or toy, indicating that showing behavior in dogs is indeed a form of functionally referential communication. Later studies confirmed that showing behavior in dogs fulfills all criteria (Leavens 2004; Leavens et al. 2005) of intentional referential communication (Gaunet 2010; Gaunet and Deputte 2011; Heberlein et al. 2017; Savalli et al. 2014; Virányi et al. 2006).

In contrast to gaze alternation, vocalizing in itself does not qualify as showing, but rather represents an attention-getting component. Barking and whining have been described as attention-capturing signals in the past (Bekoff 1974; Bradshaw and Nott 1995; Fox 1971). In addition to gazing and vocalizing, other components of showing exhibited by dogs in hidden-object tasks have been identified in Miklósi et al.'s (2000) and other studies. Directional components include moving towards (Heberlein et al. 2016, 2017) or spending time near the hiding place, i.e., using their own position as a local enhancement cue (Gaunet and Deputte 2011; Hare et al. 1998; Miklósi et al. 2005; Savalli et al. 2014), manipulating (Gaunet 2010; Miklósi et al. 2005; Savalli et al. 2014), sniffing (Gaunet 2010; Miklósi et al. 2000; Savalli et al. 2014) or jumping at the hidden object (Hare et al. 1998); and as attention-getting components include establishing body contact with the owner (Gaunet 2008, 2010; Gaunet and Deputte 2011; Heberlein et al. 2016, 2017; Savalli et al. 2014) and moving towards the owner (Heberlein et al. 2016, 2017).

It is important to emphasize that in all studies investigating showing, owners could overall successfully use the signals provided by their dogs to find the hidden objects. Thus, showing behavior provides a powerful example of successful dog–human communication. However, in all studies on this topic so far, owners have been treated as passive receivers of the dog's showing signals. Therefore, an interesting question remains unanswered: whether owners can influence showing behavior, and thereby maybe even success as well. The above-mentioned studies outlining dog's sensitivity to human communicative signals suggest an influential potential for owners here as well.

Shared information and the principle of least effort

Past studies with human participants have shown that shared information between communication partners influences the form their communication takes and its success, for instance when both communication partners remember past discourse or share access to information in the present such as stimuli attributes (Brennan and Clark 1996; Brown-Schmidt et al. 2008, 2009; Krauss and Weinheimer 1967; Müller et al. 2019; Winters et al. 2015, 2018; Yoon et al. 2016). Apart from its positive influence on communication success, relying on shared information also often allows interlocutors to reduce their communicative effort. Zipf (1949) argued that human behavior in general is guided by the principle of least effort, that is, people try to spend as little effort as possible on the problems they face by taking current and future situations into account. This strategy proved to be effective on the individual as well as the collaborative level (Clark and Wilkes-Gibbs 1986).

Taken together, this implies that humans use shared information to optimize effort and, thus, achieve an optimal trade-off between efficiency and communicative success. At this point, there is relatively little empirical work demonstrating whether these factors influence communication in species other than humans or even cross-specific communication.

In a study by Scheider et al. (2011), dogs searched longer and more often at an empty location a human pointed at, in a condition in which they had previously found food in the presence of that human, than dogs without such context information. This study demonstrates that such additional information not only affects dogs' behavior but also their interpretation of human communication. However, this study investigated searching/choice behavior and not showing. Heberlein et al. (2017) delivered an indication that showing might be sensitive to shared information between dog and human as well. They found that dogs exhibited less showing behavior if the human partner and the dog shared the knowledge about the correct hiding location, in contrast to when only the dog observed the hiding procedure. Furthermore, in a study by Gaunet and Deputte (2011), dogs positioned their bodies differently depending on the height of the target location. This study is particularly relevant since shared information represents the spatial layout of the experimental set-up, like in the current study. However, the findings of Gaunet and Deputte (2011) only illuminate the sensitivity of a (directional) component of showing behavior to the spatial set-up. Thus, it remains unclear whether and to what degree showing behavior as a whole is affected by the spatial set-up.

At the time of this study, no research could be found that specifically investigated whether dogs follow the principle of least effort in their communication in general or with humans in particular. However, generally, behavior research in humans as well as non-human animals has adopted the idea that organisms strive to save energy and minimize effort (Menzel 1973; Mowrer and Jones 1943; Sparrow and Newell 1998; Tsai 1932; Waters 1937). Moreover, several studies found Zipf's (1949) principle of least effort to apply to animal communication (Doyle et al. 2011; Hanser et al. 2004), specifically in dolphins (Ferrer-i-Cancho and Lusseau 2009; McCowan et al. 1999), squirrel monkeys (McCowan et al. 2002), formosan maquaques (Semple et al. 2010), bats (Luo et al. 2013), and to some extent common marmosets (Ferrer-i-Cancho and Hernández-Fernández 2013) which speaks in favor of the generalizability of Zipf's principle of least effort.

In general, the long commensal history of dogs and humans is suggested to have driven dogs to develop communication patterns that follow the same rules as those of humans (Fitch et al. 2010; Miklósi et al. 2004; Schleidt and Shalter 2003; Topál et al. 1998). Accordingly, crucial factors that have been found for human communication could apply to dog–human communication as well.

The present study

In the current study, we examined whether present and past shared information between dogs and their owners, as well as the owner's behavior, influence the form and the success of human–dog interactions in a hidden-object task. The set-up, similar to Miklósi et al. (2000), enabled only dogs to witness the hiding of their toy while owners re-entered the room afterwards. Thus, dogs had to show their owners where the toy had been hidden to get it back and play with their owners. Two different conditions manipulated present shared information in the form of the spatial set-up: The distance between the possible hiding places was either small (*close* condition) or big (*far* condition), therefore requiring either high or low precision in indicating of the target location. The order in which pairs went through these conditions represented different communication histories, i.e., shared information about the past. Dogs could make use of information about the present (i.e., condition) as well as their memories from their first session (i.e., communication history) to adjust their communication strategies which in turn might influence success in finding the hidden toy.

Hypotheses

Building on the aforementioned literature, four hypotheses are proposed regarding the communicative behavior between dogs and their owners:

H1: success of communication Dogs are able to successfully show the location of the hidden object to their owner. Based on this hypothesis, we predict that a greater proportion of showing referring to the correct location predicts greater success.

H2: spatial set-up The distance between the boxes affects success and form of dog–owner communication. Regarding this hypothesis, we predict that (a) performance will be better in the far compared to the close condition, i.e., there will be a main effect of condition, and that (b) the form of communication will differ between conditions.

H3: communication history Past interactions between dogs and owners constrain future communicative behaviors. Based on this hypothesis, we predict that (a) the starting condition determines the showing strategy dogs use throughout the whole procedure, i.e., dogs use relatively more high-effort strategies starting with close than with far. This has direct implications concerning performance: (b) pairs perform better if they start with close than when they start with far. Thus, we expect an interaction between condition and session regarding showing effort as well as performance (an in-depth description of these predictions can be found in Online Resource 1).

H4: principle of least effort Dogs always use the minimal effort strategy for a given context. Here, the prediction is that the far condition should be characterized by relatively less high-effort strategies than the close condition. This should hold irrespective of the order in which pairs completed the conditions. Thus, this hypothesis predicts a main effect of condition regarding showing effort, but no interaction of condition and session.

Note that H3 and H4 contradict each other. Although the influence of communication history and the principle of least effort are not necessarily mutually exclusive, in this set-up we wanted to examine the isolated contributions of the two factors.

In addition to these hypotheses, the set-up of the study also gave the opportunity to look at the interaction of dogs' and owners' behaviors. Regarding this part of the showing paradigm, however, existing literature does not allow precise predictions. Therefore, we analyzed this relationship exploratively to provide a first look at the interactive part of showing. First, we examined whether the owners' behavior can influence their dogs' proportion of correct showing and thereby, indirectly, the pair's success. Second, we examined the owner's influence on showing effort.

Materials and methods

Subjects

The 32 pairs that took part in this study were normal pet dogs of various breeds and their owners. Two pairs had to be excluded during testing because of health problems of the dog, leading to a final sample size of 30 dog–owner pairs. Of these dogs, 18 were female and 12 were male (mean age 5.8 years, range 2–13 years), whereas 24 of the owners were female and 6 were male (for detailed information about pairs see Online Resource 1 and 2). Dogs were recruited from the DogStudies database of the Max Planck Institute for the Science of Human History in Jena. Selection criteria for dogs were high toy motivation and the ability to fetch inert objects (which was additionally tested explicitly; see Sect. Pretest). All dogs were healthy individuals with no known sight or hearing problems and no known aggression towards humans.

Materials and set-up

In the test room, four small boxes (8 cm × 15 cm × 20 cm) were attached to the windowsills which constituted the four possible hiding places. They were numbered from 1 to 4, so the owners could identify each box for their choices in the test. In the close condition, boxes were put up 17 cm apart from each other, while in the far condition, boxes were positioned 90 cm apart from each other (Fig. 1). For the owners, a chair with an accompanying questionnaire was placed in the middle of the room on which owners had to check the supposed target box (for detailed information about materials and set-up see Online Resource 1).

Procedure

Each dog–owner pair visited the laboratory twice within 1 week. Only one condition, comprising four trials, was tested per session (i.e., per day) with an inter-trial break of ~10 min. Conducting all eight trials in one session was decided to be too demanding for most dogs. While owners were instructed for the test, dogs could freely explore the test room.

Pretest

Before the actual test, a pretest was conducted. The owner was instructed to sit on the chair facing the dog sitting in ~2 m distance. If necessary, one experimenter held the dog by their collar. The dog's favorite toy was now put between the two parties and the owner was instructed to call the dog to bring the toy. Owners were told to do so in a natural manner, as they would in a typical playing or training context

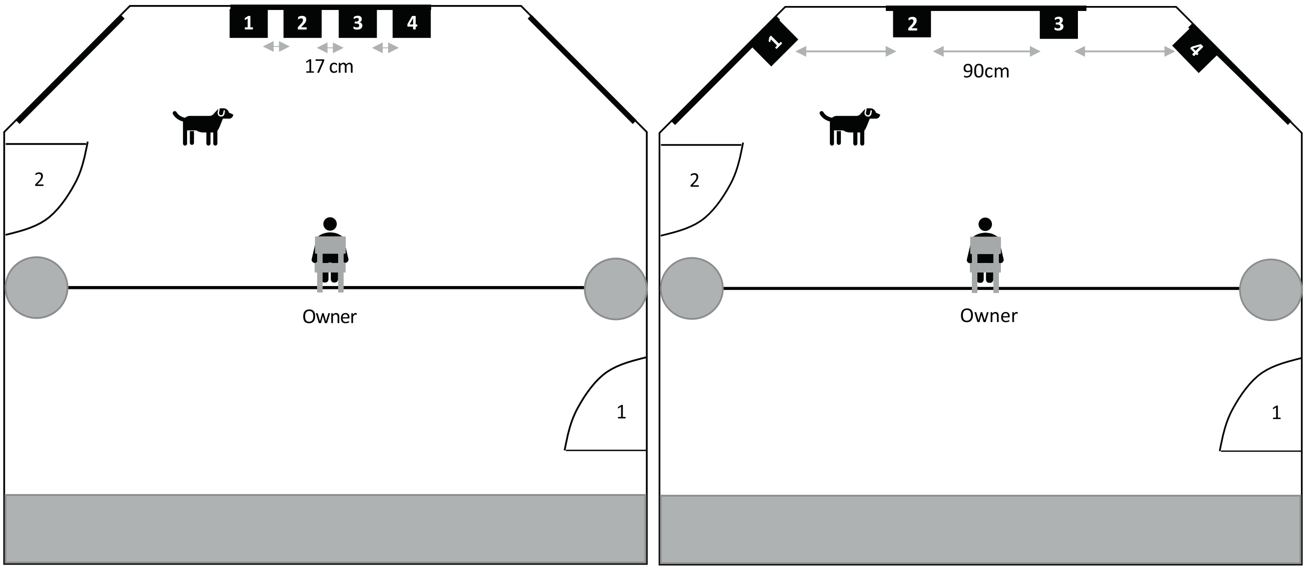

Fig. 1 Set-up of the close condition (left) and the far condition (right). The four possible hiding places (numbered 1–4) were fixed on the windowsills of the room. The owner, seated on a chair, was positioned in the middle of the room which could be entered through two doors (1 and 2). One camera was positioned above the boxes, one was on the sideboard behind the owner

since the aim of this study was to investigate the typical communication of the pairs. If the dog did as requested, the pair was allowed to play for a short amount of time. The exact duration of play varied between subjects because of different play styles but was kept approximately constant within subjects to avoid unintended differential rewarding (e.g., we either kept constant how often the toy was thrown and fetched or, if pairs preferred other play styles like tug-of-war, the duration of play time was kept constant). If a dog failed to bring the toy right away it had one more chance to do the task correctly before being excluded from the study. All dogs successfully completed the pretest. This procedure was repeated at the beginning of each new trial to re-establish the play context.

Test

Immediately after the short play session, the owner handed over the toy to experimenter 1 (E1). Experimenter 2 (E2) left the room with the owner through door 1 (see Fig. 1).[1] Now, E1 first gently waved the toy in front of the dog's face to get its attention (this was repeated whenever the dog averted its gaze from the toy, accompanied by calling the dog by its name). E1 then put the toy into the target box and closed it. Immediately, the box was reopened and this procedure was repeated one more time to assure that the dog really processed where the toy had been hidden. Meanwhile, E2 guided the owner around the room to door 2 (see Fig. 1) and waited for the signal from E1 which was given as soon as E1 had closed the box and left the room. E2 now opened the door and let the owner inside the room.

We also wanted to investigate the effect of behavioral restrictions on communication. Previous research has shown that a standardized, but nevertheless unnatural setting, can inhibit dogs' natural behavior and conceal their actual abilities (e.g., Bräuer et al. 2013). Therefore, the following procedure was divided into two phases with differing degrees of standardization (since this manipulation hardly yielded any effects, most results will not be discussed here and can be viewed in Online Resource 1).

Phase 1: The owner entered the room and directly sat down on the chair. During phase 1, owners were not allowed to stand up and walk around. Other than that, no constraints were put on communication between dogs and owners. After 1 min had elapsed, one of the experimenters signaled the owner from outside the room to fill in the questionnaire which also marked the end of phase 1. The owner now had to check the box in which he or she assumed the toy is located (i.e., make their choice for phase 1).

Phase 2: As soon as the owners had checked the questionnaire, they were allowed to stand up and move around freely within the test room. Here, the only communicational constraint was that owners were not allowed to open the

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[1] In the case of two pairs (see Online Resource 2), the dogs did not pay any attention to the toy anymore as soon as the owner had left the room. Thus, it was decided that the owners could stay inside the room, but they had to cover their eyes and ears during the hiding procedure. This way, the owners remained naïve and the dogs were attentive towards the toy.

boxes unless they wanted to make a choice. Phase 2 lasted a maximum of 1 min, hence, in contrast to phase 1, owners had the possibility to make their choice before 1 min had passed, even directly after filling in the questionnaire without further interacting with their dog. However, if owners had not opened a box after 1 min, experimenters prompted them by calling “Wählen!” (German for “Choose!”). The box that was opened in phase 2 could be different from the choice made in phase 1. If the pair chose correctly in phase 2, they could play together as a reward (again duration of play varied across but not within subjects). If the wrong box was opened, the experimenters would enter the room and open the correct box to show the toy to both the dog and the owner, but the pair was not allowed to play.[2] Choices for phase 2 were coded live by the experimenters and back-checked from tape afterwards.

In contrast to previous studies, the current set-up only prevented smaller dogs from accessing the boxes. Consequently, some dogs retrieved the toy on their own.[3] If dogs retrieved the toy already in phase 1, before owners could check the questionnaire, the respective box was taken as choice for both phases because in this case it was unambiguous for the owner which box was the correct one. If owners did not check a box on the questionnaire and the dog did not retrieve the toy, the choice for phase 1 was coded as *0* and subsequently as incorrect choice because it neither overlapped with the target box nor did it indicate a correct inference from the dog’s behavior. In between trials dogs had no access to their favorite toy or any other toys. Online Resource 3 displays a video of the procedure.

Design

Order of conditions was counterbalanced across subjects. Order of boxes was semi-randomized across conditions, with the stipulations that the same box could not be target in two consecutive trials within a session and that each box had to be target twice for each dog. The number of the first box was counterbalanced across subjects. Due to excluded pairs and problems during the test, the final distribution is slightly uneven: Seven pairs started with box 1, ten with box 2, six with box 3 and seven with box 4.[4]

Behavioral coding

All behaviors were coded using Solomon Coder software (Péter 2017) which was set-up with a sensitivity of 0.20 s. For dogs, seven different behaviors were coded: gazes directed at each of the boxes and the owner, movements directed at each of the boxes and the owner, time spent near each box, jumping/standing upright in front of each of the boxes, vocalizations, whether the dog opened the boxes and whether the dog retrieved the toy on its own.

For owners, the following behaviors were coded into one variable *owner behavior*: owners’ gazing at the dog, gazing at the boxes (i.e., one specific box or the general direction of the boxes), pointing at the boxes, nodding in the direction of the boxes, showing empty hands, shrugging, approaching the boxes, talking (any utterances by the owner, i.e., including laughing, sneezing, coughing) and calling the dog by its name (including obvious nickname versions of the dog’s name, e.g., Sue for Susi, but no other kinds of nicknames that were given, e.g., honey). This variable is very broadly defined, since, for an explorative analysis of the interaction of owner and dog, the variable should cover a wide range of possibly influential behaviors. (We also conducted analyses with owner behavior separated into non-verbal prompting, talking and calling the dog’s name which can be seen in Online Resource 1).

All dog- and owner-related variables were coded in terms of frequency, and time point relative to all other behaviors (both the dog’s and the owner’s), i.e., how often and when they happened. All behaviors that were necessary for the calculation of showings (see below) were additionally coded in terms of duration, i.e., when they started and when they ended relatively to all other behaviors. Solomon Coder provides a timetable of all behaviors (dog’s and owner’s) as output as well as automatically calculates frequencies and durations of variables.

To assess the inter-coder reliability, 20% of the videos (i.e., 6 pairs) were coded by a second observer, naïve to the hiding location and the purpose of the study. Agreement between the two coders was calculated using Spearman rank order correlation, and inter-coder reliability was assessed according to the limits proposed by Cicchetti (1994). Accordingly, mean inter-observer reliability was good for frequencies of gazes ($r=0.74$), and excellent for durations of gazes ($r=0.82$), frequencies ($r=0.78$) and durations of the dog’s movements ($r=0.82$), frequencies ($r=0.97$) and durations ($r=0.96$) of dogs spending time near each box, frequencies ($r=0.98$) and durations ($r=0.99$)

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[2] In 10 trials, there were problems with the procedure. Sensitivity analyses were run in which these cases were excluded (see Online Resource 1) but results did not change in regard to the predictions.

[3] Again, sensitivity analyses were run excluding phases with retrieval (see Online Resource 1). Results did not change in regard to the predictions.

[4] Analyses were run to determine a possible effect on performance and behavior (see Online Resource 1). The resulting patterns of success and choice rates did not reflect this uneven distribution.

Table 1 List of combinations of directional components and attention-getting components forming showing.

Directional component	Attention-getting component
Gaze at box	Gaze at owner
	Move towards owner
	Vocalize
Move towards box	Gaze at owner
	Move towards owner
	Vocalize
Time near box	Gaze at owner
	Move towards owner
	Vocalize
Jump/stand upright in front of box	Gaze at owner
	Move towards owner
	Vocalize
Open box	Gaze at owner
	Move towards owner
	Vocalize

Both alternations and overlaps of directional and attention-getting components classify as showing. For alternations, order of the two components does not matter.

of jumping/standing upright at the boxes as well as opening boxes ($r=0.92$) (Spearman rank order correlation coefficients for each behavior per box can be seen in Online Resource 1). For dog vocalizations, coders reached good agreement for frequencies ($r_s = 0.74$, $p<0.001$) and excellent agreement for durations ($r_s = 0.77$, $p<0.001$). Lastly, inter-coder reliability was excellent for owner behavior ($r_s = 0.97$, $p<0.001$).

To specify showing behaviors, we generalized the definition for gaze alternation that Russell et al. (1997) initially used for chimpanzees and Miklósi et al. (2000) transferred to dogs, to include other showing behaviors as well: The directional component has to be followed directly and within two seconds by the attention-getting component or vice versa (i.e., order of components does not matter). Therefore, the above-mentioned behaviors were divided into directional components and attention-getting components (Miklósi et al. 2000). All 15 possible combinations of these components form the showing behaviors analysed in this study (see Table 1).

Since the initial definition focused on gaze alternation (Miklósi et al. 2000; Russell et al. 1997), it stated that the two components have to occur in succession. In this study, however, the two components could also occur simultaneously (e.g., spending time near a box while gazing at the owner). Therefore, both alternations and (partial or complete) overlaps of the above-mentioned behaviors were defined as showing. Showings were calculated based on the timetables provided by Solomon Coder using a script programmed with Python (further details regarding behavioral coding, flowcharts. depicting the employed algorithm and an example of the generated output can be seen in Online Resource 1).

For analyses regarding showing effort, low-effort showing was defined as the least effortful showing strategy: gazing at a box plus gazing at the owner (i.e., gaze alternation). Similarly, high-effort showings were defined as all showings involving the most effortful behavioral component: jumping/standing upright plus any of the three attention-getting components (i.e., gazing at the owner, moving towards the owner or vocalizing). However, since many dogs did not exhibit jumping/standing upright at all, the second most effortful showing strategy was added as well: moving towards a box plus moving towards the owner.

Statistical analysis

All analyses were done with R software (version 3.6.3; R Core Team 2020), the code can be viewed in Online Resource 4. In line with the Cumming's propositions of "new statistics" (Cumming 2014, p. 7) and the Publication Manual of the American Psychological Association (APA 2010), raw estimations and effect sizes will be reported and discussed independent of, and in addition to, their significance status ($\alpha=0.05$) and with regard to their respective confidence intervals. Raw data can be found in Online Resource 2. Results of analyses adjusted for outliers are displayed in Online Resource 1.

Overall success, i.e., whether pairs chose correctly or not, was investigated with a one-sample *t* tests against chance (25%) for each phase since two different measures of performance were used in phase 1 and 2 (i.e., questionnaire versus opening box). Two-sided, paired *t* tests were calculated to assess differences in performance between phases and differences in frequencies of the different showing types between conditions.

For all other effects, we applied a model comparison approach. Models were compared based on their respective Akaike information criterion (AIC; Akaike 1974) value. The respective model with the smallest AIC was chosen as final model, and to test for significant differences between the models a Chi-square test was applied (results of all calculated models and comparisons can be found in Online Resource 1). Whenever the program responded a warning of nonconvergence, the respective model was optimized using the BOBYQA algorithm (Powell 2009). For each analysis, rows including missing values for a variable of interest were excluded. According to the study design, session, trial and phase were always treated as one nested variable (i.e., phases were nested within trials which were nested within sessions) which is henceforth referred to as *time*.

To investigate the effects on success, generalized linear mixed-effects models (GLMM) with a binomial distribution

Table 2 Mean frequency, accuracy and choice rate of each type of showing behavior of a pair per phase within a trial

Directional component	Gazing at owner	Moving towards owner	Vocalizing
Frequency			
Gazing at a box	9.29	0.99	0.46
Moving towards a box	3.42	4.10	0.36
Spending time near a box	**12.38**	7.52	0.83
Jumping/standing upright at a box	0.57	0.37	0.11
Opening a box	–[a]	0.03	*0.01*
Accuracy			
Gazing at a box	0.38	0.36	0.43
Moving towards a box	0.30	0.31	0.47
Spending time near a box	0.29	*0.25*	0.31
Jumping/standing upright at a box	0.53	0.53	0.68
Opening a box	–[a]	0.58	**1.00**
Choice rate			
Gazing at a box	0.39	0.33	0.42
Moving towards a box	0.33	0.33	0.53
Spending time near a box	0.30	*0.26*	0.35
Jumping/standing upright at a box	0.64	0.65	0.77
Opening a box	–[a]	0.67	**1.00**

The highest numbers are written in bold, the lowest in italics

[a] Opening a box plus gazing at the owner was not exhibited at all

were calculated using the R package lme4 (version 1.1–19; Bates et al. 2018). Since the outcome variable was binary (i.e., correct vs. incorrect), a logit transformation was applied, i.e., the dependent variable for models was the probability of pairs choosing correctly rather than incorrectly.

For the investigation of effects on the proportion of correct showing and showing effort, linear mixed-effects models (LMM) were calculated. For this, we used the R package lme4 (version 1.1–19; Bates et al., 2018), and *p* values were calculated using the lmerTest package (version 3.0–1; Kuznetsova et al. 2017). Showing effort was defined as the frequency of high-effort showings relative to the sum of frequencies of high- and low-effort showings, i.e., the proportion of high-effort showing. Hence, higher values for this variable indicate higher showing effort.

Results

Overall success

Results show that pairs as a group chose correctly significantly above chance level in phase 1 ($M=53.75$, SD = 24.82, $t[29]=11.81$, $p<0.001$, Cohen's $d=2.16$, 95% CI [1.23, 3.05]) as well as in phase 2 ($M=59.58$, SD = 24.93, $t[29]=13.04$, $p<0.001$, Cohen's $d=2.38$, 95% CI [1.42, 3.31]). Moreover, both of these effects are of substantial size. Performance in phase 2 was significantly better than in phase 1 ($t[29]=-2.25$, $p=0.032$, Cohen's $d=0.23$, 95% CI [−0.28, 0.74]).

Distribution of showing types

Overall, showings involving gazing, moving or spending time near a box were used more readily than showings involving vocalizing, jumping/standing upright or opening boxes (see Table 2). But interestingly, those behaviors that were used less often by dogs corresponded more with the target box and the owner's choice than behaviors dogs exhibited more frequently (see Table 2).

Dogs used the following showing strategies significantly more often in the far condition: gaze alternation (i.e., gazing at box plus gazing at owner; far: $M=9.84$, SD = 7.34, close: $M=8.75$, SD = 6.96, $t[239]=1.99$, $p=0.048$, Cohen's $d=0.15$, 95% CI [−0.03, 0.33]), moving towards box plus gazing at owner (far: $M=3.68$, SD = 3.25, close: $M=3.16$, SD = 3.25, $t[239]=-2.33$, $p=0.021$, Cohen's $d=0.16$, 95% CI [−0.02, 0.34]) and moving towards box plus moving towards owner (far: $M=4.69$, SD = 4.57, close: $M=3.51$, SD = 4.01, $t[239]=-4.64$, $p<0.001$, Cohen's $d=0.27$, 95% CI [0.09, 0.45]). Strategies that were exhibited significantly more often in the close condition were: spending time near box plus gazing at owner (close: $M=12.97$, SD = 8.62, far: $M=11.79$, SD = 7.43, $t[239]=2.58$, $p=0.010$, Cohen's $d=0.15$, 95% CI [−0.03, 0.33]) and spending time near the box plus vocalizing (close: $M=1.04$,

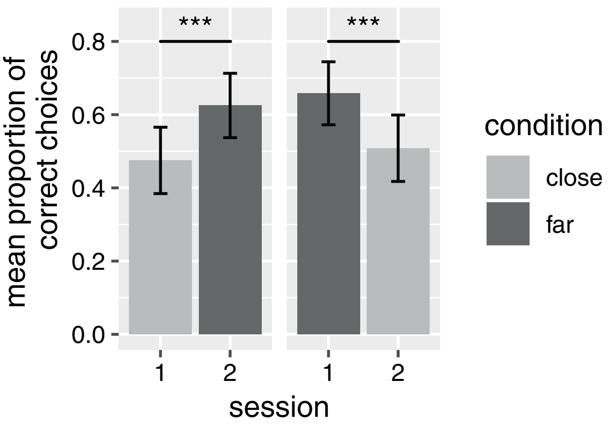

Fig. 2 Mean proportion of correct choices (with standard errors) by condition and session. Note that the differences across sessions within a condition (e.g., close in session 1 vs. close in session 2) did not reach significance, neither for close, nor for far. Significance code: ***$p < 0.001$

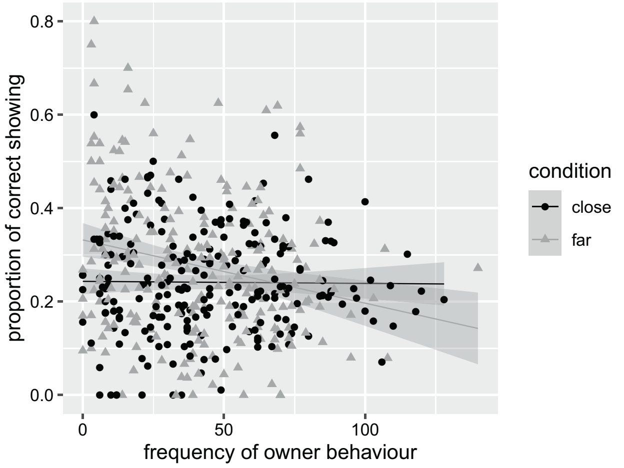

Fig. 3 Proportion of correct showing (with standard errors) by frequency of owner behavior and condition

SD = 3.18, far: $M = 0.62$, SD = 1.73, $t[239] = 2.30$, $p = 0.022$, Cohen's $d = 0.16$, 95% CI [−0.01, 0.34]). No significant differences were found for the other showing types (see Online Resource 1), indicating similar distributions of these strategies in the two conditions.

Effect of correct showing, condition and time on success

The final model describing the effect of the proportion of correct showing on success (prediction 1b) displayed a large and significant effect of correct showing ($\beta = 6.81$, SE = 1.03, $z = 6.62$, $p < 0.001$). Thus, a higher proportion of correct showing significantly increased the probability of choosing the correct box. Additionally, time showed a significant effect of trial in session 1 ($\beta = -0.40$, SE = 0.15, $z = -2.64$, $p = 0.008$) indicating a decline in performance over trials in session 1.

Results of the final model investigating the effect of condition (prediction 3), time and their interaction on success (prediction 4b) show a significant main effect of condition ($\beta = 0.78$, SE = 0.21, $z = 3.71$, $p < 0.001$), i.e., pairs performed better in the far condition than in the close condition (see Fig. 2). Moreover, time showed a significant effect of trial in session 1 again ($\beta = -0.47$, SE = 0.14, $z = -3.21$, $p = 0.001$), indicating that there was a significant decline in the performance over trials in session 1. Conversely, since adding the interaction of condition and time did not improve the model, this suggests that the performance in a respective condition did not depend on whether it was completed first or second (see Fig. 2).

Effect of condition and time on showing effort

Results of the final model for the effect of condition (prediction 5), time and their interaction (prediction 4a) on showing effort displayed a significant effect of phase in session 1 ($\beta = -0.05$, SE = 0.01, $t[420.37] = -6.43$, $p < 0.001$) and 2 ($\beta = -0.05$, SE = 0.01, $t[420.75] = -6.65$, $p < 0.001$), suggesting that, in both sessions, showing effort was significantly higher in phase 1 than in phase 2. Thus, overall, time displayed a significant effect on showing effort. In contrast, since model comparisons revealed that the addition of condition as main effect or interaction did not improve the model, the implication is that there is no effect of condition or its interaction with time on showing effort.

Correlation between showing accuracy and seconds

Showing accuracy (i.e., whether the respective showing behavior referred to the correct box or not) correlated significantly with seconds passed within a respective trial ($r = 0.016$, $t[19410] = 2.24$, $p = 0.025$, 95% CI [0.002, 0.030]). This indicates that showing accuracy very slightly increased with passing time.

Effect of owner behavior on correct showing

Owner behavior exhibited no significant main effect on the proportion of correct showing ($\beta \approx 0.00$ SE ≈ 0.00, $t[388.00] = -0.39$, $p = 0.694$), indicating that the owner's behavior did not overall benefit or worsen the dog's proportion of correct showing. However, owner behavior significantly interacted with condition ($\beta \approx 0.00$, SE ≈ 0.00, $t[436.70] = -2.75$, $p = 0.006$) in that the owner's influence impeded the dog's correct showing in far but hardly affected

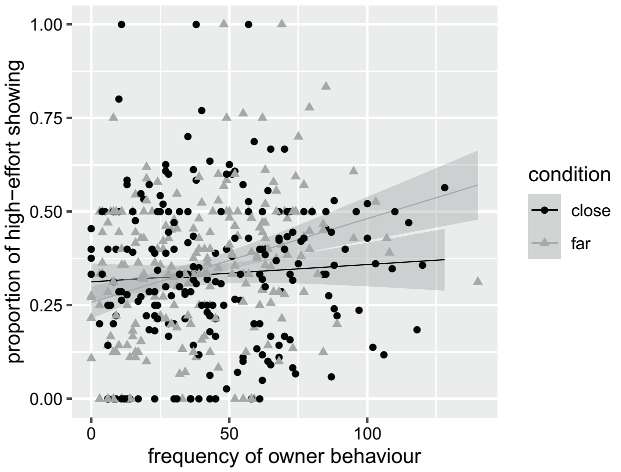

Fig. 4 Proportion of high-effort showing (with standard errors) by frequency of owner behavior and condition

it in close (see Fig. 3). The main effect of condition reached significance as well ($\beta = 0.08$, SE = 0.02, $t[432.10] = 3.80$, $p < 0.001$) indicating that the proportion of correct showing was overall higher in far than in the close condition. But due to the significant interaction the main effect should not be interpreted in isolation (Zar 1999).

Effect of owner behavior on showing effort

Owner behavior showed no significant main effect on showing effort ($\beta \approx 0.00$, SE ≈ 0.00, $t[384.60] = 0.19$, $p = 0.849$), indicating that the owner's behavior did not overall increase or decrease the dog's showing effort. However, owner behavior significantly interacted with condition ($\beta \approx 0.00$, SE ≈ 0.00, $t[425.90] = 2.52$, $p = 0.012$; see Fig. 4), indicating that the owner's influence greatly increased showing effort in the far condition but hardly increased it in close. The effects of time were similar to the ones detected in the analyses concerning predictions 3a and 4.

Discussion

The first aim of the present study was to determine the relationship of present and past shared information with strategies as well as success of dog–owner communication. Second, this study aimed at exploring the influence owners have on success and form of their dog's showing behavior. Results demonstrated that showing behavior in dogs is a means to successfully communicate the location of a hidden object to their owner. Analyses indicated no effect of communication history, neither on showing effort nor on success. The spatial set-up affected success but not showing effort. Owner behavior was found to have an overall negative effect on correct showing and generally increased showing effort.

Communication about the hidden object's location

First, since we found that success rates of pairs were significantly above chance level, we could replicate the findings of previous showing studies (Gaunet 2008, 2010; Gaunet and Deputte 2011; Hare et al. 1998; Heberlein et al. 2016, 2017; Kaminski et al. 2011; Miklósi et al. 2000; Piotti and Kaminski 2016; Savalli et al. 2014; Virányi et al. 2006): dogs engage in showing behavior as defined by Miklósi et al. (2000) to successfully indicate the location of a desired hidden object to their owners. Moreover, the key to success in the current task proved to be dogs showing their owners the correct box. Results demonstrated that the more dogs addressed the target box with their showing behavior relative to all other boxes, the higher the respective pair's chances of choosing correctly became. This effect was significant in absence of a mere improvement of performance over time. To the contrary, performance even slightly decreased over the first four trials of the experiment. Thus, the first hypothesis is supported by the current data: Dogs are able to achieve successful communication with their owners about the hiding location of their favorite toy by means of showing.

Given that the analyses demonstrated that showing behavior was the driving force in this experiment, an interesting question is whether dogs only show the correct location to their passive owners or if owners can actively influence success in this task as well. Thus, we explored whether owners had an influence on the proportion of correct showing and thereby, indirectly, on whether they found the toy or not. Results suggested that owners did indeed influence how correctly their dogs showed but not necessarily in the most obvious way. We found that owners overall negatively impacted their dog's proportion of correct showing. In other words: the more owners pushed their dogs to show them the hidden toy, the less they showed the correct box and the more they showed just any box. This effect seemed to be stronger in far than in close. Although at this point it remains possible that the described effect rather operates in the opposite direction, i.e., the proportion of correct showing affects the owner's behavior, this explanation seems unlikely since owners did not know the correct location in this study.

The overall detrimental effect of owners pushing their dogs fits with findings from several other studies. Range et al. (2009) found that ostensive cues (Csibra and Gergely 2009; Sperber and Wilson 1986), i.e., verbal or nonverbal signals indicating the signaller's communicative intention, have an activating potential regarding dogs' behavior. Some of the owners' behaviors in the current study are ostensive cues: looking at the dog, talking in a high-pitched voice and calling the dog by its name (Topál et al. 2014). As Kaminski et al. (2011) outlined, ostensive cues like that can activate behavior, including indicative behavior (i.e., showing), diffusely. Consequently, as in the present study, Kaminski et al. observed that, if dogs do not know what exactly they are supposed to show to their owners, they show just any location. One might argue that encouragement, both verbal and non-verbal, was beneficial for most dogs in the beginning. But with time passing, ongoing asking by the owner, especially without direct reinforcement such as praise, seemed to tell the dogs that they had not displayed the right behavior yet. Thus, they did not know anymore what to show, and, therefore, tried out other options, i.e., showing other boxes. However, results of our explorative analyses did not reflect such a pattern. Since the owner's influence did not interact with session, trial or phase, the effect of owner behaviors on dogs' showing did not vary as a function of time. Moreover, our analyses showed that showing accuracy did not negatively correlate with time. Accordingly, a dog's showing did not get worse over the course of a trial. Thus, the effect of owner behavior on the proportion of correct showing rather seems to be a matter of active versus passive owners as a general characteristic. In line with this, in Kaminski et al.'s study (2011), the diffuse activation effect only occurred if the hidden object was only desirable to the owner and therefore, the dog did not know what to do. It did not occur when the dog desired the hidden object. However, it is still possible that this diffuse activation effect played a role in the present study albeit not developing over time. In one example this pattern was extremely obvious because the dog responded to the owner's cues by fetching the lids of random boxes suggesting that the dog did not know what the actual task was.

Various authors mention another factor that could explain the negative effect of the owner's pushing on correct showing which is more or less independent of the dog's understanding of the task: ostensive signals generally seem to induce a "ready-to-obey" attitude in dogs leading to all following signals, like pointing, being understood as a command or instruction (Kaminski et al. 2011, 2012; Kirchhofer et al. 2012; Kis et al. 2012; Topál et al. 2009; Topál et al. 2014; but see Scheider et al. 2013). Moreover, a large body of research has demonstrated that dogs have a strong tendency to abandon their own initial (usually correct) choice in favor of another option if it is ostensively cued by a human (Erdőhegyi et al. 2007; Marshall-Pescini et al. 2011, 2012; Plourde and Fiset 2013; Prato-Previde et al. 2008; Szetei et al. 2003; Topál et al. 2009). This implies that dogs either more or less blindly follow humans' instructions or value the information provided by humans over their own knowledge. In our study, owners often pointed at boxes, asking their dogs "Is it here?". This way, owners might have accidentally deceived their dogs into directing showing behavior at the wrong box.

In our study, however, the owner's behavior did not simply decrease correct showing. The effect was mainly prevalent in the far condition; while in the close condition, the effect was weak or absent. A possible explanation could be the aforementioned activation effect of human ostensive signals (Erdőhegyi et al. 2007; Kaminski et al. 2011; Marshall-Pescini et al. 2011, 2012; Plourde and Fiset 2013; Prato-Previde et al. 2008; Range et al. 2009; Szetei et al. 2003; Topál et al. 2009, 2014). Dogs might have been stimulated too much by their owners for a setting as easy as the far condition. Possibly, in the close condition, a considerable amount of encouragement was necessary to motivate dogs to try to solve such a hard task, or at least not harmful. Contrarily, in the far condition, too much encouragement might have led dogs to be overly motivated and therefore exhibit diffuse (showing) behavior and/or abandon their own initial choice for the owner's (accidentally) cued choice. Nevertheless, this interpretation of the interaction of owner behavior with condition remains highly speculative at this point and needs further investigation.

Sensitivity to spatial set-up and communication history

The second hypothesis of this study examined sensitivity of dog–human communication to the spatial set-up of the interaction setting. The prediction that performance should be better in the far condition than in the close condition could be confirmed, supporting the hypothesized effect of the spatial set-up on success of dog–owner communication, i.e., distance between boxes did affect performance of pairs. Moreover, the form of dog–owner communication varied between conditions as well. Showing strategies that were used more often in far all contained gazing and movements as directional and attention-getting components. Conversely, showing in the close condition always contained vocalizations. However, this could also be attributed to higher excitement in the harder condition. But remarkably, in close, dogs predominantly gave their owners directions by positioning their body near the box they wanted to show. This strategy is much more precise and, therefore, adapted to the context of the close condition. In contrast, the strategies employed in far, i.e., movements and gazes, could occur from afar as well as close to the boxes and, hence, are less precise. Interestingly, showings involving jumping/standing upright or opening boxes did not vary according to the spatial set-up although owners clearly preferred them for making their choices. This marks a mismatch in communication between dogs and owners.

In summary, this study provides further evidence that, similar to the case of human interactions (Brown-Schmidt et al. 2008; Krauss and Weinheimer 1967; Müller et al. 2019; Winters et al. 2015, 2018), shared knowledge about the communicational context influences success of interspecies communication between dogs and humans as well, at least when this shared knowledge concerns spatial cues. This adds to the study by Gaunet and Deputte (2011) who delivered the first evidence that showing behavior in dogs (although their study only focused on one component of showing) might be sensitive to the spatial context of the experimental set-up.

Hypothesis 3 stated that past interactions should constrain future communicative behavior. First, results did not confirm the prediction that dogs use more high-effort strategies when they start with the close condition. Second, we predicted that performance should reflect an effect of communication history as well. However, pairs did not perform better if they started with the close condition. Thus, the results did not confirm this prediction either. Therefore, hypothesis 3 was not supported by the current data; hence, no evidence could be found that shared information about past interaction affects dog–human communication.

Based on the current findings, communication history does not seem to play the same role in dog–human communication as it does in human communication (Brennan and Clark 1996; Brown-Schmidt 2009; Yoon et al. 2016). A possible explanation could be that this hypothesis was based on the theory that, through the domestication process, dogs might have evolved a communication system analogous to that of humans (Fitch et al. 2010; Miklósi et al. 2004; Schleidt and Shalter 2003; Topál et al. 1998). However, the study by Heberlein et al. (2016) demonstrated that hand-raised and extensively socialized wolves perform just as well as dogs in a showing task. This suggests that socialization might play a bigger role in showing than domestication, i.e., the shared evolution of humans and dogs. Moreover, showing object location is commonplace in non-domesticated captive apes (e.g., Call and Tomasello 1994; Leavens and Hopkins 1998; Leavens et al. 1996; Woodruff and Premack 1979) which is also an indicator that showing behavior might be a product of ontogeny rather than phylogeny.

It is also possible that dog–owner pairs were indeed influenced by past interactions but not within the timeframe of our experiment or observable on a group level. Miklósi et al. (2000) argued in their study that dog–owner pairs might develop unique and individualized communication systems and signals, with specific reference to ontogenetic ritualization (e.g., Tomasello and Call 1997; Tomasello et al. 1994). The behavioral observations during the experiment clearly indicated individual differences in behavior, both on the part of the dog and the owner. For instance, some pairs heavily relied on vocal communication (both dog and human) whereas others almost completely relied on non-verbal communication. In addition, some owners reported having employed scenarios similar to the experimental set-up into their playing routines before and others reported encountering this kind of situation for the first time. Therefore, some pairs might already have developed individual strategies to solve such situations and others have not. Consequently, the possibility that dog–human dyads are influenced by their communication history should not be dismissed yet and should be investigated again in future studies, possibly focussing more on individual differences.

The principle of least effort and the owner's influence on it

The fourth hypothesis stated that dogs always use a strategy that minimizes effort for a given context, i.e., they follow the principle of least effort (Zipf 1949). However, the predicted pattern that dogs should use relatively more high-effort strategies in close and relatively more low-effort strategies in far, irrespective of order of conditions, was not confirmed by the current results. Showing effort rather varied by time than by condition. Thus, we could not find evidence that dogs follow the principle of least effort like humans do (Zipf 1949).

It is possible, however, that an effect of the spatial set-up on dogs' showing effort (i.e., the principle of least effort) was concealed by the interaction between dogs and owners. From the behavioral observations, it appeared that owners usually incited their dogs to show more precisely and therefore more effortfully, i.e., they did rarely accept low-effort strategies like gaze alternation, even if they would have sufficed. As the results of this study demonstrate, owners also based their decisions more often on high-effort showings. Therefore, owners might have effectively enforced a ceiling effect for showing effort which might have concealed differences in showing effort between and within conditions.

We found that owner behavior generally increased showing effort. The increase was stronger in far, where showing effort was originally predicted to be low, than in close, where showing effort was predicted to be high. Presumably, this way, the owner's influence effectively eliminated the predicted difference in showing effort and, therefore, the hypothesized effect of the principle of least effort.

At this point, it is not completely clear whether owners did in fact influence showing effort or whether showing effort rather influenced the owners' behavior. However, the latter case seems substantially hard to interpret and, hence, rather unlikely, as the direction of the effect would suggest that owners pushed their dogs more, the more effortfully they showed. Moreover, the explanation that the owner's behavior generally increased showing effort fits with the activating effects of ostensive human communication described earlier. Nonetheless, this effect remains somewhat uncertain and needs further investigation, possibly also employing other operationalizations of showing effort.

Limitations and implications for future research

Inferences about the effects of the owner's influence on the proportion of correct showing and effort can only be made with caution since these variables were not manipulated experimentally (i.e., influence versus no influence). Future studies should aim at implementing this to get a clearer picture of the dog–human interplay.

One very interesting point this study could illuminate over and above other studies is the importance of different types of showing. Past studies have mainly focused on gazing and gaze alternation. While the current study also found this to be an important type of showing behavior, it appeared to be less important for success in the task since it converged little with the target box or the owner's choice. In other words: it constituted only a moderately precise showing strategy from both the dog's and the owner's point of view. Other showing types seemed to be much more informative, especially showing involving jumping at the target box and vocalizing. Thus, in future studies, these behaviors should be investigated in addition to gaze alternation.

Conclusion

In summary, this study confirmed that dogs use showing behavior to successfully communicate the location of a hidden object to their owner and, moreover, demonstrated that success in such a hidden-object paradigm can be truly attributed to dogs showing the target location. This study also indicated for the first time that owners can influence their dog's showing accuracy (and thereby success) but that such influence tends to be negative rather than positive. This finding fits with previous literature that found human ostensive signals to be diffusely activating and potentially 'accidentally deceptive' for dogs. Moreover, owners can influence how effortfully their dogs show, generally increasing effort, especially when the task was easier. Regarding the effect of communication history, this study could neither find an effect on showing effort (strategies) nor on success in the task. In contrast, an effect of the spatial set-up was found for success, with pairs performing better when hiding places where further apart, however, not for showing effort (strategies), i.e., there was no evidence from this study that dogs followed the principle of least effort. The latter could, however, be concealed by human influence since owners enforced high-effort showing especially in the condition where effort was predicted to be low. Future research with bigger samples should focus on further illuminating the complex effects of the owner's influence on canine showing behavior and its efficiency.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval This observational study adhered to the Guidelines for the use of Animals in Research of Germany. Approval was obtained from the ethics committee of the Max Planck Society (processing number 2019_17).

Consent for participation/publication All dog–owner pairs took part voluntarily and owners signed an informed consent form prior to the tests.

Availability of data and material Additional information, raw data and a video of the procedure can be found in Online Resources 1–3, in the online version of this article. The python script used for management of behavioral data is available from the corresponding author on reasonable request.

Code availability The R code written to analyze the data in this study is available in the online version of this article (Online Resource 4).

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ORIGINAL PAPER

Domestic dogs conceal auditory but not visual information from others

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Abstract A number of studies have shown that dogs are sensitive to a human's perspective, but it remains unclear whether they use an egocentric strategy to assess what humans perceive. We investigated whether dogs know what a human can see and hear, even when the dogs themselves are unable to see the human. Dogs faced a task in which forbidden food was placed in a tunnel that they could retrieve by using their paw. Whereas the dogs could not see the experimenter during their food retrieval attempts, the experimenter could potentially see the dog's paw. In the first experiment, dogs could choose between an opaque and a transparent side of the tunnel, and in the second experiment, they could choose between a silent and a noisy approach to the tunnel. The results showed that dogs preferred a silent approach to forbidden food but they did not hide their approach when they could not see a human present. We conclude that dogs probably rely on what they themselves can perceive when they assess what the human can see and hear.

Keywords Social cognition · Domestic dogs · Perspective taking

Introduction

Taking the visual perspective of others is a highly adaptive skill for social living animals (Kummer et al. 1996). To know what others can see is not only helpful when individuals hide from each other (Kummer 1982) while competing over food (Bräuer et al. 2007; Emery and Clayton 2001; Hare et al. 2000; Kaminski et al. 2006) but also in a communicative context, where senders should understand that recipients need to attend to their signal to receive it (Kaminski et al. 2004; Liebal et al. 2004). Numerous species seem to have some understanding about what others are seeing (e.g., chimpanzees: Bräuer et al. 2007; Hare et al. 2000; Melis et al. 2006; rhesus macaques: Flombaum and Santos 2005; Western scrub jays: Dally et al. 2006) or at least are sensitive to the attentional state of others (wolves: Udell et al. 2011, great apes: Kaminski et al. 2004, capuchin monkeys: Hattori et al. 2007, dolphins: Xitco et al. 2004, goats: Kaminski et al. 2005, see also Rosati and Hare 2009 for a review about primates).

Domestic dogs have also been tested in their perspective-taking abilities using three basic experimental approaches. First, dogs have been tested in a situation in which they can beg for food. In the study of Gácsi et al. (2004), dogs could choose between two eating humans based on either the visibility of the human's eyes or direction of the face. Dogs begged more from the attentive than from the inattentive human, indicating that they were sensitive to human attention. In the second experimental approach, dogs were given a command, either to do a certain action (i.e., lie down) or to refrain from doing something (i.e., do not eat the food). The human either looked at the dog or was distracted, having eyes closed or back turned. Dogs obeyed the command better when the human was attentive, and therefore, it was concluded that they are sensitive to human attention (Call et al. 2003; Gácsi et al. 2004; Schwab and Huber 2006; Virányi et al. 2004). Note that in all these situations, dogs could rely on the orientation of the body, the orientation of the head, the visibility of the eyes, and could use them as a cue to obey

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or to beg. Relying on certain stimuli could also be the explanation for the findings of the study of Bräuer et al. (2004). In that study, forbidden food was placed behind different kinds of barriers. The authors found that dogs were sensitive to whether or not the presented barrier was effective or ineffective at obstructing a human's vision. Dogs ate more forbidden food when the barrier was large compared to small or had a window, so that the human could see either the approach to or the taking of the forbidden food. However, it is possible that the dogs' behavior was based on their sensitivity to stimuli, such as seeing certain human body parts instead of their understanding of the human's visual access to the food.

Kaminski et al. (2009) took a different approach that went beyond explanations based on using the presence of certain stimuli to assess whether one is being watched. They tested dogs in a cooperative situation in which the subjects were asked to fetch a toy. Two toys were placed on the dog's side of two small barriers (one opaque and one transparent). In the experimental condition, a human sat on the opposite side of the barriers, such that only the toy behind the transparent barrier was visible to her. She then told the dog to fetch the toy. Dogs preferentially fetched the toy that the experimenter could see, namely from behind the transparent barrier. Dogs did not have this preference in the two control conditions, in which the human could see either both or neither of the toys. The authors concluded that even in the absence of behavioral cues, dogs were sensitive to humans‘ visual access, even if it differed from their own.

However, one alternative interpretation is that dogs preferred the transparent barrier simply because they wanted to sustain visual contact with the human while fetching the toy (Kaminski et al. 2009). Also, in the other two experimental approaches, dogs could have relied on whether the human or his eyes were visible. In most cases, the egocentric strategy of assuming that "When I see you (and your eyes) then you see me" is very successful (Kummer 1982). However, if animals are really able to take the visual perspective of others, then they should be able to understand the perspective of the other *independent* of their own perspective.

Melis et al. (2006) investigated this question with chimpanzees. They used a competitive situation in which chimpanzees competed with a human for food. The human sat inside a booth, with one piece of food to her left and one to her right. She could retract either piece of food from her chimpanzee competitor's reach as needed. The chimpanzees could approach either side of the booth unseen and then could reach for the food through one of two tunnels. One tunnel was opaque and one was transparent. The chimpanzees preferred to reach through the opaque tunnel, indicating that they could take the visual perspective of the competing human, and that they actively concealed information from her. The important point here is that the chimpanzees could *not* solve the problem on the basis of what they themselves saw—because they could not see the human while they reached for the food. In other words, they could not rely on the egocentric strategy "When I see you, then you see me." In the current study, we wanted to investigate whether dogs are also able to judge what a human can see when they are not able to see the human.

Melis et al. (2006) suggested that if subjects are also able to conceal information in a modality other than the visual, this would show a deeper understanding of the other's perceptual states. Indeed, they found evidence that chimpanzees knew what humans can hear by using the same basic procedure described above but with auditory information (but see Bräuer et al. 2008). Again, chimpanzees competed for food with a human who sat inside the booth. But now, both tunnels were clear and the human was looking away, but one of the tunnels made a loud noise when it was opened. Chimpanzees preferentially reached through the silent tunnel, successfully concealing their taking of the food from the human competitor. The authors concluded that chimpanzees can actively manipulate the auditory perception of others by concealing information from them. Santos et al. (2006) found similar results with rhesus macaques using silent and noisy containers with food inside them. Monkeys selectively choose the silent container over the noisy container, suggesting that they knew that the noisy container might alert the human competitor.

There is also evidence that dogs are sensitive to what humans can hear. Kundey et al. (2010) also tested dogs using containers rather than tunnels. Dogs could choose to eat food from a silent or a noisy container. Subjects preferred to eat from the silent container when the human was *not* looking at them. In contrast, they had no preference when the human was looking at them. The authors concluded that the dogs tried to retrieve food silently only if silence was relevant to obtaining food unobserved by a human gatekeeper. In contrast to other studies, the food during the test was not forbidden but the experimenter had forbidden the dogs to take food prior to the test. More importantly, dogs could see the human while taking the forbidden food. Thus, the use of an egocentric strategy, such as trying to be silent when the human's eyes are not directed at them, is still viable.

In sum, a number of studies have shown that dogs are sensitive to human perspective but it remains unclear whether they use an egocentric strategy to assess what humans can hear and/or see. In the current study, we investigated whether dogs' perspective taking goes beyond this egocentric strategy. We used the basic setup as Melis et al. (2006), except that the dogs did not compete with the human, but food was forbidden by the human. In the first study, we investigated whether dogs know what a human can see even when they are unable to see the human. While the dog is retrieving forbidden food with her paw, she *cannot* see the experimenter but the experimenter can potentially see the dog's paw. Would the dogs conceal their approach to the forbidden food by retrieving the food from an opaque as opposed to a transparent tunnel? In the second study, we investigated whether dogs would conceal their approach by avoiding the production of auditory cues. Would they prefer a silent as opposed to a noisy approach to the forbidden food?

Experiment 1: Concealing visual information

Methods

Subjects

Seventy-eight dogs (41 females and 37 males) of various breeds and ages (see Table 1) participated in this study. Additionally, 42 dogs had to be excluded because they showed signs of discomfort without the owner or did not pass the pretest. All subjects had been living as pets with their owner and had therefore received the normal obedience training typical of domestic dogs. The dog owners were not present during the test and were not informed about the design and the purpose of the study before it started. Subjects were tested individually with only the experimenter present in the room.

Materials

Testing took place in the "dog-bungalow" of the MPI EVA in Leipzig in a quiet room (8.70 m × 4.00 m × 2.85 m) with two doors. Figure 1 shows the experimental setup. The room was separated into two parts by 1.80-m-high movable walls with the test apparatus in the middle. During training, the outer parts of these walls were removed so that the dog could walk around and get familiar with the apparatus. During test trials, the dog was always in part A and the experimenter in part B (or outside) of the room (see Fig. 1).

The apparatus had an hour glass shape and was 1.66 m long. Its width was 0.48 m in the middle and 0.83 m at the ends. The apparatus was constructed from wood and open on the experimenter's side so she could get inside to place the food in the middle of the tunnel. The tunnel was made of Plexiglas and was located in the middle of the apparatus. The opening of the tunnel in the middle of each side of the apparatus was 0.06 m wide and 0.27 m high. The dog could reach into the tunnel from the right or left side. A black cover was put on one side of the tunnel making it opaque—so that when a dog reached through, the experimenter could not see the dog's paw. The other side remained transparent. From the dog's side, there was a 0.10-m wide Plexiglass gap in the apparatus. Through this gap, the dog could see the tunnel and the experimenter. In that gap, there was one hole (diameter 0.04 m) 0.56 m above the ground, which was used to show the food to the dog at the beginning of each trial.

There was a separate training tunnel with the same size, but half as long as the tunnel used in the test. It was placed beside a wall in part B of the room and was only used for training.

Procedure

Training and pretest The dogs had to learn to get the food from the tunnel using their paws. They were therefore trained to get food from a tunnel outside the apparatus. This training tunnel, half as long as the one used in the test, was attached to the wall in part B of the testing room. The experimenter put the food in the training tunnel and encouraged the dog to get it out with its paw (in the test

Table 1 Breed, gender, and age of the participating dog subjects

Experiment	Breeds	Gender	Age (years)
Experiment 1: Concealing visual information	2 Airedale Terrier, 4 American Staffordshire Terrier, 3 Border Collies, 1 Cocker Spaniel, 1 Great Dane, 6 German Shepherds, 1 English Bulldog, 1 Flat Coated Retriever, 10 Golden Retriever, 1 Husky, 15 Labradors, 1 Magyar Vizsla, 1 Malinois, 16 Mixed breeds, 1 Portuguese Water Dog, 1 Rhodesian Ridgeback, 1 Schapendoes, 1 ShibaInu, 2 Tibet Terrier, 2 Weimaraner, 1 Welsh Terrier	33 Males (16 neutered) 39 Females (26 neutered)	Range: 1–10 Mean: 4.47
Experiment 2: Concealing auditory information	1 Airedale Terrier, 1 American Staffordshire Terrier, 1 Australian Cattle dog, 2 Australian Shepherds, 1 Beagle, 1 Berger des Pyrenees, 3 Border Collies, 1 Cocker Spaniel, 1 DogoCanario, 2 German Pinscher, 4 German Shepherds, 5 Golden Retriever, 1 Husky, 5 Labradors, 3 Magyar Vizsla, 5 Malinois, 20 Mixed breeds, 1 Parson Jack Russel Terrier, 1 Rottweiler, 1 Weimaraner	30 Males (10 neutered) 30 Females (18 neutered)	Range: 1–11 Mean: 4.05

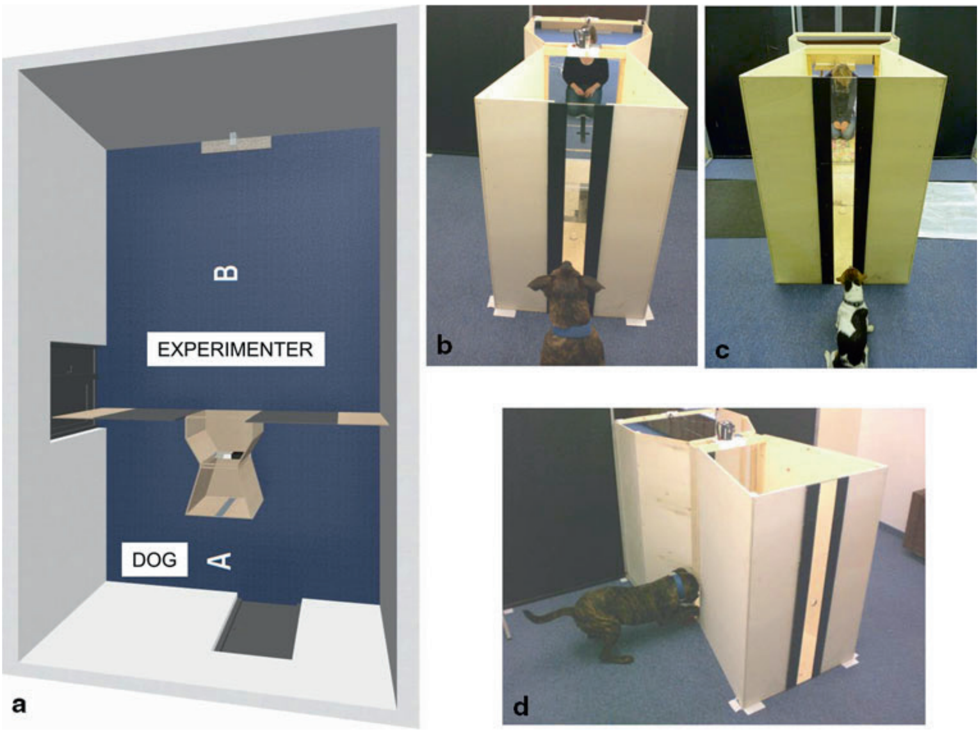

Fig. 1 Experimental setup: **a** plan view of the room and the apparatus, **b** apparatus from the view of the dog in Experiment 1, **c** apparatus from the view of the dog in Experiment 2, **d** approach to the tunnel

tunnel attached to the apparatus, the food was located in the middle and dogs could reach for it from both sides). Every trial the experimenter placed the food deeper in the tunnel so that the dog had to insert her paw further in order to get the food. This procedure was repeated until the experimenter could put the food at the very end of the tunnel close to the wall and the dog was able to get it. In every second training trial, the experimenter put the black cover on the tunnel so that the dog got used to it and did not develop a preference for the opaque or the transparent tunnel. Before the test trials began, each dog had to pass a pretest consisting of getting the food out of the training tunnel within 1 min, four times in a row. In addition to the training, dogs were allowed to explore the test apparatus, so that they could see it from every side. But prior to the test, they never had to retrieve food from the tunnel of the apparatus.

Test The experimenter entered the apparatus in part B of the testing room (see Fig. 1). Then, the dog was sent into part A of the room by a second person who then left the room and closed the door. At the beginning of each trial, the dog was called to the Plexiglas gap where the experimenter showed her/him a piece of food. The experimenter put the food into the tunnel while talking to the dog according to the condition (see below). Then, the experimenter sat on the predetermined place opposite the dog or left the room (Non-social Control). The dog now had the chance to get the food from the tunnel, either from the opaque or from the transparent side. The experimenter always looked straight ahead through the Plexiglas gap and did not react to the dog's behavior. After 1 min, the trial was over. The experimenter took the food from the tunnel if it was still there, and the dog was called out of the room by the second experimenter. The dogs were randomly assigned to one of the three conditions. Each dog was given one trial only.

Experimental condition (visual): While putting the food into the tunnel, the experimenter forbade the dog from taking the food ("Nein" or "Aus") and moved one meter backwards to the predetermined position.

Non-social control (visual): While putting the food into the tunnel, the experimenter forbade the dog from taking the food ("Nein" or "Aus") and then immediately left the room.

Motivation control (visual): While putting the food into the tunnel, the experimenter motivated the dog to take the food ("Hol Dir das Leckerli!") and moved one meter backwards to the predetermined position.

One side of the tunnel was always opaque (blocked by the black cover) and the other side transparent. The sides were alternated between dogs, so that in each condition for half of the dogs, the left side was opaque, and for the other half, the right side was opaque.

Scoring

All trials were scored from the videotapes. We coded two dependent measures: where and when the tunnel was approached. An approach was defined as the dog putting one part of the body (paw or nose, usually both) into the tunnel so that it was potentially visible to the experimenter. We coded:

(a) side of the first approach—whether the visible or the opaque side was approached (This also included a few unsuccessful reaches for the food.)
(b) latency to approach: latency from the moment the food was placed inside the tunnel until the dog first approached one side of it.

A second coder, blind to the experimental hypothesis, coded 20 % of the videotapes. All behaviors were scored perfectly reliably (side of the first approach: Cohen's Kappa = 1.0, $N = 20$, latency to approach: Spearman = 0.999, $N = 16$).

We concentrated in our analysis on the subjects that tried to take food from the apparatus during the trial. Note that from the dog's perspective, it is not "wrong" not to approach since the food is forbidden. 11 dogs were excluded from the analysis because they did not approach the tunnel at all: 4 in the Experimental Condition, 5 in the Non-social Control, 2 in the Motivation Control. We used Fisher's exact and Binominal test to compare between conditions and against chance, respectively. We used the Kruskal–Wallis and Mann–Whitney *U* tests to compare the latencies across conditions.

Results

Figure 2 presents the number of dogs who first approached the hidden or the visible side of the tunnel in the three conditions. There were no significant differences between conditions in the side approached (Fisher's exact test $P = 0.747$). Moreover, dogs showed no preference for the hidden tunnel in any of the conditions (Binominal test, $P > 0.424$ for all three conditions).

Overall, there were no significant differences between conditions in the latency to approach the tunnel (Kruskal–Wallis $\chi^2(2) = 4.63;\ P = 0.099$). Nonetheless, we compared the conditions and found that subjects approached the food faster when they were encouraged to take it than when the food was forbidden and the human stayed in the room (Mann–Whitney $U = 168.0$, $n1 = 21$, $n2 = 25$, $P = 0.037$).

Discussion

The dogs showed no preference for approaching the tunnel from the hidden side when the food was forbidden.

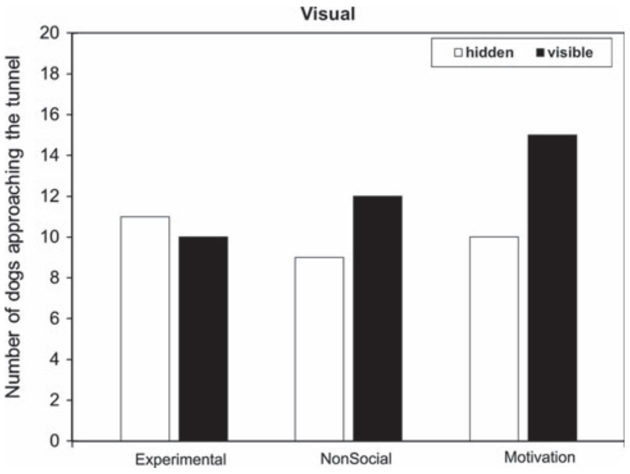

Fig. 2 The number of dogs approaching the hidden and the visible side of the tunnel in the three conditions of Experiment 1

This means that, unlike the chimpanzees tested by Melis et al. (2006), dogs did not conceal their approach to the forbidden food. These results provide no evidence that dogs can assess what humans can see independent of their own perspective, a result that is apparently at odds with some of the data reported in previous studies (e.g., Kaminski et al. 2009). In the following, we therefore analyze the various aspects of the current task in more detail. At the beginning of the trial, dogs have to *assess* what the human can and cannot see—in particular that the human cannot see into the opaque part of the tunnel. They also have to *understand* that this is the tunnel they are going to put their paw inside, although from the side of the apparatus, they can only see the entrance hole of the tunnel. Finally, they have to *remember* not only that the food is forbidden but also that the human is still there (in the experimental condition).

Kaminski et al. (2009) found that dogs were sensitive to human perspective even when it differed from their own. In that study, the dogs distinguished the toy the human could see from the one the human could not see, although the dogs themselves could see both toys. Thus, dogs might be able to assess from their starting point what the human can see. A number of studies have also shown that dogs are able to remember and obey a command that was given one minute ago (Call et al. 2003; Gácsi et al. 2004; Schwab and Huber 2006; Virányi et al. 2004). However, the crucial point in our study might be that the dogs could not see the human while they put their paws inside the tunnel. Dogs not only had to remember that the human was still there, but also to keep in memory that the experimenter was still looking at them and potentially seeing the paw in the transparent tunnel. It might be too challenging for a dog to remember what view the human had when the dog was at the starting point and to keep that in mind while they are taking the food. In fact, Kaminski et al. (2009) found no evidence that dogs knew what others have seen in the recent past. More specifically, dogs failed to differentiate between the two toys on the basis of whether or not the human had seen them. Kaminski et al. (2009) concluded that dogs may be unable to engage in perspective taking based on the memory of past events. It is possible that in the current study, dogs could not take into account what the human could see because there was a delay between visual cues at the starting point (where they could see the human and the tunnel) and the moment in which they put their paw into the tunnel.

However, it is also possible that dogs know what humans can see independently of their own egocentric view, but the setup of the experiment was too complicated for them. Dogs had to learn to use their paws to retrieve the food. From their starting point, they had to approach the food on the side of the apparatus. They had to understand that the holes on the sides of the apparatus lead into the tunnel, and they had to make a choice between the two parts of the tunnel. Thus, it is possible that dogs did not understand how the apparatus worked and therefore showed no preference for the opaque side of the tunnel.

In Experiment 2, we wanted to investigate whether dogs would conceal their approach to hidden food in the auditory modality. We used exactly the same method as in Experiment 1. Thus, we could also investigate whether dogs did not prefer the hidden tunnel in Experiment 1 because they were simply unable to cope with the setup. If dogs were sensitive to what humans can hear in the same setup, this would suggest that dogs' performance in the current experiment is not due to the challenging setup but to the fact that they do not understand what humans can see independent of their own egocentric view.

Experiment 2: Concealing auditory information

In Experiment 2, we investigated auditory perspective taking. Kundey et al. (2010) found that dogs prefer to eat food from a silent container when a human is not looking at them. Here, we used the setup of Experiment 1 so that dogs could not see the human while they reached for the food but added an auditory cue to one side of the tunnel. If dogs can take humans' auditory perspective, they should approach the forbidden food from the silent side of the tunnel. Moreover, if dogs show such a preference for the silent side, this would also indicate that dogs can cope with the complexities of the apparatus.

Methods

Subjects

Sixty-three dogs (32 females and 31 males) of various breeds and ages, who had not taken part in Experiment 1, participated in this experiment (see Table 1). A further 7 dogs had to be excluded because they showed signs of discomfort without the owner or did not pass the pretest. As in Experiment 1, the dogs were family dogs and were tested individually by one experimenter who was not the owner. Most of the dogs were familiar with the testing facilities as they had participated in other experiments about social cognition.

Materials

Materials were similar to the first experiment with two exceptions, see Fig. 1c: First, both sides of the tunnel in the apparatus were transparent. Second, two distinct mats (135 cm long × 81 cm wide) were used. They were placed in front of each side of the apparatus and extended into the tunnel (see shape of the mats in Fig. 1c). The dogs were able to see the mats from their starting position and had to walk over one to approach the food. One mat was white and produced a noise when the dogs walked over it because it was made of crinkly plastic foil (=noisy side). The other mat was black, it was a normal mat and produced no noise when the dogs walked over it (=silent side).

Procedure

Training and pretest were similar to Experiment 1 except that the training tunnel was transparent. Instead, the mats were put in front of, and inside, the tunnel (in the same way that they would later be put into the tunnel of the apparatus during the test.) After every training trial, the experimenter changed the mat so that each subject got experience with both mats. Additionally, there was an obedience task before the beginning of the test in which the experimenter made sure that the dog would not take the forbidden food on the floor for 30 s. This was to make sure that the dogs obeyed the command not to take the food.

The test procedure was similar to Experiment 1 except that when the experimenter stayed in the room, instead at looking through the Plexiglas gap she closed her eyes and oriented her face downwards. The dogs were randomly assigned to one of the three conditions and received a single trial.

Experimental condition (auditory): While putting the food into the tunnel, the experimenter forbade the dog to take the food ("Nein" or "Aus") and moved one meter backwards to the predetermined position, closed her eyes, and oriented her face downwards.

Non-social control (auditory): While putting the food into the tunnel, the experimenter forbade the dog to take the food ("Nein" or "Aus") and then immediately left the room.

Motivation control (auditory): While putting the food into the tunnel, the experimenter motivated the dog to take the food ("Hol"s Dir" or "Hier ist das Futter") and moved one meter backwards to the predetermined position, closed her eyes, and oriented her face downwards.

The side of the tunnel where the noisy mat was located was alternated between dogs, so that in each condition for half of the dogs, the left side was noisy and for the other half, the right side was noisy.

Scoring

Scoring was identical to Experiment 1. We coded the side of the first approach and the latency to approach. A second coder, blind to the experimental hypothesis, coded 20 % of the videotape. All behaviors were scored perfectly reliably (side of the first approach Cohen's Kappa $= 1.0$, $N = 12$, latency to approach: Spearman $= 1.0$, $N = 11$). Again, we restricted the analysis to the subjects that tried to take food from the apparatus during the trial, and therefore we had to exclude 13 dogs (6 in the Experimental Condition, 3 in the Non-social Control, and 4 in the Motivation Control). We used the same statistical analyses as in Experiment 1.

Results

Figure 3 presents the number of dogs who first approached the silent and the noisy part of the tunnel in the three conditions. There was a significant difference between conditions in approached side (Fisher's exact test $P = 0.033$). Moreover, dogs in the Experimental condition preferentially approached the silent tunnel (Binominal test, $P = 0.007$), whereas they showed no such preference in the other two conditions (Binominal test, Nonsocial Control $P = 1.000$, Motivation Control $P = 0.815$).

There were significant differences between conditions in the latency to approach the tunnel (Kruskal–Wallis $\chi^2_2(2) = 15.72$; $P < 0.001$). Subjects approached the food faster when they were encouraged to take it than when the food was forbidden (Motivation Control vs Experimental Condition, Mann–Whitney $U = 39.5$, $n1 = 15$, $n2 = 18$, $P < 0.001$) and the experimenter left the room (Motivation Control vs Nonsocial Condition, Mann–Whitney $U = 55.0$, $n1 = 17$, $n2 = 18$, $P = 0.001$). There was no difference in the latency to approach between the two conditions in which the food was forbidden (Mann–Whitney $U = 109.0$, $n1 = 15$, $n2 = 17$, $P = 0.484$).

Discussion

The dogs preferred to approach the forbidden food from the silent side of the tunnel. One might argue that the dogs just wanted to avoid walking on the crinkly mat and that is why they preferred to approach the side with the silent mat. However, the dogs did not prefer either side in the control conditions in which the food was not forbidden (Motivation Control) or when the human left the room (Non-social Control).

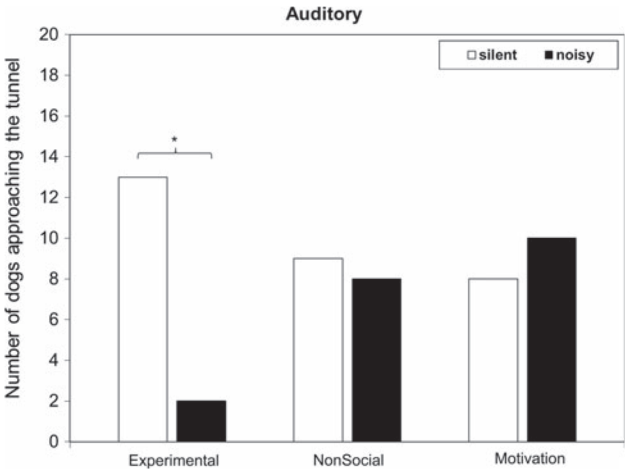

Fig. 3 The number of dogs approaching the silent and the noisy side of the tunnel in the three conditions of Experiment 2

In accordance with the findings of Kundey et al. (2010), our results indicate that dogs can take into account what humans can hear. We showed that even with this challenging apparatus, dogs chose the silent tunnel. There were three main differences between the current study and the study of Kundey et al. (2010). First, in our study, the human forbade the dog to take the food. Second, we used the Motivation Control in which there was objectively no reason to prefer the silent tunnel because the experimenter allowed the dog to take the food; Kundey et al. (2010) used a Looking Condition in which the human saw the dog approaching the containers. And third, and most important, in the current study, dogs could *not* see the human while they took the forbidden food. But it is likely that they remembered that the human was there and behaved appropriately: they approached silently. Thus, we replicated and extended the findings of Kundey et al. (2010).

General discussion

When taking forbidden food from a tunnel, the dogs preferred to be silent, but not to be hidden. Compared to previous studies (Call et al. 2003; Gácsi et al. 2004; aKaminski et al. 2009; Schwab and Huber 2006; Virányi et al. 2004), dogs in the current task could not rely on what they themselves could see when attempting to take the food. To solve the current task, dogs had to infer that the human would see them, although they could not see the human. Unlike chimpanzees tested in this setup, dogs did not conceal their approach. Once the human was out of sight, they failed to take her perspective into account, thus suggesting that in visual perspective-taking tasks, dogs rely on an egocentric strategy “When I see the other, then the other sees me.”

Interestingly, dogs could solve the task when it was presented in the auditory modality, that is, when they had to take into account that the human could hear, rather than see, their approach to the food. In that situation, they walked on the silent mat to get the forbidden food out of the tunnel. The question is why dogs could solve the problem in the auditory but not in the visual modality. One possible explanation for this difference is that the silent/noisy mats were more salient for the dogs than the opaque/transparent tubes. Moreover, hearing might be more important for dogs than vision, and therefore their appreciation of what others can and cannot hear can be deployed more flexibly. However, although dogs are able to hear ultrasound, and can localize sound sources more precisely than humans, they mainly rely on olfaction and not on hearing (Miklósi 2007, Chapter 6).

Another explanation may be based on the intrinsic differences between the way visual and auditory information is propagated. Whereas two subjects can have a completely different view–for example, when they stand opposite each other, both subjects will hear the same sound when they are in one room. The crucial point here is that while the dog is approaching the tunnel on the crinkly mat, s/he can hear it her/himself. Thus, in that moment, she can hear what the human can (and should not!) hear. In other words, she can use the egocentric strategy “When I hear the noise, then the other hears it.” By contrast, in Experiment 1 in the moment when she puts her paw into the tunnel, she cannot see what the human can see. In this sense, the problem is easier to solve in the auditory compared to the visual modality.

Note also that the dogs produced and controlled the noise themselves. This was also the case in the studies and reports in which primates showed sensitivity to what others can hear: Chimpanzees and rhesus macaques avoided a noisy tunnel in an experimental competitive setup (Melis et al. 2006; Santos et al. 2006). Subordinate chimpanzees may suppress vocalizations in mating contexts (de Waal 1986) and refrain from producing food calls that might attract dominants when they encounter food resources that can be monopolized (Brosnan and de Waal 2003). Moreover, at the borders of their home ranges, chimpanzees avoid making noises that might alert their neighbors (Watts and Mitani 2001) and often remain silent more than they normally would when hunting for monkeys (Boesch and Boesch-Achermann 2000). Similarly, Western scrub jays (*Aphelocoma californica*) reduced auditory information during caching by avoiding a noisy tray to reduce the chances of cache theft by conspecifics (Stulp et al. 2009). In all these studies, subjects could control whether or not they themselves produced a noise. In contrast, when the noise is produced by someone else even chimpanzees fail to take into account what others can hear. Bräuer et al. (2008) tested pairs of chimpanzees competing over two pieces of food. One piece of food was hidden by the experimenter in a very noisy manner, the other was hidden silently. Previous studies have shown that subordinate chimpanzees avoided the piece of food that the dominant could see (Bräuer et al. 2007; Hare et al. 2000).

In contrast, Bräuer et al. (2008) found that chimpanzees did not avoid the food piece that was placed with a noise, although they were able to locate the hiding place using the noise. The authors suggested that producing the noise, as opposed to hearing the noise, may have substantially simplified the problem. Subjects may have learnt the consequences of making sounds in certain situations, while lacking a full understanding of what others can hear.

This could also be the case for domestic dogs. During their life with humans, dogs have the opportunity to learn to be silent when doing something forbidden. Moreover, there could even be a predisposition to be silent in critical situations for carnivores, but also for prey species. For example, dogs’ ancestors, wolves, try not to be detected when stalking prey (Peterson and Ciucci 2003). The interesting finding in our study is that the dogs did not just prefer to be silent when they approached the forbidden food, but that they distinguished between a situation in which the human could hear them and a situation in which the human was absent and therefore could not hear them. This suggests that dogs do not simply use strategies such as approaching forbidden food silently but that their sensitivity to what humans can hear is flexible. However, it is possible that they have learned over the course of their experiences with humans to approach forbidden food silently only in cases when a human is in the room.

In conclusion, dogs prefer a silent approach to forbidden food but they do not hide their approach when they cannot see a human present. It is likely that dogs rely on what they themselves can perceive when they assess what the human can see and hear. Thus, they prefer the silent approach because in that moment, they hear what the human can hear. It is conceivable that this sensitivity to what others can hear is widespread in the animal kingdom. Future studies about perspective taking should also take into account which modality is important in which situation.

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Conflict of interest We declare that the experiments comply with the current laws of Germany. We also declare that we have no conflict of interest.

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I do not understand but I care

The prosocial dog

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Prosocial behaviour benefits another individual and occurs voluntarily. It may have a cognitive and a motivational component. The actor who benefits a recipient – for example by solving her/his problem (1) must recognize the recipient's goal and understand how to fulfil it and (2) has to be motivated to support the recipient.

In the current paper I will review recent studies on prosocial behavior in dogs and I will compare them to studies with primates. I will address the cognitive and motivational skills required for the actor in order to support the recipient.

I conclude that dogs and also chimpanzees display a number of prosocial behaviours, but there are remarkable differences. In contrast to humans, which have an outstanding biological predisposition to benefit others, dogs and chimpanzees only do so under certain conditions.

Keywords: comparative cognition; helping; cooperation; domestic dogs; fairness

1. Introduction

Everyone knows "Lassie", the collie dog that helps people that are in danger. She rescues them from the water, she informs about them about dangers, she seeks for help if someone is injured and she would probably even share her food with them.

Behaviour like this, which aims to benefit another individual or group of individuals and occurs voluntarily, has been subsumed under the general term prosocial behaviour (Wispe, 1972) and can be regarded as a special case of cooperation (Melis & Semmann, 2010). Some authors use the term "helping" in the same way as "prosocial behaviour" and define it as a behaviour that increases the direct fitness of another individual (Bshary & Bergmüller, 2008; Lehmann & Keller, 2006). Others use the term "prosocial behaviour" as a generic term, which includes several kinds of behaviour such as comforting, sharing and informing and instrumental helping (Hay, Caplan, Castle, & Stimson, 1991; Liszkowski, Carpenter, Striano, & Tomasello, 2006; Warneken & Tomasello, 2009a, 2009b).

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In the current paper I will use the latter terminology and concentrate on prosocial behaviours that are beneficial for one individual (the recipient) and potentially involve a cost to the actor (Bshary & Bergmüller, 2008; Jensen, 2012a, Melis & Semmann, 2010; Warneken & Tomasello, 2009a, 2009b). I will take a comparative approach to discuss under what circumstances dogs and other animals behave prosocially.

The first question that arises is about the ultimate mechanism, i.e. how prosocial behaviour has evolved. When an actor increases the direct fitness of the recipient, this behaviour must also lead to an increase in the fitness of the actor to be evolutionarily advantageous. The actor can either obtain indirect benefits or direct benefits (Bshary & Bergmüller, 2008, Hamilton, 1964; Jensen, 2012a; Melis & Semmann, 2010; Trivers, 1971; Yamamoto & Tanaka, 2009a).

The classical example for indirect benefits for the actor is cooperative breeding. In a number of species not only the parents but also other members of the group take care of the offspring. As such, these helpers incur in costs in order to support, defend and feed others' offspring (see Burkart, Hrdy, & Van Schaik, 2009). This can be explained by kin selection which is the evolutionary strategy that favours the reproductive success of the helpers' relatives, who largely share the same genes, even at the cost that these helpers do not invest in their own reproduction (Bshary & Bergmüller, 2008, Hamilton, 1964; Jensen, 2012a; Yamamoto & Tanaka, 2009a). It has been argued that cooperative breeding has evolved in cases where breeding requires a lot of effort, i.e. when it is especially costly. For example, a pair of wolf parents would be unable to rear their puppies on their own. In these cases it is more beneficial for subordinate animals to invest in their siblings, nieces or nephews instead of in their own puppies, which would probably not survive (Emlen & Wrege, 1988, Mcgowan, Hatchwell, & Woodburn, 2003, Coppinger & Coppinger, 2001, Thornton & McAuliffe, 2006, see Hamilton, 1964).

But an actor can also obtain direct benefits, even if s/he is not related to the recipient. The classical explanation here is reciprocity: although the fitness of the actor is temporarily reduced, it is expected that the recipient will act in a similar manner at a later time (Trivers, 1971). Recently, more detailed theories about different forms of reciprocity were developed (see Bshary & Bergmüller, 2008; Jensen, 2012a,b; Melis & Semmann, 2010 for reviews), such as indirect reciprocity (when poor reciprocators are avoided because they have a bad reputation and when good reciprocators get a higher chance of receiving help even from subjects they have had no direct interactions with previously, Alexander, 1987), and pseudo-reciprocity (when the return benefits are the consequence of self-serving behaviour by the recipient, Connor, 1996).

Whereas some forms of reciprocity probably require cognitive capacities (Stevens & Hauser, 2004; Melis & Semmann, 2010), this is probably not true for cooperative breeding. For example it is unlikely that a wolf makes a conscious decision to help her siblings. It is more likely that this is an innate behaviour. Also humans are not always consciously calculating how to increase their inclusive fitness when they behave prosocially, but psychological mechanisms that promote prosocial behaviors were probably evolutionary advantageous (Barcaley, 2011).

A second central question that arises is on the proximate mechanisms of prosocial behaviour, i.e. on the preconditions for prosocial behaviour and the reason why individuals benefit others. Here I will especially focus on whether non-human individuals benefit others on purpose and whether they understand what they do when they support others. I will concentrate on the immediate costs and benefits of single (or few) acts, as I am mainly interested in psychological mechanisms that impel the actor to behave prosocially (Bshary & Bergmüller, 2008; Jensen 2012a, Melis & Semmann, 2010).

Warneken & Tomasello (2009a) have first argued that instrumental helping has two main components: (1) a cognitive and (2) a motivational component. The cognitive task that the actor has to solve is to understand the situation. This actually involves two subtasks: (a) The actor must recognize the recipient's goal (i.e. "Lassie" has to understand that the swimmer wants to reach the save shore) and (b) the actor must know how to fulfil that goal, (i.e. "Lassie" has to know the solution for the problem – pulling the swimmer to the shore). The motivational component contains the question of whether the actor is willing to benefit the recipient. "Lassie" could recognize the swimmer's problem and she could understand how to solve it, but she might simply not care. Thus, besides the cognitive component, another precondition for helping others is being motivated to do so (Warneken & Tomasello, 2009a). A related question would be whether these motives are truly "altruistic" or unintended by-products of selfish motives (see Clavien, 2012; Jensen, 2012a,b), but this is not the focus of the current review.

Although these two preconditions were first postulated for instrumental helping only (Warneken & Tomasello 2009a), they might also apply to other forms of prosocial behaviour such as informing (Bullinger, Zimmerman, Kaminski, & Tomasello, 2011, Kaminski, Neumann, Bräuer, Call, & Tomasello 2011, Liszkowski, et al., 2006) and sharing (Stevens & Gilby, 2004). In the first case the informer has to understand what information the recipient needs and in the second case the donor has to understand that the recipient wants food – and both have to be motivated to benefit the recipient (see below).

In this paper, I will focus on informing, instrumental helping and sharing, as these are the three forms of prosocial behaviours that have been studied most in dogs and other animals. The majority of experimental studies about prosocial behaviour have been conducted with chimpanzees, since they are our closest living relatives and hence an appropriate model to study the evolution of cooperation (see Amici &

Bietti, Albiach-Serrano, this volume). However, another reasonable animal model for studying prosocial behaviour is the domestic dog. Although the initial reason why dogs were domesticated 15,000 years ago remains unknown, they were subsequently bred and kept for various purposes including protection, hunting, herding, and later also for rescue, search, service and guide purposes (Serpell, 1995; Svartberg & Forkman, 2002). This means domestic dogs might have been selected for cooperating with humans and therefore have developed some special skills especially in the social communicative domain (Hare & Tomasello, 2005, Kaminski & Marshall-Pescini, 2014 see also Price, 1984). However, it remains unclear how much of their prosocial behaviour is innate and how much is trained (Miklósi, 2007; Naderi, Miklósi, Doka & Csányi, 2001; Ruusila & Pesonen, 2004). So the question here is whether dogs that behave prosocially towards humans actually understand human intentions and are motivated to support them for the sake of being prosocial, rather than simply being trained to follow certain commands or react to particular situations in certain ways (Bräuer, Schönefeld, & Call, 2013). In other words, the question is whether the story of "Lassie" is only fiction or has some true background.

2. Informing

Being prosocial does not necessarily mean pulling someone out of the water or sharing food with him. It can also be extremely beneficial for the recipient to receive important information.

Many animals follow each other's gaze in order to receive extra information about the environment (apes: Bräuer, Call, & Tomasello, 2005; monkeys: Call, Hare, & Tomasello, 2001; Amici, Aureli, Visalberghi, & Call, 2009; goats: Kaminski, Call, & Tomasello, 2005; corvids: Schloegl, Kotrschal, & Bugnyar, 2008 and even tortoises: Wilkinson, Mandl, Bugnyar, & Huber, 2010). The to date unanswered question is whether the actor, i.e. the one that looks somewhere, has the intention of informing the recipient about important events in their environment. Only then can gaze following be regarded as prosocial behaviour, as the actor does intend to give the information the recipient is using.

Whereas gaze following might be widespread in the animal kingdom, there is one species that shows outstanding skills at using other informative cues – the domestic dog. Dogs use various cues from conspecifics (Hare & Tomasello, 1999) and also from humans in order to locate hidden food (see Kaminski & Marshall-Pescini, 2014 for a review) and might even perceive the communicative intent, i.e. that the human wants to provide them with information about the location of the hidden food (Kaminski & Nitzschner, 2013).

The question is whether dogs also provide humans with information when necessary. A number of studies have shown that dogs – without special training – informed naïve humans about the location of hidden food or toys (Miklósi, Polgárdi, Topál, & Csányi, 2000; Savalli, Ades, & Gaunet, 2014; Virányi, Topál, Miklósi, & Csányi, 2006).

However, in all these studies dogs informed humans about objects that were rewarding for them, thus, their action was beneficial for them and not for the human, and can therefore not be regarded as prosocial behaviour. Consequently Kaminski et al. (2011) investigated whether dogs would assist a naïve human to find a hidden object and varied whether the object was valuable either to the dog, the human, both or neither (see Figure 1). The object was hidden by a helper in one of four locations in a room. The dog witnessed the hiding process, but the human was absent and therefore unaware of the location of the object. As in previous studies dogs showed naïve humans the location of the hidden objects that were interesting for themselves (Miklósi et al., 2000; Savalli et al., 2014; Virányi et al., 2006). However, dogs also sometimes indicated the location of objects in which they were not interested (i.e. a hole punch, a vase). Moreover, when only the human was interested in the object, dogs often performed an informative showing behaviour, albeit indicating the wrong location of the object. In addition, the rate of indicating did not decrease over time. Thus, dogs seemed to be motivated to support or at least willing to please the human, perhaps prompted by the human's utterances and search behaviour. But they were unable to infer the human's goal in that situation (Kaminski, Neumann, et al., 2011).

In a similar paradigm great apes showed a different performance (Bullinger et al., 2011; Zimmermann, Zemke, Call, & Gómez, 2009). Subjects witnessed how a tool was hidden out of reach for them. They then had the opportunity to inform a human experimenter about the position of that tool by pointing at it. The experimenter then either used the tool to retrieve a reward for the pointing subject (so the pointing was selfish) or to retrieve the reward for herself (so the pointing was prosocial). This means that in the first trial subjects could not know what the experimenter would do, but as trials passed they could learn which tool was beneficial for them, and which one was only beneficial for the human experimenter. Chimpanzees and other apes informed humans about the location of hidden tools, but only if it was beneficial for them – this means their pointing was selfish. If the tool was irrelevant to the apes, the rate of indicating decreased over time until it nearly extinguished (Bullinger et al., 2011; Zimmermann et al., 2009). Bonobos pointed more often when the tool was potentially beneficial for the human experimenter, but they did not seem to distinguish whether the human really needed the object or not (Zimmermann et al., 2009). For chimpanzees (and probably also for the other great ape species) it might be more natural *not* to inform others, as they live in a competitive environment (Bräuer, Call, & Tomasello, 2007; Hare, Call, Agnetta, & Tomasello, 2000; Hare & Tomasello, 2004).

Figure 1. Set-up of the study by Kaminski et al. (2011). Above: the four objects were introduced according to four different conditions, which varied in terms of to whom the objects were valuable. Middle: the object was hidden by a helper in one of four locations in the presence of the dog. Then the experimenter searched for the hidden object. Below: dogs mainly indicated the location of objects that were valuable for them, but did not differentiate between objects the experimenter was and was not interested in (Picture: Alex Chauvel, copyright Springer 2014)

In contrast humans reliably provide others with various kinds of information – and it is possible that the unique features of the human eye evolved as a device for providing others with information (Kobayashi & Kohshima, 2001, Tomasello, Hare, Lehmann, & Call, 2007). Before they are able to speak, children point in order to inform an adult about a hidden tool. They point regardless of whether they benefit from this, they remain motivated over time (Bullinger et al., 2011; Liszkowski et al., 2006), and they even gesture appropriately for knowledgeable versus ignorant adults, i.e. they seem to understand when their information is needed (Liszkowski, Carpenter, & Tomasello, 2008). Thus human children at that early age already fulfil both of our preconditions: they are motivated to benefit others without an immediate benefit, and they understand when this is needed.

In sum, human children start very early to provide others with necessary information, whereas domestic dogs and great apes do not. For the dogs it is probably a lack of the ability to infer the other's goal while for the apes this might be a question of motivation.

3. Instrumental helping

Instrumental helping is one kind of prosocial behaviour and it is defined as acting for another individual who is faced with an instrumental problem and unable to reach her behavioural goal (Warneken & Tomasello, 2006, 2009a, 2009b).

Bräuer et al. (2013) first raised the question of whether dogs would help a human. As other studies had shown that dogs have problems to understand the human goals and intentions (Kaminski et al., 2011, see also below) the aim of this study was to make the human goal as obvious as possible for the dog. Bräuer et al. (2013) used a set-up in which a human tried to enter a target room in order to get a key. The tested dog could open the door to the target room by pushing a button. The help conditions in which the human expressed that she wanted to enter the target room were compared to a control condition in which the human did not try to enter the room. Bräuer et al. (2013) found that dogs did not help when the human simply tried to open the door. But dogs helped if the human explicitly communicated her goal to them in a natural way, i.e. without a predetermined series of actions. When dogs helped, they continued to open the door over trials without receiving any reward (Bräuer et al., 2013). This study confirms that dogs were highly motivated to help but had problems inferring the human's goal if it was not communicated clearly.

But also chimpanzees help others in a variety of situations, such as in agonistic and feeding contexts (see Yamamoto & Tanaka, 2009a for a review). Chimpanzees reliably help humans in out-of-reach tasks but not in tasks that involve physical obstacles, wrong results or wrong means (Warneken & Tomasello, 2006). Chimpanzees also help conspecifics. For instance, they can open a door for an unrelated group mate and they help a group mate obtain a tool (Melis, Hare, & Tomasello, 2008; Melis et al., 2011; Warneken et al., 2007, but see Albiach-Serrano, this volume), or release a latch that allows another chimpanzee to gain access to a tool or food (Melis et al., 2011). In a recent study by Yamamoto, Humle and Tanaka (2012), a chimpanzee recipient needed a special tool in order to receive a juice reward from an apparatus. Subjects selected the appropriate tool from a random set of seven objects and transferred it to the recipient, indicating that they understood what their partner needed. This targeted helping was observed only when the helpers could visually assess their partner's situation. These results support the argument that chimpanzees understand conspecifics' goals in this situation (see also Melis & Tomasello 2013). Thus, in all these studies chimpanzees fulfil both of the preconditions: they obviously recognize the other's goal and they are also motivated to help without receiving any benefit such as a reward or praise in various situations (see also Warneken et al., 2007).

However, although chimpanzees and dogs do help in some situations, there is no doubt that humans are unique in the way they help each other (Bshary & Bergmüller, 2008; Jensen, 2012a,b; Melis & Semmann, 2010; see Amici, this volume). In their second year, human toddlers already help non-related adults to reach their instrumental goals (Warneken, Chen, & Tomasello, 2006; Warneken, Hare, Melis, Hanus, & Tomasello, 2007). Interestingly, young children's motivation to help seems to be intrinsic. Warneken et al. (2007) found that the provision of material rewards is not necessary to elicit helping behaviour or to increase its rate. In fact, children who had received material rewards helped less in subsequent trials than children who had not received any reward (Warneken et al., 2007; Warneken & Tomasello, 2008, but see Prinz, 2007). They conclude that this so-called over-justification effect suggests that these early helping behaviours in young children are intrinsically motivated and that socialization practices involving extrinsic rewards can undermine this tendency (Warneken et al., 2007).

In sum, dogs help humans only when the other's goal is made very obvious to them, chimpanzees help conspecifics and humans in some situations whereas humans are outstanding instrumental helpers (see Jensen, Vaish & Schmidt 2014 for a review).

4. Sharing

The third kind of prosocial behaviour I want to consider is sharing resources. This can be defined as a situation where the resource owner shows tolerance and allows a partner animal to consume a part of her food, although she has the ability to fight and try to keep all of her food (Hadjichrysanthou & Broom, 2012).

Surprisingly, to my knowledge there is no published study about how domestic dogs share food with each other. It is well known that wolves – dogs' closest living relatives – provide their offspring with food, which is probably an innate behaviour (Coppinger & Coppinger, 2001, see above). Interestingly dogs have reduced cooperative breeding tendencies compared to wolves, and puppies are rarely fed by group members other than their mother (Bonanni & Cafazzo, 2014). In addition, there is some indirect evidence that dogs do not divide food in equal shares. In a recent study about cooperative problem solving, the two partners could share the spoils after they solved the problem, but one of the partners often monopolized food, even if it was presented in two bowls (Bräuer, Bös, Call, & Tomasello, 2013).

A different, but somehow related question is whether dogs show other regarding preferences by *providing* others with food. This is usually tested in a set-up in which subjects have a choice between pulling two trays. In one tray, there is food for the subject and a conspecific partner, whereas in the other tray there is food for the subject only (Figure 2, see Jensen, 2012a; Bräuer & Hanus, 2012 for reviews). In a pilot study dogs showed no preference to deliver food to the partner even if this would not result in extra costs to themselves (Chaumette, Dale, Dania, Marshall-Pescini, & Range, 2014). With a similar set-up two non-food tokens are used instead of the trays. One token leads to a prosocial outcome and the other to a selfish one (Amici, Visalberghi, & Call, 2014; Horner, Carter, Suchak, & de Waal, 2011). According to preliminary results of another on-going study dogs did not differentiate between the prosocial option in both – subject and partner receive food, and the selfish option in which only the subject receives food (Dale, Chaumette, Dania, Marshall-Pescini, & Range, 2014).

These preliminary results suggest that dogs either have problems to understand these paradigms (as they are cognitively too demanding), or have no other regarding preferences towards conspecifics. However, as dogs prefer humans as social partners and were probably originally selected to behave prosocially towards humans (Kaminski & Marshall-Pescini, 2014, see also above), it seems not unlikely that they would provide humans with food if they had the chance to do so.

Whereas there are many open questions about sharing and other-regarding preferences in domestic dogs, there have been a number of studies about sharing in other species (see Stevens & Gilby, 2004 for a review). Also chimpanzees do share food with each other. However, compared to humans there is a difference in terms of *how* chimpanzees share (usually not actively, Ueno & Matsuzawa, 2004; Silk, Brosnan, Henrich, Lambeth & Shapiro, 2013, Stevens, 2004; and usually not fairly, see below), *with whom* they share (Boesch, 1994, see below) and *why* they share (to avoid costly harassment from the beggar, Stevens, 2004; to enhance the welfare of closely related group members and to strengthen social relationships with favoured partners, Silk et al., 2013).

When chimpanzees hunt monkeys, not only the involved hunters get portions of the meat but bystanders do as well, i.e. members of the group that are around when the monkey is killed (Boesch, 1994). Thus chimpanzees in this case share independently of what effort each subject has invested in the cooperative hunt. By contrast, human children share the spoils after collaboration equitably (Hamann, Warneken, Greenberg, & Tomasello, 2011; Melis, Schneider, & Tomasello, 2011; Warneken, Lohse, Melis, & Tomasello, 2011).

Chimpanzees were also tested whether they show other regarding preferences, i.e. whether they are willing to provide others with food at no extra costs for themselves. When chimpanzees have a choice between a tray with food for themselves and a partner and a tray with food for themselves only, they do not preferentially deliver food to their partners (Jensen, 2012a; Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005, see Figure 2).

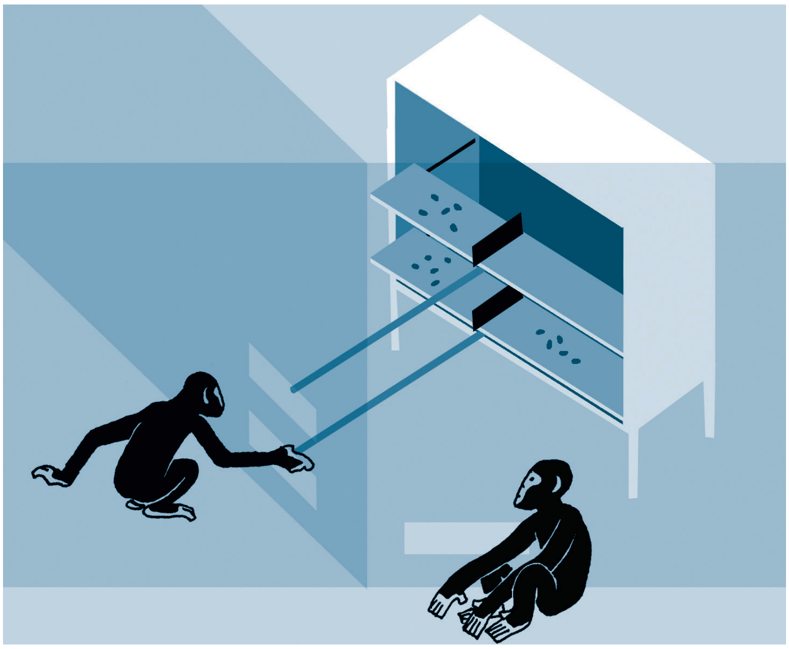

Figure 2. Basic set-up to test other-regarding preferences in primates. Subjects have a choice between a tray with food for themselves and a partner and a tray with food for themselves only (Picture: Alex Chauvel, copyright Springer 2014)

Chimpanzees were also tested in the token-task in which they have the choice between two tokens. Although in one study subjects provided food to a partner by selecting a prosocial token over a selfish one (Horner et al., 2011), they failed to do so when proper control conditions were introduced (Amici et al., 2014).

Another related question is whether animals have a sense of fairness when they share food. This sense would allow animals to compare their own efforts and subsequent outcomes with those of others, and thus to evaluate and react to inequity. A growing number of studies have investigated how subjects react to unequal situations that humans would perceive as 'unfair' (see Bräuer & Hanus, 2012 and Brosnan & de Waal, 2014 for reviews).

One experimental setup that was often used to investigate fairness in animals is a situation in which a subject and her partner participate in a task, but receive rewards of different value. The question is whether the subject refuses to participate in the task if she witnesses the partner obtaining a more attractive reward for the same effort. Range, Horn, Virányi, & Huber (2009) tested domestic dogs using a task in which dogs had to give their paw to an experimenter. They found that subjects did not react to differences in the quality of food that the partner received. However, dog subjects showed sensitivity toward the inequity of rewards when they themselves did not receive a reward. Then they differentiated between situations in which the partner was rewarded compared to an asocial control situation. The authors conclude that dogs might show a primitive version of inequity aversion (Range et al., 2009).

But also for apes, there is only weak evidence for a sense of fairness (i.e. Bräuer, Call, & Tomasello, 2006; Bräuer, Call, & Tomasello, 2009; Brosnan, Schiff & de Waal, 2005, Brosnan et al., 2015). Although apes are attentive to what a partner is receiving, they do not seem to be able or motivated to compare their own efforts and outcomes with those of others at a human level. They are mainly interested in maximizing their own benefit, regardless of what others may receive (Bräuer & Hanus, 2012, Jensen, 2012a, but see Brosnan & de Waal, 2014).

In sum, there are not many studies on sharing and other regarding preferences in dogs. Preliminary results suggest that they do not share nor provide conspecifics with food, which might again be a problem of understanding the situation, rather than a problem of motivation. Chimpanzees do not share food actively, do not provide others with food voluntarily and might share mainly to avoid costly harassment from the beggar. In contrast, humans actively provision others with food, share the spoils equally after collaboration (e.g. Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012) and are also unique in terms of the way they share, using their sense of fairness (e.g. Fehr & Fischbacher, 2003).

5. Discussion

In summary, dogs show some kinds of prosocial behaviours, but there are remarkable differences in comparison with chimpanzees and humans. Dogs are highly motivated to please humans, but they often have problems understanding the situation. This probably involves both the recognition of the recipient's goal and knowledge of how to fulfil that goal.

Dogs' problem to interpret others' behaviour as goal-directed has also been shown in several other situations. For example it is unlikely that dogs understand intentions when they imitate a conspecific (Kaminski, Nitzschner, et al., 2011; but see Range, Virányi & Huber 2007). There is also no evidence that dogs recognize the human goal in a communicative situation, when they are deceived by a human (Petter, Musolino, Roberts & Cole, 2009). However, in a habituation-dishabituation paradigm, dogs might be able to attribute intentions to an animate (a human) but not an inanimate (a black box) agent interacting with an object (Marshall-Pescini, Ceretta & Prato-Previde, 2014). More evidence about recognition of intentions and goals comes from communicative situations, in which dogs probably react to several ostensive cues in order to behave appropriately (see Topál, 2014 for a review). But overall dogs seem to have difficulties interpreting others' behaviour as goal-directed (see Bräuer, 2014 for a review).

Dogs might not only have problems to recognize the recipient's goal when the other needs help or information or simply food, but in some situations dogs might also lack the knowledge on how to fulfil the recipient's goal. Macpherson & Roberts (2006) tested whether dogs seek help in an emergency situation. Dogs' owners feigned a heart attack, and a bystander was available to which dogs could go for help. In contrast to "Lassie" dogs did not solicit help from the bystander. It is likely that dogs did not know how to intervene in that situation (Macpherson & Roberts, 2006). However, it is also possible that they did not perceive the situation as an emergency case, as the owners just acted as if they had a hard attack. In other words, the emergency was not real – and dogs might perceive that.

Indeed, there is growing evidence that dogs alert to real epilepsy and diabetes seizures, and might even be able to predict them, even when they were not trained to do so (Dalziel, Uthman, McGorray, & Reep, 2003; Lim, Fisher, & Burns-Cox, 1992). Whether dogs have the motivation to support the owner in that situation or whether they are simply aroused because the owner smells and behaves in an unusually way remains an open question. Also Macpherson & Roberts (2006) report a greater attentiveness to the owner in the emergency conditions of their study. They suggest that this indeed could be a sign that the dogs showed concern for the victim's situation.

Overall there is evidence that dogs' difficulty in helping situations lies in perceiving the human's goal and knowing how to intervene, rather than in their willingness to support them. If the goal is presented by means of a clear communicative signal, dogs do help reliably and without receiving a reward (Bräuer et al. 2014). That leads to the question of whether it can be still considered as informing, helping or sharing if the recipient has to send a strong signal in order to elicit these prosocial behaviours. Some authors have argued that these behaviours should occur also in the absence of signals for them (Stevens, 2004; Burkart, Fehr, Efferson, & van Schaik, 2007; Melis et al., 2011).

This may be a criterion that excludes most non-human animals, since it appears that communicative signals are the main source by which individuals perceive that the recipient needs support. Not only in dogs, but also in chimpanzees, a key factor determining prosocial behaviour is whether the recipient provides cues signalling the need for help (Melis et al., 2011; Warneken et al., 2007; Warneken & Tomasello, 2006; Yamamoto & Tanaka, 2009a,b). Melis et al. (2011) have argued that the cues provided by the recipient may signal to the potential actor to 'do something', triggering her motivation to support the recipient. Another possibility is that actors simply help recipients to terminate the recipient's requests (Albiach-Serrano, this volume, Melis et al., 2011, see also Yamamoto et al., 2012). In other words actors might feel harassed by the signals of the recipient and simply want the recipient's requests to stop. But note that also human children help more reliably in the presence of such signals (Warneken et al., 2007; Warneken & Tomasello, 2006, 2007).

Although chimpanzees are not as motivated to please or benefit others as dogs and humans, and although they might only help to terminate the recipient's requests, they have no problems with the cognitive component of prosocial behaviour. As also shown in other situations, chimpanzees are able to recognize others' goals and know how to fulfil them (Call, Hare, Carpenter, & Tomasello, 2004, Buttelmann, Carpenter, Call, & Tomasello, 2007, see Call & Tomasello, 2008 for a review). Thus the reason why chimpanzees sometimes fail to behave prosocially might not be their inability to recognize the recipient's goal but rather a lack of motivation to benefit others.

In contrast there is no doubt that humans instead fulfil both preconditions for prosocial behaviour and have an outstanding biological predisposition to benefit others (i.e. Jensen, Vaish & Schmidt 2014, Tomasello, et al., 2012, see Amici, this special issue).

Future studies should further investigate both the cognitive and the motivational component of prosocial behaviour in non-human animals. They should show whether there is a real difference in the motivation of humans and animals to help, share and inform. It is likely that this motivation also depends on the social system of a given species (i.e. Burkart, Hrdy, & Van Schaik, 2009, Jensen, 2012a). In this respect dogs, with their special domestication history (as they were probably selected to cooperate with humans), might represent a better model to study prosociality than great apes.

Concerning the cognitive component, it would be interesting to investigate what species other than chimpanzees (and capuchin monkeys, Phillips, Barnes, Mahajan, Yamaguchi & Santos 2009) are truly able to recognize the recipient's goal. For dogs it should be investigated what aspect of communication makes the human goal obvious, and whether dogs with special training (such as service dogs) are especially skilful when it comes to perceiving the human's goal or whether they are simply more easily guided to the goal.

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Author's bionote

Juliane Bräuer's main research interest is comparative cognition. She conducts experimental studies following a comparative approach, that is, selecting meaningful groups for comparisons to learn about how and why certain cognitive skills might have evolved. Thus, she is especially interested in investigating what cognitive skills different species have evolved in order to survive in their ecological niche. So far she has studied all four great ape species, domestic dogs, but also wolves, swine and human children. She started her research with conducting experimental studies on visual perspective taking and communication in dogs and apes. Currently her research interests also include future planning, inequity aversion and cooperation. Besides these topics, that fall in the category of social cognition, she is also interested in tool-use behaviour and mental time travel.

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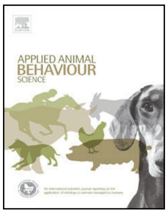

When do dogs help humans?

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ABSTRACT

Here we investigate whether domestic dogs (*Canis familiaris*) engage in instrumental helping towards humans without special training. We hypothesized that dogs would help a human if the human's goal was made as obvious as possible. Therefore we used a set-up in which a human attempted to enter a compartment within a room (the "target room") in order to get a key. The dog could open the door to the target room by pushing a button. We varied the way in which the experimenter expressed how she wanted to enter the target room (reaching, pushing the door, communicating with the dog) and the relationship between human and dog (owner versus stranger). Dogs helped in two situations: (1) when the human pointed at the button and (2) when the humans communicated naturally to the dogs, i.e. without a predetermined series of actions. In these situations, dogs continued to open the door without receiving any reward. We therefore conclude that dogs are motivated to help and that an experimenter's natural behaviours facilitated the dogs' recognition of the human's goal. Interestingly the identity of the experimenter had no influence on the behaviour of the dogs.

1. Introduction

In recent years there has been an unprecedented interest in the area of prosocial behaviour in nonhuman animals. A behaviour which aims to benefit another individual or group of individuals and occurs voluntary has been subsumed under the general term prosocial behaviour (Wispe, 1972). There are four types of prosocial behaviour (Warneken and Tomasello, 2009a): comforting (Zahnwaxler et al., 1992), sharing (Hay et al., 1991), informing (Liszkowski et al., 2006) and instrumental helping. Especially instrumental helping, defined as acting for another individual to achieve its behavioural goal (Warneken and Tomasello, 2006, 2009a, 2009b), has received considerable attention.

Helping involves a cost to the actor and a benefit to the recipient and it has a cognitive and a motivational component. The actor who helps to solve a recipient's problem (1) must recognize the other's goal and (2) has to be motivated to help (Warneken and Tomasello, 2009b).

Recent studies suggest that human children have a biological predisposition to help others, even non-relatives, with their instrumental goals. Human infants start instrumentally helping others at the age of 14 months (Warneken and Tomasello, 2007). In studies by Warneken et al. (2006, 2007) it was shown that 18-month-old children help in various situations. In one example, when a human experimenter accidently dropped an object on the floor, the child gave it back to him, and in another, the child opened a cabinet door for him when he was not able to do it himself. In the control conditions in which the experimenter did not need help, the children did not perform these actions (Warneken and Tomasello, 2006, 2007). Children also reliably point to inform a human about a hidden tool. They point regardless of whether they benefit, and they remain motivated over time (Bullinger et al., 2011; Liszkowski et al., 2006).

Warneken et al. (2007) found that the provision of material rewards is neither necessary to elicit helping behaviour nor to increase its rate. In fact, children who had received

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material rewards helped less in subsequent trials than children who had not received any reward. The fact that material rewards decreased even 20-month-olds' motivation to help led the authors to conclude that there is an intrinsic motivation in humans to help others (Warneken et al., 2007; Warneken and Tomasello, 2008).

Chimpanzees also help others in a variety of situations such as in agonistic and feeding contexts. However, researchers have noted remarkable differences in the helping behaviour of the two species. Like human children, chimpanzees reliably help humans in out-of-reach tasks (Warneken and Tomasello, 2006). They seem to recognize the other's goal, i.e. they hand the object to the human when she needs it and reaches for it. They are also motivated to help without receiving any benefit such as reward or praise (Warneken et al., 2007). However, chimpanzees have failed to help without being requested to do so in all previous studies. Perhaps in these types of tasks the chimpanzees have problems inferring the human's goals or they do not know how to intervene (Warneken and Tomasello, 2006). In other situations when chimpanzees are clearly able to recognize the human's goal they do *not* help. Several studies have shown that chimpanzees and other apes inform humans about the location of hidden tools but only if it is beneficial for them – i.e., when the human uses the tool to retrieve a reward for the ape. If the object is irrelevant to the chimpanzee or orang-utan, the rate of indicating decreases over time until it is nearly extinguished (Bullinger et al., 2011; Zimmermann et al., 2009). Bonobos produce more 'gifts' but they do not seem to distinguish whether the human needs them or not (Zimmermann et al., 2009).

Chimpanzees also help conspecifics in situations similar to those mentioned above. For instance, they can open a door for an unrelated group mate and they help a group mate to obtain a tool (Melis et al., 2008; Warneken et al., 2007) or release a latch that allows another chimpanzee to access a tool or food (Melis et al., 2011). In contrast, other studies have shown no other-regarding preferences in chimpanzees: when they had a choice, at no cost to themselves, between pulling a tray with food for themselves *and* a partner or a tray with food only for themselves they did not preferentially deliver food to their partners (Jensen et al., 2006; Silk et al., 2005). However, Melis et al. (2011) found that chimpanzees helped conspecifics to obtain food and non-food items during a situation in which the donor could not get the food herself. Interestingly, donors helped only when recipients tried to get the food or tried to get the attention of the donor. Thus, as noted previously, a key factor determining helping behaviour is whether the recipient provides cues signalling the need for help. Melis et al. (2011) argued that the cues provided by the recipient may signal to the other to 'do something', and that the donors have the motivation to help when the goal of the recipient is clear. Another possibility is that donors simply help recipients to terminate the recipient's requests (Melis et al., 2011).

In the current study, we investigated whether dogs engage in instrumental helping towards humans. The relationship between dogs and humans has existed for at least 15,000 years (Savolainen et al., 2002). During the process of domestication, dogs have evolved special social skills to read the social and communicative behaviour of humans (Cooper et al., 2003; Hare and Tomasello, 2005; Miklosi et al., 2004). They are sensitive to humans' attention and perspective (Call et al., 2003; Gacsi et al., 2004; Kaminski et al., 2011; Viranyi et al., 2004). Dogs are also very skilful in locating hidden food by using certain human-given social cues. When food is hidden under one of two cups (the so called object choice design), dogs can use cues such as pointing, gazing, bowing or a marker placed on the baited cup to find the hidden food (Agnetta et al., 2000; Hare et al., 1998; Hare and Tomasello, 1999; McKinley and Sambrook, 2000; Miklosi et al., 1998; Soproni et al., 2001, 2002). Not only are dogs able to use human's communicative cues, but they are also able to communicate the place of the hidden food to their owner (Miklosi et al., 2000).

Although the initial reason why humans domesticated dogs 15,000 years ago remains unknown, dogs were later bred and kept for various purposes including protection, hunting and herding. Since the last century, dogs have also been used for rescue, search, service and guide purposes (Serpell, 1995; Svartberg and Forkman, 2002). Despite extensive evidence of dogs helping humans, it remains unknown whether dogs are intrinsically motivated (as humans are) to help their human companions achieve their goals. In other words, it is unclear if dogs that help humans actually understand human intentions and if they are motivated to help for the sake of helping, rather than simply trained to follow certain commands or react to particular situations in certain ways.

Kaminski et al. (2011) investigated whether dogs would help a human to find a hidden object. The object was hidden in one out of four locations while the dog watched. They found that dogs showed naïve humans the location of the hidden objects. As in previous studies (Miklosi et al., 2000) the dogs had no problem indicating the location of objects in which they were interested (i.e. toys). However, they sometimes indicated the location of objects in which they were not interested (i.e. a hole-puncher, a vase). Interestingly, they showed the human the place of these objects more frequently when it was their owner (in half of the cases) than when it was a stranger (in approximately 20% of the cases). Moreover, the rate of indicating those objects did not decrease over time, suggesting that the dogs maintained their motivation to inform humans about objects in which they were not interested, even in the absence of any benefit. However, although dogs often performed this informative showing behaviour, they usually indicated the *wrong* place of the object when the human was interested in it, showing the right location in only about 15% of the cases. Thus, dogs seemed to be motivated to help or at least willing to please the human, perhaps prompted by the human's utterances and search behaviour.

The aim of the current study was to investigate whether dogs would help a human if the human's goal was made as obvious as possible. We used a set-up in which a human tried to enter a target room in order to get a key. The dog could open the door to the target room by pushing a button. If the dogs were able to understand the human's goal and were motivated to help, they should open the door when the human tries to enter the target room. In different help conditions we varied how the human expressed that she wanted to enter the target room (reaching, pushing the door, communicating with the dog) and the relationship between human and dog (owner versus stranger). We compared the help conditions with control conditions in which the human did not try to enter the room. Thus, our question was, under what circumstances dogs would help a human to open a door. We conducted three experiments and in each experiment different dogs were used.

2. Experiment 1: Ostensive cues

Here we investigated whether ostensive and other behavioural cues help dogs to realize the human's goal to open the door to the target room. Ostensive cues are communicative cues, e.g. a high pitched voice and eye contact. They are produced in order to indicate when information is relevant and help an audience to understand the communicator's intention (Csibra and Gergely, 2009; Sperber and Wilson, 1986, 1995). Dogs are sensitive to various ostensive cues (Topal et al., 2009; Viranyi et al., 2004). These cues can provoke increased arousal and greater levels of active behaviour (Range et al., 2009) as well as elicit indicative behaviour (Kaminski et al., 2011). In the current experiment the human showed her intention to the dog in various ways. In one help condition (h-SUPPORT (fixed)) the human simply looked at and reached into the target room and pushed against the door without using ostensive cues to communicate with the dog. In the other help conditions (h-GAZE, h-TALK, COMMAND) she used various ostensive and other communicative cues to communicate directly with the dog in order to make her goal as obvious as possible.

2.1. Methods

2.1.1. Subjects

Twelve dogs (*Canis familiaris*; 6 females and 6 males) of various breeds and ages (range = 1–9 years old, mean age = 4.8 years) participated in this experiment (see Table 1). All subjects lived as pet dogs with their owners in Leipzig and received normal obedience training typical for domestic dogs. The dog owners took part in the study voluntarily. During the test the owners were absent. Furthermore, owners were not informed about the design of the experiment or the specifics of their dog's task in the study until after the last session was completed.

The preconditions to participate in this experiment were that the dog had to be (1) food-motivated, (2) at least one year old and (3) able to learn to open the target door. Dogs were trained the first day to open the target door. From the 13 invited dogs all except one passed the training and participated in the test. Every dog was tested individually by the same experimenter E (KS). The study adhered to the Guidelines for the use of Animals in Research.

2.1.2. Materials

2.1.2.1. Training. The training was conducted in a training room (5.90 m × 3.60 m). Plexiglas walls were positioned to create a compartment in the room (2.45 m × 2.00 m). The target door (height 112 cm/width 80 cm) was installed on one side of the wall. The door was Plexiglas and was locked magnetically. A wooden button (30 cm × 30 cm) resting on the floor was located outside the compartment. This button had to be pushed by the dog in order to open the target door. Depending on the progress of the training, the button was placed in several positions in the room.

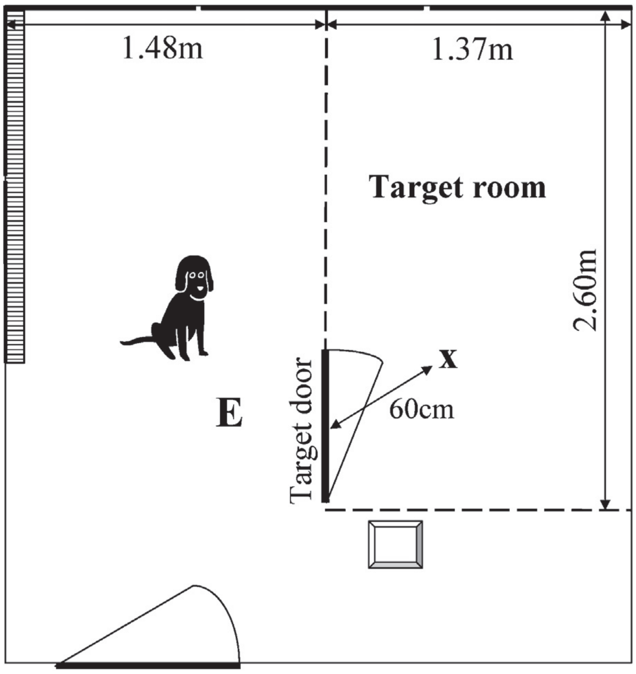

Fig. 1. Overview of the testing room for the help conditions (*x* – location of key; *E* – position of the E; ☐ – button).

2.1.2.2. Test. Fig. 1 shows the testing room (3.60 m × 2.90 m). As with the training room, there was a compartment surrounded by Plexiglas walls. This was the target room, which could be accessed by a door in the same way as it could be accessed during training. Also the button used was identical to the one used in training, and it was placed directly in front of the target door. E either stood in front of the target door (helping conditions) or sat upon a low windowsill opposite the target door and read a book. The dogs could move freely about the room throughout the duration of the test. In the target room there was a bunch of keys (from now on called key) or one piece of food for the dog, depending on the conditions.

2.1.3. Procedure

2.1.3.1. Training and warm-up. During training, dogs learned in three steps that when they pressed the button, the target door would open. In the first step, each dog learned to push the button. The dog was rewarded with pieces of food and praise when s/he put his/her paw on the button (for example by walking over it). In the second step, the button was associated with the target door. E stood in the compartment and the target door was closed. The button was located next to the target door. E pointed at the button, calling the dog's name and in this way encouraged the dog to press the button. Again the dog was rewarded with praise and food. In the final step, the dogs had to be

Table 1
Name, breed, gender and age of the subjects in each experiment.

Subject	Breed	Gender	Age (years)	Experiment
Alma	Mongrel (Irish Setter)[b]	Female[a]	5	1
Baghira	Mongrel (Shepherd dog)[b]	Female[a]	5	1
Balou	Schapendoes[b]	Male[a]	8	1
Bazi	Mongrel[b]	Male	1	1
Emmi	Weimaraner[b]	Female	5	1
Fara	Mongrel (Shepherd dog × Border Collie)	Female[a]	8	1
FeFo	Parson Russell Terrier	Male[a]	1	1
Filou	Mongrel (Australian Shepherd)[b]	Male[a]	9	1
Gonzo	Labrador[b]	Male	5	1
Linus	Golden Retriever[b]	Male[a]	6	1
Motte	Mongrel	Female[a]	1	1
Zosi	Mongrel	Female[a]	4	1
Amy	Magyar Vizsla	Female	7	2
Blue	French bulldog	Male	2	2
Caja	Mongrel (Doberman)[b]	Female	7	2
Chester	Beagle	Male	4	2
Felix	Mongrel[b]	Male[a]	5	2
Gordo	Mongrel (Dogo Canario × Doberman)	Male	3	2
Judy	French bulldog	Female	2	2
Lara	Golden Retriever	Female	1	2
Lea	Mongrel (Leonberger)[b]	Female	9	2
Migo	Jack Russel Terrier[b]	Male	1	2
Nilsson	Mongrel[b]	Male[a]	2	2
Susi	Mongrel (American StaffordshireTerrier)	Female	2	2
Aaron	Eurasier[b]	Male	3	3
Aimee	Collie[b]	Female	2	3
Atze	Wire-haired dachshund	Male[a]	5	3
Benji	Mongrel[b]	Male[a]	5	3
Jasper	Gun dog	Male	1	3
Karou	Berger des Pyrenees[b]	Male	3	3
Kira	Mongrel (Pit bull)[b]	Female[a]	5	3
LucaH	Podenco[b]	Female[a]	1	3
LucaS	Labrador	Female	3	3
Maxl	Shepherd dog[b]	Male	2	3
Maya	Mongrel (Tibetan Spaniel)	Female[a]	2	3
Via	Doberman	Female	1	3

[a] Castrated.
[b] Participated in a dog course such as puppy school, obedience, agility, rescue or companion dog training.

able to open the target door without any help (or request) within 1 min. More specifically, E showed a piece of food to the dog and placed it on the ground in the compartment. Then E stepped back and looked at the ground while the dog pressed the button to open the door and fetched the food. This final step was repeated three times on the second day to make sure that the dog remembered the task.

The dog was trained until s/he was able to complete the final step of the task. This took on average 75 min including a number of breaks to keep the dog motivated. If a dog did not learn the task within 2 h, s/he was excluded from the study. Note that dogs did not learn any particular command to press the button. Instead, E used different words to encourage the dog, such as “Come here!”, “Give paw!” and “Go on it!”.

Warm-up trials were conducted on days 2–5 prior to every test to ensure that dogs were able to transfer the learned association between pressing the button and opening the door from the training room to the testing room. The warm-ups were similar to the final step of the training (see above), except that they were conducted in the testing room. Thus, E was in the target room, placed a piece of food on the ground, and the dog had to open the door by pressing the button and eat the food within 1 min of the E placing the food. There were two warm-up trials on the second day, conducted after the final step of the training. A third warm-up trial was performed only if the dog required verbal encouragement from the experimenter during the first two trials. Within three trials all dogs managed to solve the task without additional encouragement. On days 3–5 there was only one warm-up trial prior to the test trials.

As in other studies (see for example Bullinger et al., 2011) training was needed to teach the dogs the potential helping behaviour, i.e. to press the button in order to open the target door. We tried to keep the training as short and as different from the test conditions as possible (for example in contrast to the test E was inside the target room and she avoided to use specific commands).

2.1.3.2. Test. Each test trial began when E and the dog entered the testing room together. The target door was closed and inside the target room there was either a key (helping conditions) or a piece of food (food condition). E then preformed various patterns of behaviour depending on the condition (see below). If the dog pushed the button to open the target door, E either showed no reaction (food condition) or entered the target room, picked up the key, went back and sat on the windowsill and read the booklet (helping conditions). The dog was not praised for opening the door in either condition. After 1 min the trial ended, and E left the room with the dog.

Dogs were presented with five conditions. In four help conditions (marked by an "h") E needed help to open the target door because the key was in the target room. The design of the h-SUPPORT (fixed) condition was the basis for the procedure of the other three help conditions. In each of these three help conditions, E added various ostensive cues to make her goal as obvious as possible. In the fifth condition (FOOD) we tested whether the dog was motivated and still able to open the door. These were the five conditions:

h-SUPPORT (fixed): The key was inside the target room. E stood in front of the target door. She tried to enter the target room in order to get the key. Therefore she performed three actions: (1) *looking* – staring into the target room through the target door, (2) *movements* towards the target door – pushing and shaking the target door and (3) *reaching* for the key above the target door). These three actions were carried out in a predetermined order: 10 s looking/10 s movements/10 s looking/10 s reaching/10 s looking/10 s movements.

h-GAZE: The procedure was the same as in condition h-SUPPORT (fixed) with the addition of E alternating her gaze once between the dog and the key in the target room during the phases *looking* and *reaching*.

h-TALK: The procedure was the same as in condition h-GAZE with the addition of E talking to the dog with a high pitched voice while she looked to the key inside the target room. She used the following sentences: "Oh, where is my key?/There is my key!/How can I get it?/I want my key!/How did it get there?/Usually this door is not closed." The order of these sentences was always the same. Dogs were never addressed by their name.

COMMAND: The procedure was the same as in condition h-GAZE with the addition of E saying "Open!" in a commanding tone, while she alternated her gaze, moving towards the target door and reaching for the key. Note that this command was not used during training. We used it here to test whether dogs would open the door because they heard any command.

FOOD: One piece of food was inside the target room. E took the booklet and sat on the low windowsill opposite from the target door. She then read the booklet during the remainder of the trial.

Each dog received four trials per condition. These 20 trials were presented in four sessions. Each session included five trials, one of each condition, that were presented in randomized order. Dogs received one session per day. Thus, after the training on the first day, they received the four sessions from day two to day five. To keep the dogs motivated and focused, there was a break of at least 10 min between trials.

2.1.4. Scoring and data analysis

All data was coded from the video material by the same person (KS). Our main dependent variable was whether the dog pushed the button to open the target door within the 60 s of the trial. Additionally, we coded whether the dog entered the target room after s/he had opened the target door, i.e. whether she moved inside the target room with the whole body.

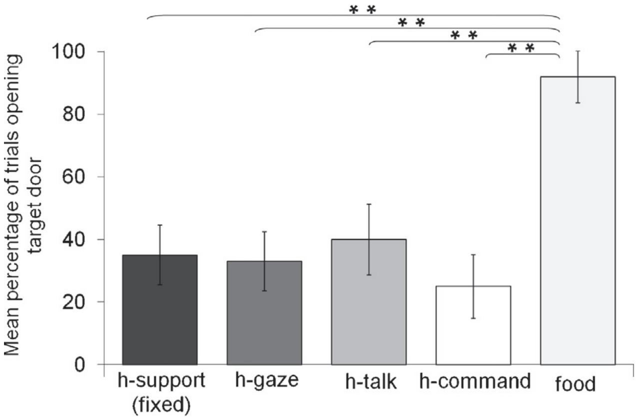

Fig. 2. Experiment 1: Mean percentage of trials in which the dogs opened the target door (mean ± SE) in the five different conditions (*$P \leq 0.05$; **$P \leq 0.01$).

We coded whether the dogs sat or lay down before s/he opened the target door (or before the trial was over in case s/he did not open the door). Sit/lie was defined as any posture in which the dog's hindquarters touched the ground, including scratching behaviour. This variable allowed us to check whether dogs' body posture differed between conditions.

Finally we coded what E did just before the dog opened the door in all conditions (except the food condition). This was defined as the behaviour of E within the 2 s before the dog pressed the button. This measure included movements towards the target door, reaching for the key above the target door, gaze-alternation between dog and key, or no detectable behaviour.

Whether the dogs opened the target door and entered the target room was unambiguous. An independent observer who was not familiar with the purpose of the study coded 25% of all trials randomly selected. The level of agreement was excellent for "open target door" (*Kappa* = 1.00, $N = 60$), "enter target room" (*Kappa* = 1.00, $N = 39$) and "sit/lie down" (*Kappa* = 1.00, $N = 60$) and good for "E's behaviours before dogs pressed the button" (*Spearman correlation* $r_s = 0.82$, $N = 15$).

All statistical tests were two-tailed and the alpha level was set to 0.05. We used nonparametric statistics: Friedman test and Wilcoxon signed rank tests for comparison of the conditions.

2.2. Results

Fig. 2 shows the mean percentage of trials in which dogs opened the target door in the five conditions. There were significant differences between the conditions (Friedman test: $\chi^2 = 22.989$, $N = 12$, $P < 0.001$). The dogs opened the target door significantly more often in the FOOD condition compared to all help conditions (Wilcoxon: FOOD vs. h-SUPPORT (fixed): $T = 55.00$, $N = 10$, $P = 0.002$; FOOD vs. h-GAZE: $T = 55.00$, $N = 10$, $P = 0.002$; FOOD vs. h-TALK: $T = 52.00$, $N = 10$, $P = 0.010$; FOOD vs. COMMAND: $T = 55.00$, $N = 10$, $P = 0.002$). All dogs except one opened the target door in the FOOD condition in every session. There were, however, no significant differences between the

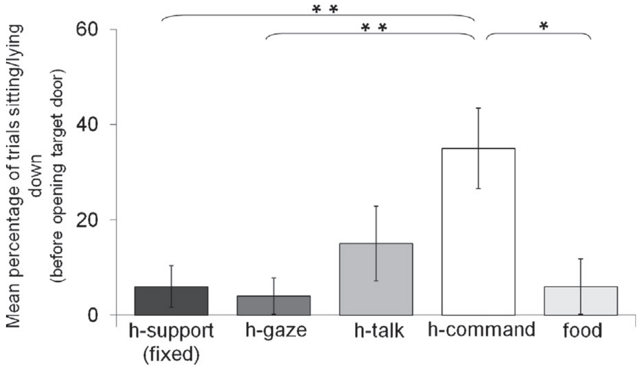

Fig. 3. Experiment 1: Mean percentage of trials (mean ± SE) the dogs sat/lay down before they opened the target door ($^*P \leq 0.05$; $^{**}P \leq 0.01$).

help conditions. Moreover, the number of trials in which dogs opened the target door did not change over sessions, indicating that there was no learning or decrease in motivation to open the door (Sessions 1 and 2 vs. Sessions 3 and 4, Wilcoxon tests, non-significant for all five conditions: h-SUPPORT (fixed): $T = 20.00$, $N = 8$, $P = 1.000$; h-GAZE: $T = 10.00$, $N = 5$, $P = 0.750$; h-TALK: $T = 9.00$, $N = 5$, $P = 1.000$; COMMAND: $T = 6.50$, $N = 4$, $P = 0.750$; FOOD: $T = 0$, $N = 0$, $P = 1.000$).

Dogs entered the target room in 86% of the trials after they had opened the door, but there were no significant differences across conditions (Friedman test: $\chi^2 = 8.571$, $N = 4$, $P = 0.053$). Fig. 3 shows that there were significant differences between the conditions in the mean percentage of trials in which dogs sat/lay down (Friedman test: $\chi^2 = 19.927$, $N = 12$, $P < 0.001$). The dogs sat/lay down in significantly more trials when E gave a command than in the other conditions (Wilcoxon: COMMAND vs. FOOD: $T = 42.50$, $N = 9$, $P = 0.020$; COMMAND vs. h-SUPPORT (fixed): $T = 36.00$, $N = 8$, $P = 0.008$; COMMAND vs. h-GAZE: $T = 36.00$, $N = 8$, $P = 0.008$) except for the h-TALK condition (Wilcoxon: COMMAND vs. h-TALK: $T = 25.50$, $N = 7$, $P = 0.078$). None of the other comparisons were significantly different.

In trials in which dogs opened the door they did so after E had reached for the key in more than 20% of the trials in the helping conditions. In the COMMAND condition dogs pressed the button mainly after movements towards the door (25%) and gaze alternation (35%, see supplementary material).

2.3. Discussion

Dogs opened the target door when there was food in the room but they rarely did so for the human regardless of how she communicated her intention. The question this raises is why dogs did not help the human. Next we discuss several possibilities.

We can rule out that their lack of helping behaviour was due to their inability to open the door because they opened it nearly in every trial when they could obtain food for themselves. This is similar to the findings of Kaminski et al. (2011) in which dogs reliably indicated the place of an object in which they themselves were interested.

One possibility is that dogs just opened the door for the food because they had learned that in the training session. They did not do so in the other conditions because the situation differed from the training session. However, the training session also differed from the FOOD condition and, more importantly, dogs did open the door in the other conditions in about 30% of the trials.

If we consider that dogs did more than simply repeating what they had learned there are two possibilities. Either dogs failed to grasp what the experimenter wanted or they simply were not motivated to help. Although the latter explanation could account for the results of two of the helping conditions, it cannot explain their failure in the command condition. In that condition, dogs received a command to perform an action, which is a familiar situation for dogs and one to which they have learned to respond by complying. In the current experiment, dogs were requested to push the button and to open the target door, but dogs did not do so. Interestingly, we found that dogs sat/lay down more often in the COMMAND condition compared to the other conditions (except condition h-TALK). Scheider et al. (2011) also found that when pointing gestures were paired with an imperative command-like tone of voice without a meaningful context (e.g., there was nothing to retrieve or inspect), dogs sat or lay down in the direction of the pointing gesture. Scheider et al. (2011) interpreted this as evidence that the imperative tone of voice triggered obedient and even submissive behaviour, as can be seen in the findings of the current study. It is also possible that dogs sat/lay down simply because they were confused or frustrated because they did not know how to react.

Thus, dogs may have been willing in principle to comply but they had not previously learned how, to comply to the command “open!” and could not infer from the human’s behaviour what they were supposed to do. It is conceivable that dogs failed to open the door not because they were unmotivated to comply (at least in the command condition) but because they failed to grasp the human’s goal. In the next two experiments we investigated these motivation and goal attribution hypotheses further. In experiment 2 we presented another set of ostensive cues designed to make the human’s goals more transparent, in order to see whether dogs would help more when they received this further assistance. In experiment 3 we attempted to boost the motivation to help by enrolling the owners in the test, hoping that dogs would be more willing to help their owners than strangers.

3. Experiment 2: The pointing gesture

In this experiment the dogs received additional information to make the goal of the human more obvious. Therefore we used a pointing gesture (pointing towards the button) in order to show the dogs what they had to do. Studies have shown that dogs spontaneously respond to variations of human pointing gestures in multiple types of situations (Hare and Tomasello, 1999; Miklosi et al., 2005; Scheider et al., 2011; Soproni et al., 2001). In addition to the pointing condition, we introduced a baseline condition, in which the human was not interested in the content of the target room. This was to rule out that the dogs opened the target door just because they had learned to open it when the human was present – irrespective of the human's need for help.

3.1. Methods

3.1.1. Subjects

Twelve dogs (*Canis familiaris;* 6 females and 6 males) of various breeds and ages (range = 1–9 years old, mean age = 3.75 years) participated in this second experiment (see Table 1). These dogs had not participated in experiment 1. The preconditions to participate in the experiment were the same as in experiment 1. From 13 invited dogs all except one passed the training and participated in the test.

3.1.2. Materials and procedure

Materials were the same as in experiment 1. The same was true for the training, warm-up and the test procedure, – except that the conditions were different. The experimental design was the same as in experiment 1: each dog received four trials per condition, presented in four sessions.

The four conditions differed from each other in the contents of the target room and in E's interest in the content. There were two helping conditions marked by the letter "h":

h-SUPPORT (fixed): This was similar to the condition h-SUPPORT (fixed) in experiment 1. The key was inside the target room and E tried to enter the target room using the three actions: *looking, movements* and *reaching*. The only difference to experiment 1 was the order and the latency of the actions (20 s looking/10 s movements/20 s looking/10 s reaching).

h-POINT: The procedure was the same as in condition h-SUPPORT (fixed). In addition, E pointed to the button twice during the action *looking*. The pointing gesture was accompanied by gaze alternation. While E looked at the dog, her arm was in front of her body, but when she looked at the button her arm and the forefinger was outstretched and pointed towards the button.

NO INTEREST: The key was inside the target room. E took the booklet and sat on the low windowsill opposite from the target door. She then read the booklet during the remainder of the trial. If the dog opened the target door, the E did not react at all and continued reading.

FOOD: The procedure was exactly the same as in FOOD condition in experiment 1. Food was inside the target room and E sat at the low windowsill and read the booklet during the remainder of the trial.

3.1.3. Scoring and data analysis

We coded again the variables "open target door", "enter target room" and "E's behaviours before dogs pressed the button" using the same basic definition as in experiment 1. "E's behaviours before dogs pressed the button" this time also included pointing. We did not code the variable 'dog sat/lay down' because dogs sat/lay down only in very few trials. Again an independent observer coded 25% of the original video material for reliability purposes. The levels of agreement for "open target door" (*Kappa* = 1.00, $N = 48$, $P < 0.001$), "enter target room" (*Kappa* = 1.00, $N = 33$, $P < 0.001$) and "E's behaviours before dogs pressed the button" (*Spearman Correlation* $r_s = 0.90$, $N = 24$) were perfect. We used the same statistical tests as in experiment 1.

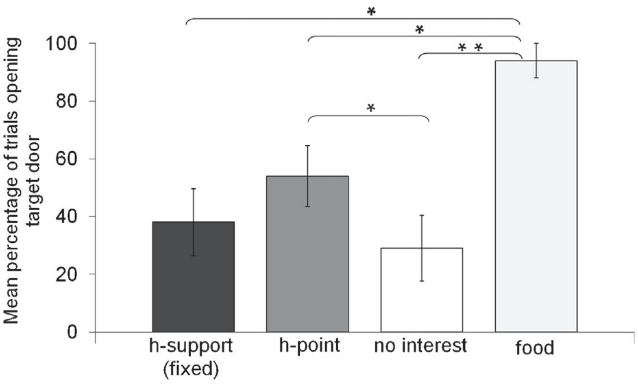

Fig. 4. Experiment 2: Mean percentage of trials in which the dogs opened the target door (mean ± SE) in the four different conditions ($^*P \leq 0.05$; $^{**}P \leq 0.01$).

3.2. Results

Fig. 4 shows the mean percentage of trials in which dogs opened the target door in the four conditions. There were significant differences between the conditions (Friedman test: $\chi^2 = 17.633$, $N = 12$, $P < 0.001$). The dogs opened the target door significantly more often in the FOOD condition compared to all other conditions (Wilcoxon: FOOD vs. h-SUPPORT (fixed): $T = 51.00$, $N = 10$, $P = 0.014$; FOOD vs. h-POINT: $T = 48.50$, $N = 10$, $P = 0.027$; FOOD vs. NO INTEREST: $T = 45.00$, $N = 9$, $P = 0.004$). Moreover, the dogs opened the target door significantly more often in the h-POINT condition compared to the NO INTEREST condition (Wilcoxon: $T = 41.50$, $N = 9$, $P = 0.027$). However, there was no significant difference between the baseline NO INTEREST condition and the other help-condition, h-SUPPORT (fixed). As in experiment 1 there was no increase or decrease in the number of trials in which dogs opened the door over sessions (Sessions 1 and 2 vs. Sessions 3 and 4, Wilcoxon tests, non-significant for all four conditions: h-SUPPORT (fixed): $T = 7.50$, $N = 4$, $P = 0.625$; h-POINT: $T = 18.00$, $N = 8$, $P = 1.000$; NO INTEREST: $T = 5.00$, $N = 4$, $P = 1.000$; FOOD: $T = 1.00$, $N = 1$, $P = 1.000$). After dogs had opened the target door, dogs entered the target room in 81% of all trials, but there was no difference between conditions (Friedman test: $\chi^2 = 6.614$, $N = 5$, $P = 0.086$).

In the h-SUPPORT condition dogs opened the door mainly after E had reached for the key and moved towards the door. In contrast in the h-POINT condition dogs pressed the button after E had pointed to the button in 46% of the cases (see supplementary material).

3.3. Discussion

Dogs helped the human to open the door if the human displayed her goal very clearly by using a pointing gesture directed towards the button. In that condition, dogs opened the door more often than when the human was uninterested in the content of the target room (but less than for themselves). Moreover, when dogs pressed the button they often did it immediately after E had pointed to the button. Therefore, the failure to help in experiment 1 could be attributed, at least partly, to the type of cue given by the experimenter. One key question, however, is how dogs understand the pointing gesture, as informative or imperative.

Szetei et al. (2003) tested dogs in an object-choice task, in which the human experimenter pointed towards the incorrect location, the one without food. Even when dogs had witnessed the baiting process and therefore knew where the food was hidden, they followed the pointing cue and went to the empty cup. Szetei et al. (2003) concluded that the dogs understood the pointing gesture as an imperative cue (i.e., a command) rather than an informative cue (see also Petter et al., 2009). However, Scheider et al. (2013) found different results with a similar set-up. In their study, when dogs had witnessed the baiting process, they chose the baited cup, even when the human pointed to the empty cup. Scheider et al. (2013) concluded that dogs are able to understand the human pointing as an informative gesture. One possible reason for this difference between the two studies is that Scheider et al. (2013) presented the pointing gesture accompanied by gaze alternation. Scheider et al. (2013) argued that it is conceivable that dogs might have needed gaze alternation to construe pointing as an information cue about the location of the hidden food.

In the current study, the dogs had learned during the training how to open the target door. To make the dogs approach the button during training, E also sometimes pointed to the button. This could have influenced the dogs' behaviour in the test (although, note that other cues used in the training – such as high pitched voice – did not lead to increased opening of the door in the test). Dogs may then have interpreted the human-given pointing cue as an imperative gesture ("Go there!"). But it is also possible that dogs perceived the pointing gesture as information ("Help me by pushing the button.") rather than as a command. Two facts seem to support this assumption. First, the pointing gesture was accompanied by gaze alternation, as it had been Scheider's et al. (2013) study, which might have been crucial for the dogs' recognition of the gesture as informative. Second, there was no decrease of performance in the pointing condition. If dogs perceived the gesture as imperative, they should have opened the target door less often over trials, as they did not receive any reward for their action. Indeed, Elgier et al. (2009) found that dogs stopped following the pointing cue in an object choice task when their choice was unrewarded because the human pointed to the wrong container.

The results of experiment 1 and 2 suggest that the motivation to help the human exists in dogs, but they need a strong cue such as a pointing gesture to understand what to do. However, it is also possible that dogs' helping behaviour depends on the individual person they are going to help. In the study by Kaminski et al. (2011), dogs indicated the location of a non-desired object more frequently to the owner than to a stranger. Thus, it is conceivable that dogs are more likely to open the door for the owner than for a stranger. Dogs may prefer to help the owner for two reasons: first, because they are more motivated to help her as they have a close relationship, and second because it is easier for dogs to understand the owners' goal because they have had more experience interpreting and responding to her particular behaviours. To investigate whether the identity of the human would influence the helping behaviour of the dogs, we conducted a third experiment.

4. Experiment 3: Owner versus stranger

In this experiment, we investigated two aspects that could influence dogs' helping behaviour. First, we wanted to know whether the identity of the human would change the dogs' performance. Therefore we tested the same dogs with the owner and with the stranger, hypothesizing that dogs would prefer to help the owner as was found in Kaminski et al's (2011) study. Second, we wanted to know whether the natural behaviour of the experimenter – in contrast to the predetermined order of actions in experiment 1 and 2 – would improve the performance of the dogs. Therefore the human was allowed to perform the actions to express her goal however she wanted, including calling the dog by his/her name.

4.1. Methods

4.1.1. Subjects

Twelve dogs (*Canis familiaris;* 6 females and 6 males) of various breeds and ages (range = 1–5 years old, mean age = 2.75 years) participated in the third experiment (see Table 1). Only dogs naïve to the test and not involved in one of the other two experiments were tested. The preconditions to participate were the same as in the previous experiments. 18 dogs were invited but six dogs did not pass the training and were excluded from the study. In contrast to the previous experiments owners were present during some conditions (see below).

4.1.2. Materials and procedure

Materials were similar to the previous experiments. The same was true for the training procedure, warm-up, and the test. The only difference was that dogs were trained by a third person, so that dogs had not experienced the apparatus associated with the person that later tested them, neither with the stranger, nor with the owner. Dogs received three different conditions:

h-SUPPORT (natural): The key was inside the target room and the human (E or the owner) tried to enter the target room. In contrast to the h-SUPPORT (fixed) conditions of the previous experiments there was no predetermined order of actions. The human was allowed to do anything to make her goal as obvious as possible such as reach for and point to the key, push the target door, bend down to the dog etc. She could talk to the dogs but only using the following sentences: "Open the door! Have a look! I want my key! Where is my key? How do I get there?" and the name of the dog. However, the human was *not* allowed to use different phrases (such as a fetch command) and to point to the button.

NO INTEREST: The procedure was the same as in the NO INTEREST condition of experiment 2: The key was inside the target room and the human read the booklet during the trial.

FOOD: The procedure was the same as in the FOOD condition of experiment 1 and 2.

For the h-SUPPORT (natural) condition the owners were told to show their dog that they wanted to get into the target room in order to get the key. They were instructed to follow certain rules while they showed their intention (for example not pointing to the button, see above). The third person, who also trained the dogs, could watch the owner during each trial on a monitor. In the three cases in which owners did not follow the instructions (i.e. praising the dog for opening the door, not retrieving the key after the dog opened the door, using a command that was not allowed), the trial was repeated.

Again each dog was tested in four trials per condition. These 12 trials were presented in four sessions. These sessions included three trials, one of each condition, that were presented in randomized order. In two sessions, the owner was the experimenter, and in two sessions the stranger (KS) was the experimenter. During each day of testing, dogs were presented with two sessions, one with the owner, and one with the stranger. Six dogs started with the owner-session and the other six dogs with the stranger-session. Thus, after the training on the first day, dogs received two sessions on the second day and two sessions on the third day.

4.1.3. Scoring and data analysis

We coded again the variables “open target door”, “enter target room” and “E’s behaviours before dogs pressed the button” using the same definition as in the previous experiment. Again an independent observer coded 25% of the original video material randomly selected for reliability purposes. The levels of agreement for “open target door” (*Kappa* = 1.00, $N = 36$, $P < 0.001$), “enter target room” (*Kappa* = 1.00, $N = 32$, $P < 0.001$) and “E‘s behaviours before dogs pressed the button” (*Spearman Correlation* $r_s = 0.93$, $N = 12$) were perfect. We used the same statistical tests as in experiment 1 and 2.

4.2. Results

Fig. 5 shows the mean percentage of trials in which dogs opened the target door in the three conditions for the two experimenters. There were no significant differences between the owner and the stranger as experimenter (Wilcoxon: h-SUPPORT (natural): Owner vs. Stranger: $T = 6.00$, $N = 3$, $P = 0.250$; NO INTEREST: Owner vs. Stranger: $T = 22.50$, $N = 9$, $P = 1.000$; FOOD: Owner vs. Stranger: $T = 1.50$, $N = 2$, $P = 1.000$). For that reason the data for owner and stranger were then combined. There were significant differences between the conditions in the number of trials in which dogs opened the target door (Friedman test: $\chi^2 = 12.054$, $N = 12$, $P = 0.002$).

Dogs opened the target door significantly more often in condition FOOD and h-SUPPORT (natural) compared to the NO INTEREST condition (Wilcoxon signed rank test: FOOD vs. NO INTEREST: $T = 36.00$, $N = 8$, $P = 0.008$; h-SUPPORT (natural) vs. NO INTEREST: $T = 62.50$, $N = 11$, $P = 0.007$). There were, however, no significant differences between the help condition, h-SUPPORT (natural) and the FOOD condition. (Wilcoxon: $T = 13.00$, $N = 6$, $P = 0.625$). As in the previous experiments there was no increase or decrease in the number of trials in which dogs opened the door over sessions (Sessions 1 and 2 vs. Sessions 3 and 4, Wilcoxon tests, non-significant for all three conditions: h-SUPPORT (natural): $T = 3.00$, $N = 2$, $P = 0.500$; NO INTEREST: $T = 27.00$, $N = 8$, $P = 0.289$; FOOD: $T = 4.50$, $N = 3$, $P = 0.750$).

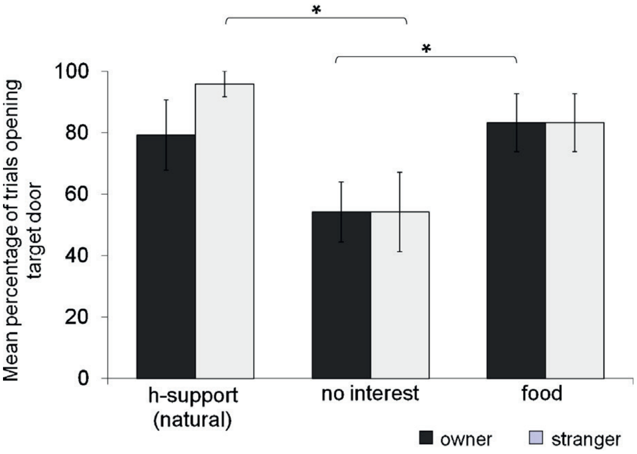

Fig. 5. Experiment 3: Owner versus stranger. Mean percentage of trials (mean ± SE) in which the dogs opened the target door in the three conditions for the two experimenters (*$P \leq 0.05$; **$P \leq 0.01$).

When dogs had opened the target door, they entered in 86% of the trials. There were significant differences across conditions (Friedman test: $\chi^2 = 7.724$, $N = 11$, $P = 0.016$). Dogs entered the target room significantly more often in the FOOD condition compared to the h-SUPPORT (natural) condition (Wilcoxon: $T = 33.50$, $N = 8$, $P = 0.039$).

When dogs opened the door in the h-SUPPORT condition they pressed the button mainly after the human had reached for the key (43%) or pointed at the key (32%, see supplementary material).

4.3. Discussion

The results of experiment 3 support the hypothesis that dogs will help humans when their goal is made more apparent. Dogs opened the target door for the human when the human tried to get into the target room. Interestingly, dogs opened the door for the human as often as for themselves. This suggests that dogs were highly motivated to help the human because they did so without receiving any reward or praise for their behaviour in the help condition.

Dogs differentiated between the situation in which the human needed help and the situation in which she was not interested in opening the target door. This is similar to findings with children and chimpanzees who performed the target behaviour more often in conditions in which the human really needed help (Warneken et al., 2007; Warneken and Tomasello, 2006, 2007). In contrast to the children and chimpanzees, dogs did not distinguish between the object the owner needed for a certain activity and a non-target object that was irrelevant for the owner (Kaminski et al., 2011). This result contrasts with what we found in the current study. Perhaps this difference between studies is due to the different set-up. When the human tries to open a door and reaches for an object, this may be more obvious for the dogs than when she is searching for an object that she has used before.

There is an alternative explanation for why dogs in the current experiment opened the door preferentially when the human required help. Instead of gauging the goal of the human, dogs may have been much more aroused when the human communicated her goal than when she was not interested and read the booklet. Because dogs were aroused by the behaviour of the human, they did what they had learned in the training–they pressed the button. This would be similar to the low-level interpretation of chimpanzees' helping behaviour in the study of Melis et al. (2011), that they do not recognize the intentions of the conspecific but 'do something' until the signalling stops. However, we think that this explanation is unlikely because dogs did not press the button in all the other helping conditions in the earlier experiments in which the human was also very active. Moreover, in experiment 3, dogs helped to open the door even though they had no previous experience with the experimenter (owner/stranger) and the apparatus, having been trained by a third person. Thus, it seems to be more likely that dogs perceived the human's goal instead of just being aroused.

In this alternative explanation based on arousal, one would expect that dogs are more aroused when the owner – instead of a stranger – shows activity. But interestingly, dogs did not differentiate between the owner and the stranger being the experimenter. In contrast to other studies (Kaminski et al., 2011) dogs did not help the owner more than a stranger. This is surprising because dogs have a close relationship with their owner (Gacsi et al., 2001). It is possible that their motivation to help is not dependent upon the identity of the recipient, as the same is true for human children (Warneken and Tomasello, 2006, 2007) and apes (Warneken et al., 2007).

5. General discussion

Dogs, in the current study, helped a human to open a door to a target room if the human explicitly communicated her goal to the dog. The results suggest that dogs are willing to help if they recognize the human's goal. They opened the door for the human as often as for themselves and they continued to do so over trials even without being rewarded.

One could argue that dogs opened the door during the experiments because they had learned it in the training and were intermittently rewarded in the food condition. In other words, training might have formed the expectation that pushing the target button will result in a food reward also during the test. But there are four reasons that make this possibility unlikely. First, in each of the three experiments dogs received the food condition–and were therefore intermittently rewarded–but they did not open the door often in the help conditions of experiment 1 and 2. Second, we found no change in the door-opening frequency within experiments. Third, although in experiment 3 there was no difference between the help condition and the food condition, dogs entered the target room less in the help condition than in the food condition indicating that they did not expect a reward. Fourth, one could argue that dogs opened the door more often in the help condition of experiment 3, because the interval between a rewarded food condition and the other conditions was shorter because there were fewer conditions than in the other experiments. However, the pattern of frequent opening in the help condition of experiment 3 but not in the other experiments appeared already in the first session in which all dogs were once rewarded in the food condition (see supplementary material). Overall, this indicates that dogs indeed helped without getting a reward and not because they were trained to do so.

The study raises the question of what aspects of the human's behaviour make her goal perceivable for the dog. Actions towards the closed target door were not sufficient to elicit helping. Ostensive cues, such as gaze alternation between the dog and target room and talking to the dog in a high pitched voice, also did not lead to helping. Dogs only helped in two situations: (1), when the human pointed at the button – then they might have perceived the pointing gesture as information about what to do and (2), when the humans communicated naturally to the dogs, i.e. without a predetermined sequence of actions. Note that in the latter case the human basically showed the same actions as in the other helping conditions such as looking into the target room, pushing the target door, pointing to and reaching for the target object, and talking to the dog. The only different behaviour the human showed was to bend over towards the dog and to call the dog by name. However, when we examined what behaviours of the human triggered the dogs to push the button, then the pattern was quite similar in all three experiments. Dogs opened the door mainly after the human reached for the target, moved towards the door, and pointed at the button or at the target.

Thus, it is quite likely that dogs helped more in the third experiment because the human was allowed to react to the behaviour of the dog and adjust her actions accordingly. If it is really the case that this natural behaviour helped the dogs to recognize the human's goal, this has to be considered when conducting further studies about the social cognitive skills of dogs. Predetermined sequences of behaviours are used to ensure that the conditions remain comparable, but if the human is behaving too inflexibly, this might prevent dogs from exhibiting the full potential of their cognitive skills. Alternatively, it may be that the dog is simply not attributing any goals but is instead being instrumentally guided towards the human's goal.

Nonetheless, the results of the current study show that dogs only help if the human is communicating with them in a certain way. Some authors have raised the question of whether such helping, if it is to be considered pro-socially motivated, should occur in the absence of signals for help (Burkart et al., 2007; Melis et al., 2011). This may be a criterion that excludes most nonhuman animals since it appears that communicative signals are the main source by which individuals perceive that the recipient needs help. Our closest living relatives are also more likely to help a human when she communicates her goal through signals. Chimpanzees helped more when the human called the subject by name, reached for the object, or alternated her gaze between the chimpanzee and the object, than when she showed neutral behaviour (Warneken et al., 2007; Warneken and Tomasello, 2006). The same was found in helping situations between chimpanzees. If the conspecific made the goal obvious and requested help by clapping hands or banging against the cage, chimpanzees helped more often (Melis et al., 2011; Yamamoto et al., 2009).

Human children, chimpanzees and also dogs help when the goal of the recipient is obvious. The difference in the helping behaviour of the species might lie in how the goal is recognized and in subjects' level of motivation. Human children understand the intention of the recipient even if s/he is only focusing on the object s/he needs; i.e. reaching for a marker that dropped on the floor (Warneken et al., 2007; Warneken and Tomasello, 2006, 2007). Chimpanzees help frequently when the recipient not only focuses on the object but also calls the attention of the chimpanzee (Melis et al., 2011; Warneken et al., 2007; Yamamoto et al., 2009). For dogs the human goal is only obvious when the humans communicate naturally to the dogs, using ostensive cues and pointing. Regarding the motivation to help, dogs behave more like children than like chimpanzees. They seem to be highly motivated, because they continue to help over trials even without being rewarded (see also Kaminski et al., 2011). Chimpanzees seem to be less motivated to help, as in some tasks they do not help at all (Warneken and Tomasello, 2006) and in other tasks – such as showing where a tool is hidden, some species stop indicating when the tool is no longer relevant for them (Bullinger et al., 2011; Zimmermann et al., 2009).

In conclusion, dogs were highly motivated to help a human, when the human's goal was apparent by means of a communicative signal. Dogs' difficulty in such situations seems to be in perceiving the human's goal and knowing how to intervene, rather than in their willingness to help. The most effective way for a human to obtain help is to communicate with the dog in a natural way. However, this raises the possibility that dogs were instrumentally guided to the goal rather than they determined by themselves what the human wanted. Additionally, the crucial role that human signals played in dogs' responses may lead some authors to prefer terms like compliance or obedience rather than helping. However, we argue that restricting the notion of helping only to those cases without a communicative exchange is too restrictive. Therefore, we prefer to use helping in a broader sense but making a clear distinction between help preceded by a communicative request from help not preceded by it. Further studies should investigate whether dogs would help in other tasks and what aspect of communication makes the human goal obvious. Finally it would be important to investigate whether dogs with special training (such as service dogs) are especially skilful in perceiving the human's goal or whether they are simply more easily guided to the goal.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.applanim.2013.07.009.

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ORIGINAL PAPER

Domestic dogs (*Canis familiaris*) coordinate their actions in a problem-solving task

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Abstract Cooperative hunting is a cognitively challenging activity since individuals have to coordinate movements with a partner and at the same time react to the prey. Domestic dogs evolved from wolves, who engage in cooperative hunting regularly, but it is not clear whether dogs have kept their cooperative hunting skills. We presented pairs of dogs with a reward behind a fence with two openings in it. A sliding door operated by the experimenter could block one opening but not both simultaneously. The dogs needed to coordinate their actions, so that each was in front of a different opening, if one of them was to cross through and get food. All 24 dog pairs solved the problem. In study 1, we demonstrated that dogs understood how the apparatus worked. In study 2, we found that, although the performance of the pairs did not depend on the divisibility of the reward, pairs were quicker at coordinating their actions when both anticipated rewards. However, the dogs did not monitor one another, suggesting that their solutions were achieved by each individual attempting to maximize for itself.

Keywords Dogs · Cooperation · Coordination · Social cognition

Introduction

Individuals in numerous species coordinate their actions toward common goals such as building shelters, acquiring food and mates, or protecting conspecifics and the territories that they inhabit (e.g., lions: Heinsohn and Packer 1995; siamangs: Geissmann and Orgeldinger 2000; chimpanzee: Mitani 2006; Magpie-larks: Magrath et al. 2007). Hunting for mobile prey is perhaps one of the most challenging activities from the point of view of coordination since not only do individuals have to coordinate their own movements but they also have to react to (and even anticipate) the prey's actions (e.g., chimpanzees: Boesch and Boesch-Achermann 2000; wolves: Mech and Boitani 2003; wild dogs: Creel and Creel 2002; lions: Stander 1992; hyenas: Mills 1990; dolphins: Gazda et al. 2005; groupers and moray eels: Bshary and Grutter 2006). For example, chimpanzees of the Tai forest hunting for monkeys coordinate their positions within the trees in order to surround their prey. While one chimpanzee actively pursues the monkey, other chimpanzees take positions in nearby locations that effectively reduce the monkey's escape routes (Boesch and Boesch-Achermann 2000). Since the success of a chimpanzee hunting alone in the Tai forest is low, it pays for chimpanzees to hunt together (Boesch 1994). Thus, the more chimpanzees hunt together, the better they organize themselves and the higher the rate of success (Boesch and Boesch-Achermann 2000).

One question that arises when animals coordinate their actions is whether they know their partners' roles and intentions or whether they independently but simultaneously direct similar actions toward the common goal (Melis and Semmann 2010). In particular, when chimpanzees perform different roles, do they realize that they are acting together to achieve a common goal, that is, to catch the monkey? It is conceivable that chimpanzees view their partners as social tools to reach their individual goals (Melis and Semmann 2010; Warneken and Tomasello 2006). It is even possible that group hunts may simply consist of the independent, yet simultaneous, actions of a

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number of individuals who have little understanding of the roles of others (Melis et al. 2006a, b; Tomasello and Call 1997). Thus, each individual could simply assess the state of the chase at a given moment and decide what it is best for it to do (Tomasello et al. 2005).

A number of recent experimental studies have addressed the question of what animals, and in particular primates, know about their partners' roles and goals in cooperative tasks. In most of these studies, pairs of subjects are confronted with a food retrieval task in which the food is placed on a platform that is out of reach of the subjects. To be able to get the food, subjects have to cooperate by simultaneously pulling a rope. Chimpanzees can coordinate their pulling efforts, but tolerance acts as an important constraint on their ability to solve this problem. Thus, pairs of chimpanzees that share food outside the test context cooperate much better than chimpanzees that do not share food (Melis et al. 2006a, b). Bonobos are more successful than chimpanzees at solving this problem, and Hare et al. (2007) have proposed that this is due to bonobos' higher tolerance levels compared with chimpanzees. Moreover, there is strong evidence that chimpanzees have some knowledge about the role of the partner in this cooperative task (Hirata and Fuwa 2007; Melis et al. 2006a, b). They recruit a partner only when solving the problem requires collaboration, and they recruit the best collaborator (Melis et al. 2006a, b). They even coordinate their actions when there is a conflict of interests between partners about which food tray they should take—one with equal payoffs and one with unequal payoffs (Melis et al. 2009).

Recent studies have begun to address the question of animal cooperation from an experimental perspective in non-primates as well. Seed et al. (2008) found that rooks are able to coordinate their actions to pull a string attached to a food platform. However, it was unclear that these rooks knew that they needed a partner to succeed because they did not wait for their partner before pulling and they did not select the appropriate apparatus depending on whether or not the partner was present. Drea and Carter (2009) also found that spotted hyenas coordinate their actions temporally and spatially in a pulling task. As in chimpanzees and rooks, the performance of the hyenas depended on the relationship between partners—it decreased with rank-related aggression. However, unlike rooks, but like chimpanzees, the hyenas attended to each other and experienced cooperators modified their behavior to accommodate naïve subjects (Drea and Carter 2009).

One conspicuous difference between studies on human and non-human animals is the virtual absence of communicative exchanges between non-human partners either before or during the task. Thus, chimpanzee dyads tested in a stag hunt game were able to coordinate their actions to obtain the option considered to be of higher value. But instead of communicating to decide what option to select, they used a leader–follower strategy in which one partner took the lead and the other followed (Bullinger et al. 2011). Warneken et al. (2006) also found that chimpanzees participated successfully in cooperative problem-solving activities with an adult human partner. However, when the human stopped participating, the apes did not attempt to reengage him. The authors concluded that the chimpanzees used a coordinated strategy in order to achieve their own goal but had not formed a shared goal with the human (Warneken et al. 2006). Taken together, these findings suggest that when chimpanzees cooperate with others, they take their partners' role into consideration, but they seem not to form shared goals with others.

Virtually, all experimental studies on animal cooperation have used a method in which the prey is non-reactive, and therefore, the need for communication may be greatly reduced. As a consequence, we investigated whether coordination and, more importantly, communication would appear within pairs of dogs in a task in which the prey was responsive to the behavior of the partners. We selected dogs, because they are social carnivores. A number of social carnivores are reported to hunt cooperatively (see above), especially dogs' closed living relatives, wolves (Coppinger and Coppinger 2001; Mech 1970; Mech and Boitani 2003). In addition, domestic dogs might have been selected for cooperating with the humans, although it is unclear how much of their cooperative behavior is trained (Miklosi 2007; Naderi et al. 2001; Ruusila and Pesonen 2004).

To investigate how dogs coordinated their actions toward a common goal, we presented pairs of dogs with an apparatus that simulated a hunting situation in which the prey defended itself from the dogs' advances. Food placed behind a fence could be accessed by two openings in the fence. A sliding door operated by the experimenter could block either opening, but not both simultaneously. As a result, the dogs needed to coordinate their actions in order to bypass the door, reach the other side of the fence through the openings and get the food. We investigated whether (1) dogs could coordinate their actions to solve this problem, (2) their problem-solving abilities depended on the divisibility of the reward, and (3) dogs shared the effort involved in solving the problem.

Experiment 1: "One defense move only"

In Experiment 1, we wanted to investigate whether dogs are able to coordinate their actions to solve the problem and whether they understood how the apparatus worked. To make the task for the dogs as manageable as possible, the sliding door was moved only once.

Methods

Subjects

Twenty-four dogs (13 males and 11 females) of various breeds and ages (range 1–12 year olds) participated in this study (see Table 1). All subjects had been living as pets with their owners and had received the normal obedience training typical for domestic dogs. Dogs were registered in our database, and the owners decided voluntarily to take part in the study. During the test, dog owners were not present and were informed about the design of the study only after their dogs were tested. The 24 dogs were tested in 12 predetermined pairs. The dogs in each pair were familiar with each other. They met each other at least once a week, although in most cases they lived in the same household.

The preconditions for participating in this study were that (1) dogs were comfortable without the owner, (2) both partners of a pair passed the pretest, (3) dogs were within the 1–12 year age range, and (4) no serious fight between the partners occurred during testing.

Materials

Figure 1a and b depicts the apparatus, consisting of a cage (300 cm × 620 m) with a sliding door and two fences. The walls of this cage were covered with material made of straw so that dogs were not distracted, and the experimenters could look through it in order to move the doors.

The cage was divided into two parts by a central fence with two openings that could be blocked by a sliding door. The dog entrance (60 cm × 77 cm) was located on one side of the cage and could be opened from outside the apparatus by the Experimenter 2. The central sliding door could be moved from outside the apparatus by Experimenter 1 with a bar so that one of the openings in the fence could be blocked (but not both simultaneously). An additional dividing fence, perpendicular to the sliding door, increased the distance the dogs needed to cover in order to go from one opening to the other. On the furthest side of the central fence (opposite the dog entrance) was either one container with food in the middle (Non-Shareable condition) or two containers, one left and one right (Shareable condition). Experimenter 1 could enter to bait the containers from this side of the cage. All fencing, including the sliding door and access doors, was made of mesh or Plexiglas and was therefore transparent. To define when a dog was approaching the opening, there was a marking line on the floor, parallel to the central fence, ca. 30 cm away from it. We used dog sausages and dry dog food as a reward.

Procedure

Dominance test This test had two aims. First, we wanted to know whether one individual within the pair would monopolize the food, and if so, which. Second, we wanted to exclude pairs with aggressive interactions in a food competition context. The dominance test took place before the experimental test sessions began. The two dogs stood opposite each other at a distance of 2 m. Each dog was held by the collar by Experimenter 1 and Experimenter 2. A piece of food was placed on the floor at a point equidistant to both dogs. The dogs were released simultaneously so that they could approach the food. We scored which animal got the food; in the event of an aggressive interaction, the pair was excluded from the study. We conducted this test eight times. The dog that got the food in over half of the trials was considered the dominant individual. There was always a dominant individual, and in most pairs, the dominance was very clear, in as much as the subordinate got nothing or just one piece of food.

Training and pretest Training was necessary as previous studies have shown that dogs have some problems solving detour tasks spontaneously, but they can easily learn to approach a reward behind a fence (Mersmann et al. 2011; Pongracz et al. 2003). Dogs were trained individually to acquaint them with the apparatus and the procedure. In the first step, dogs were allowed to explore the apparatus for 10 min. The Experimenter 1 moved the sliding door back and forth and put food into the container. In the second step, the dogs were trained to pay attention to the sliding door while approaching the reward. They were sent into an adjacent cage, outside the apparatus. As in the test, Experimenter 1 baited the food. Then, the dog's entrance was opened, so that the dog could enter the apparatus and approach the food. In contrast to the test, the door was not moved. This training trial was repeated, and which side of the middle fence was left open was varied. To pass the pretest, the dog had to approach the food directly through the unimpeded opening to four trials in a row, twice through the right side and twice through the left side. The dogs which passed the pretest in this study did so after a mean of 18 trials. Dogs that did not pass the pretest within 38 possible training trials were not included in the study.

Test At the beginning of each trial, both members of the dog pair waited outside the apparatus in an adjacent cage. From the dogs' point of view, they could see Experimenter 1 move the sliding door over to their right-hand side leaving the left section of the sliding fence open.

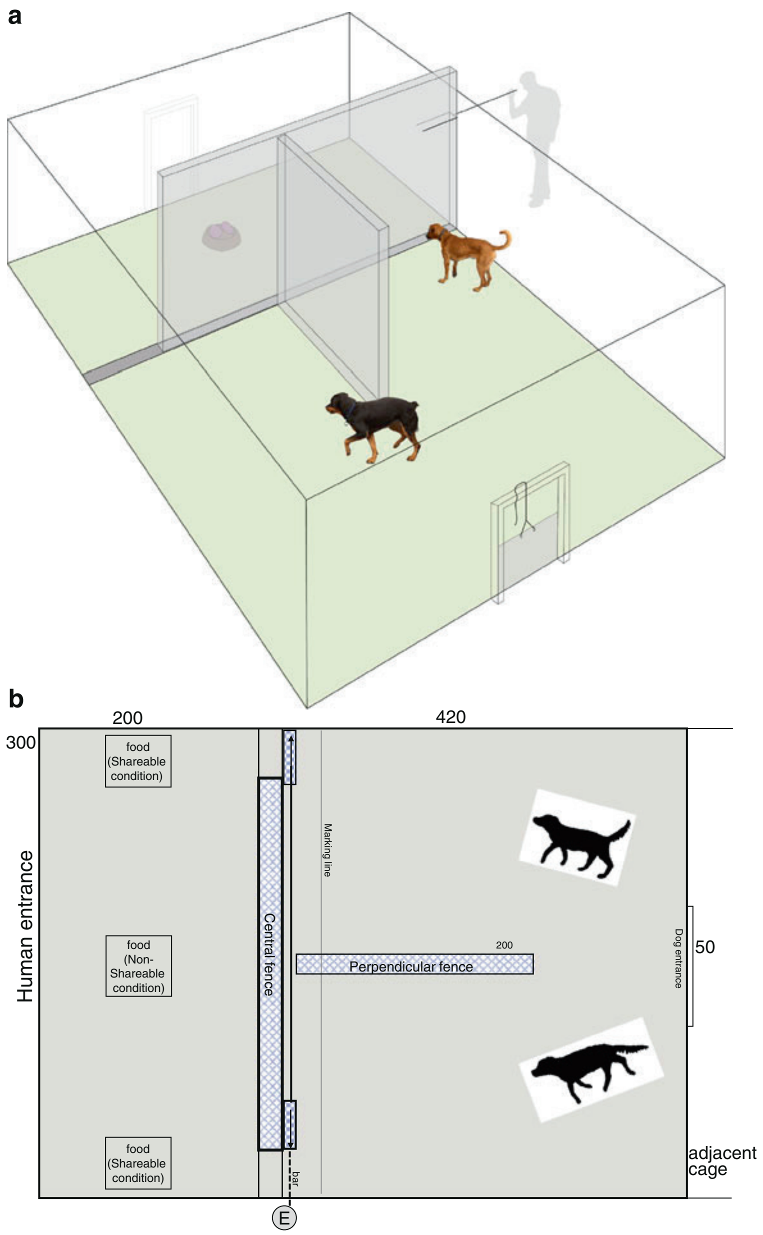
Then, Experimenter 1 entered the apparatus from the human entrance. She went to the unblocked opening, showed the two rewards to the dogs and then put them into

Table 1 Subjects included in Experiment 1 and 2

Dog	Breed	Gender	Age (years)	Participated in experiment
Wilbur	Labrador × Mongrel	M	1	One defense move only
Bruno	Labrador × Mongrel	M	1	One defense move only
Quincy	Deutscher Pinscher	M*	5	One defense move only
Pia	Deutscher Pinscher	F	5	One defense move only
Mogli	American Staffordshire × Terrier × Boxer	M*	6	One defense move only
Bolli	Mongrel	F*	5	One defense move only
Cheyenne	Malinois	F*	5	One defense move only
Fix	Malinois	M	1	One defense move only
Panda	Staffordshire Bull Terrier × Mongrel	M*	12	One defense move only
Kaya	Bardino	F*	9	One defense move only
Akira	Labrador × Mongrel	F*	10	One defense move only
Lucy	Border Collie × Mongrel	F	7	One defense move only
Emma	Golden Retriever	F	1	One defense move only
Lotti	Golden Retriever	F	1	One defense move only
Balou	German Shepherd	M*	3	One defense move only
Samson	German Shepherd	M	3	One defense move only
Paula	Mongrel	F*	4	One defense move only
Jethro	Berner Sennenhund	M	3	One defense move only
Alina	Gordon Setter × Mongrel	F*	12	One defense move only
Franzel	Zwergschnauzer	M	7	One defense move only
Laika M	Husky	F*	5	One defense move only
Elliot	Mongrel	M	2	One defense move only
Bajo	Dogo Canario	M*	2	One defense move only
Ali	Doberman × Mongrel	M*	7	One defense move only
Ace	Jack Russel Terrier	M*	5	Variable defense moves
Booker	Australian Shepherd	M*	1	Variable defense moves
Benji	Mongrel	M*	4	Variable defense moves
Aimee	Collie	F	1	Variable defense moves
Emily	Labrador	F*	7	Variable defense moves
Karah	Labrador	F*	7	Variable defense moves
Laika B	Labrador × Mongrel	F*	6	Variable defense moves
Gina	Mongrel	F	7	Variable defense moves
Maxl	Harzer Fuchs	M	2	Variable defense moves
Boscaille	Malinois	F	2	Variable defense moves
Theo	Jack Russel Terrier × Dackel	M	1	Variable defense moves
Frenz	Jack Russel Terrier × Dackel	M	1	Variable defense moves
Caja	Doberman × Mongrel	F	6	Variable defense moves
Gordo	Doberman × Mongrel	M	2	Variable defense moves
Karlo	Labrador	M*	6	Variable defense moves
Laana	Labrador	F*	7	Variable defense moves
Catie	Australian Shepherd	F	1	Variable defense moves
Susi	American Staffordshire Terrier × Mongrel	F	2	Variable defense moves
Judy	French Bulldog	F	1	Variable defense moves
Blue	French Bulldog	M	1	Variable defense moves
Karoo	Berger des Pyrenees	M	3	Variable defense moves
Lotte	German Shepherd	F*	2	Variable defense moves
Wuma	Beagle	F	3	Variable defense moves
Bubble	Beagle	F	1	Variable defense moves

* neutered

Fig. 1 Setup for Experiment 1 and 2. In the Non-Shareable condition, there was one food container in the middle (**a**, **b**). In the Shareable condition, there were two food containers that stood left and right behind the openings (**b**)



the container(s), depending on the condition. In the *Shareable condition*, Experimenter 1 put two pieces of food in a container behind the central fence on the left-hand side and two pieces in the container on the right-hand side. In the *Non-Shareable condition*, she put two pieces of food into just one container that stood behind the central fence in a central location.

Experimenter 1 went outside the cage to where she could handle the sliding door. Then, Experimenter 2 opened the dog entrance. As soon as one dog approached the opening, Experimenter 1 blocked it with the sliding fence while simultaneously leaving the other opening accessible. Experimenter 1 only ever operated the sliding fence once. Thus, when a dog approached the left open door, this door was shut. The dog had to run around the perpendicular fence to get to the right door that was open now. A dog approach was defined as crossing a line marked on the floor, that was parallel to and 50 cm away from the sliding fence, in front of the open door. The trial finished either when a dog passed through one of the openings and accessed the reward, or after 70 s had elapsed since the beginning of the trial. If the dogs did not solve the problem within 70 s, Experimenter 2 removed the rewards. After the end of the trials, both dogs were sent back through the dog entrance into the adjacent cage, and the next trial started.

Six of the dog pairs were tested in the Shareable condition, and six pairs were tested in the Non-Shareable condition. Each pair was tested for 60 trials, presented on 3 days so that they received 20 trials per day. After five consecutive trials, there was always a break of at least 10 min in which subjects could leave the testing area.

Data analysis

We scored four dependent variables: success, latency to succeed, food consumed and effort. The behaviors were defined and scored as follows:

Success the number of trials in which at least one dog managed to cross to the other side of the fence within 70 s.

Latency the number of seconds that elapsed from the moment that the dog entrance was opened until the first dog managed to cross the fence.

Eating the number of trials in which each subject ate food by putting the head into the container. For each dog pair, we calculated a food sharing index associated with this measure. This index was computed as the total number of pieces obtained by the partner who obtained the smallest number of pieces divided by the number of total pieces obtained by the other partner.

Effort the number of trials in which each subject elicited the moving and opening of the sliding door by crossing the marking line near the left opening side of the central fence. We also looked for communicative exchanges between dogs, but we detected no behaviors that could be evaluated.

A second independent observer who did not know the purpose of the study scored a randomly selected sample of trials (20 %). Reliability was excellent (Problem solving: Cohen's $\kappa = 1.00$; Latency: Spearman correlation $r_s = 0.96$, $N = 178$; Eating of the dominant pair member Cohen's $\kappa = 0.98$/of the subordinate pair member Cohen's $\kappa = 0.98$; Effort of the dominant pair member Cohen's $\kappa = 0.98$/of the subordinate pair member Cohen's $\kappa = 0.97$; $N = 180$ for all Cohen's κ).

For our statistical analyses, we used the Mann–Whitney *U* Test, Spearman correlation, Fisher's omnibus test (see Haccou and Meelis 1994) and Kendall τ coefficient of partial correlation (all two-tailed). With the latter, we correlated the behavior of one pair member with a measure of the pair's performance, while controlling for the behavior of the other pair member.

Results

Tables 2 and 3 summarize the results. The 12 dog pairs solved the problem in 95 % of the trials. There was no significant difference between conditions in the latency to solve the problem (Mann–Whitney $U = 13.0$, $n1 = 6$, $n2 = 6$, $P = 0.485$). However, it turned out that some pairs in the Shareable condition did not share the food. There was no significant difference between conditions in the sharing index (Mann–Whitney $U = 11.0$, $n1 = 6$, $n2 = 6$, $P = 0.261$). We therefore analyzed whether pairs that

Table 2 Performance of the 12 pairs in the Shareable condition in the "One defense move only" experiment

Pair: dominant–subordinate	No. of trials with problem solved	Mean latency until problem solved	Spearman correlation between latency and trial number	No. of food eaten by each subject	Sharing index (less food/more food)	No. of trials with effort for each subject
Emma–Lotti	58	6.88	$r = -0.405$, $P = 0.001$	52–56	0.93	54–6
Balou–Samson	60	10.15	$r = -0.003$, $P = 0.982$	60–56	0.93	46–17
Paula–Jethro	60	5.80	$r = 0.331$, $P = 0.010$	60–48	0.80	4–56
Alina–Franzel	57	27.74	$r = 0.005$, $P = 0.972$	44–40	0.91	30–30
Laika–Elliot	57	19.07	$r = 0.282$, $P = 0.029$	52–18	0.35	23–35
Bajo–Ali	60	5.69	$r = 0.232$, $P = 0.074$	45–60	0.75	10–51

Table 3 Performance of the 12 pairs in the Non-Shareable condition in the "One defense move only" experiment

Pair: dominant–subordinate	No. of trials with problem solved	Mean latency until problem solved	Spearman correlation between latency and trial number	No. of food eaten by each subject	Sharing index (less food/more food)	No. of trials with effort for each subject
Wilbur–Bruno	36	17.81	$r = -0.181$, $P = 0.166$	14–22	0.64	4–33
Quincy–Pia	59	19.95	$r = -0.349$, $P = 0.006$	30–29	0.97	30–29
Mogli–Bolli	60	8.51	$r = 0.326$, $P = 0.011$	42–18	0.43	46–18
Cheyenne–Fix	60	12.18	$r = 0.193$, $P = 0.139$	21–39	0.54	46–15
Panda–Kaya	60	9.87	$r = 0.102$, $P = 0.440$	39–21	0.54	28–35
Akira–Lucy	56	10.36	$r = 0.524$, $P < 0.001$	16–40	0.40	51–8

shared more often (defined by the sharing index) would solve the problem faster (defined by latency), but there was no such correlation (Spearman $r_s = 0.004$, $P = 0.991$, $N = 12$).

However, the problem was solved faster the more food was obtained by the subjects who got more food over all trials: the correlation between the number of trials on which these subjects got food and the latency to problem solution was negative and approached significance (Kendall's partial $\tau = -0.444$, $P = 0.053$, $N = 12$). In contrast, the corresponding correlation for the pair member who got less food over all trials was not significant (Kendall's partial $\tau = 0.081$, $P = 0.719$, $N = 12$).

We then looked at the correlations within individual pairs between latency to success and trial number; these are included in Tables 2 and 3. Note that here we included also the trials in which the problem was not solved, in which case we scored 70 s latency. We found three different patterns. Four pairs grew significantly slower at solving the problem (two in each condition) and two pairs grew faster at solving the problem (one in each condition). For the other pairs, we found no correlations, some of them being very fast in nearly all trials (for example, Bajo–Ali who solved the problem within 6 s on average) or showed irregular patterns (for example, Wilbur–Bruno). Fisher's omnibus test ($\chi^2 = 77.65$, $df = 24$, $P < 0.001$) showed that the distribution of these correlations differed from the null hypothesis that all correlations were zero.

We looked additionally at whether the problem was solved faster depending on the effort (approaching and waiting at one door so that the sliding door was moved and the other subject could get through the other door) of each member of the pair. We found that the latency to solve the problem depended on how much effort was invested by the individual that invested more effort in a pair. Thus, the problem was solved faster the more often this individual opened the door (number of trials with effort for the member with more effort versus latency: Kendall's partial $\tau = -0.670$, $P = 0.002$, $N = 12$). Only one pair shared the effort equally (Alina–Franzel), whereas in 7 pairs one partner opened the door in most of the trials.

Interestingly in the Non-Shareable condition, 11 out of 12 subjects sometimes opened the door for themselves when the partner did not approach the food immediately. In that case, these subjects went to the left open door so that it was shut and then went to the right door and grabbed the food before the partner approached. Thus, it was possible for them to solve the problem without a partner because the door only moved once.

Discussion

All pairs of dogs were able to solve the problem and get the reward in nearly all trials. The pairs showed different patterns independent of whether the food was shareable or not. Surprisingly, they did not solve the problem better (i.e., faster and more often) when they shared more food. However, as the door was moved only once it was possible to open the door without a partner. In some pairs, especially in the Non-Shareable condition, one subject stopped participating and did not enter the apparatus after a few trials in which she/he did not get the food. But then the other subject started to open the door for herself and solved the problem without the partner. Moreover, after a few trials, most dogs hesitated when it came to crossing the marking line in front of the open door. They approached the open door slowly and often stopped before the marking line and ran back to the—still closed—door. This suggests that they had learned that the sliding door would move. These two facts that dogs hesitated at the marking line in front of the open door and that they sometimes opened the door for themselves suggest that they knew how the apparatus worked. Whether subjects also understood the role of the partner (for example, that the partner could approach the reward earlier when the subject paid the effort) remains an open question.

Interestingly, the distribution of effort between the dogs in a pair was generally unequal. In most trials with a given pair, it was the same subject who approached the left door so that the sliding door was moved. However, it is impossible to draw the conclusion that pairs did not share the effort equally, because it was also possible for both partners to commit the same amount of effort (when both approached the left door) or for one dog to make the effort, but also take the whole reward, as she/he opened the door for her/himself.

Experiment 2: "Variable defense moves"

In Experiment 2, we changed the procedure so that the problem could not be solved without a partner.

Methods

Subjects

Twenty-four dogs (10 males and 14 females) of various breeds and ages (range 1–7 year olds) that were not tested in Experiment 1 participated in Experiment 2 (see Table 1). The preconditions for participating in this study were the same as in Experiment 1: subjects had been living as pets, owners were not present during the test, the dogs were tested in 12 pairs, and the pair members were familiar with each other.

Materials

We used the same apparatus as in Experiment 1 (See Fig. 1).

Dominance test, training and pretest

The procedure of the dominance test, training and pretest were the same as in Experiment 1.

Procedure

The basic procedure was the same as in Experiment 1.

There were two differences: First, at the beginning of the trial, the sliding door could either be on the left side so that the right side of the central fence was open or be on the right side so that the left side of the central fence was open. Second, by moving the sliding door back and forth, Experimenter 1 tried to prevent the dogs from crossing the central fence. As soon as one dog approached the opening by crossing the line on the floor (that was parallel and 50 cm away from the sliding fence), Experimenter 1 blocked it with the sliding fence, which simultaneously left the other opening accessible. When both dogs crossed the line simultaneously on both sides, the sliding door was moved once so that the door was closed in front of the dog that had approached the open side, which meant that the other dog could slip through the opening. Dogs could only solve the problem by coordinating with each other so that each approached the central fence on a particular side.

As in Experiment 1, the problem was solved when one dog managed to pass through the central fence. Experimenter 1 then stopped moving the sliding door so that the other dog could approach the reward. A trial was over once the dogs had solved the problem or after 70 s. Again, there were the same two conditions. Six of the pairs were tested in the Shareable condition, and six pairs were tested in the Non-Shareable condition, and all pairs received 60 trials.

Data analysis

As in Experiment 1, we scored Problem solving, Latency, and Eating and Effort, and we used the same definitions. In addition, we looked for communicative behavior of the dogs directed at each other, but we could not detect any behaviors for evaluation.

A second independent observer who did not know the purpose of the study scored a randomly selected sample of trials (20 %). Reliability was excellent (Problem solving: Cohen's $\kappa = 0.97$; Latency: Spearman correlation $r_s = 0.97$; Eating of the dominant pair member Cohen's $\kappa = 0.98$/of the subordinate pair member Cohen's $\kappa = 0.96$; Effort of the dominant pair member Cohen's $\kappa = 0.96$/of the subordinate pair member Cohen's $\kappa = 0.98$; $N = 180$ for all measures). We used the same statistical analyses as in Experiment 1.

Results

The 12 pairs solved the problem in 90 % of the trials within 70 s. Tables 4 and 5 summarize the results. There was no

Table 4 Performance of the 12 pairs in the shareable condition in the "Variable defense moves" experiment

Pair: dominant–subordinate	No. of trials with problem solved	Mean latency until problem solved	Spearman correlation between latency and trial number	No. of food eaten by each subject	Sharing index (less food/more food)	No. of trials with effort for each subject
Caja–Gordo	60	10.83	$r = 0.187$, $P = 0.152$	53–56	0.95	12–48
Karlo–Laana	53	7.75	$r = -0.530$, $P < 0.001$	52–48	0.92	2–51
Catie–Susi	49	18.88	$r = 0.106$, $P = 0.422$	5–45	0.11	43–6
Judy–Blue	58	14.50	$r = 0.376$, $P = 0.004$	30–53	0.57	53–5
Karoo–Lotte	60	5.87	$r = -0.106$, $P = 0.422$	60–58	0.97	0–60
Wuma–Bubble	59	6.46	$r = -0.410$, $P = 0.001$	59–58	0.98	1–58

Table 5 Performance of the 12 pairs in the Non-Shareable condition in the "Variable defense moves" experiment

Pair: dominant–subordinate	No. of trials with problem solved	Mean latency until problem solved	Spearman correlation between latency and trial number	No. of food eaten by each subject	Sharing index (less food/more food)	No. of trials with effort for each subject
Ace–Booker	54	13.30	$r = 0.290$, $P = 0.025$	47–7	0.15	7–47
Benji–Aimee	45	10.51	$r = 0.683$, $P < 0.001$	45–0	0.0	0–45
Emily–Karah	60	10.57	$r = -0.037$, $P = 0.781$	49–11	0.22	11–49
Laika–Gina	35	21.51	$r = 0.010$, $P = 0.941$	7–28	0.25	28–7
Maxl–Boscaille	60	12.63	$r = -0.216$, $P = 0.980$	47–13	0.28	13–47
Theo–Frenz	57	15.60	$r = 0.101$, $P = 0.443$	52–5	0.10	5–52

significant difference between conditions in the latency to solve the problem (Mann–Whitney $U = 11.0$, $n1 = 6$, $n2 = 6$, $P = 0.310$). As in Experiment 1, some pairs in the Shareable condition often failed to share. However, in contrast to Experiment 1, they shared significantly more often in the shareable compared with the Non-Shareable condition (sharing index: Mann–Whitney $U = 4.0$, $n1 = 6$, $n2 = 6$, $P = 0.026$). But surprisingly it was not the case that pairs that shared more solved the problem significantly faster (sharing index versus latency: Spearman $r_s = -0.55$, $P = 0.067$, $N = 12$).

In nearly all pairs, one partner usually invested the effort by approaching and waiting at one door so that the sliding door moved and the other subject could get through the open door (for two pairs even in 100 % of the trials). The latency to solve the problem depended on how much effort was invested by the individual that tended to invest more effort in a pair. The problem tended to be solved significantly faster the more often this individual opened the door (number of trials with effort for the member with more effort versus latency: Kendall's partial $\tau = -0.427$, $P = 0.053$, $N = 12$), but the corresponding correlation for the pair member who invested less effort over all trials was not significant (Kendall's partial $\tau = 0.209$, $P = 0.351$, $N = 12$).

Moreover, pairs solved the problem faster the more often one individual took on the responsibility for engaging more in effort (effort of one pair member divided by effort of both members versus latency: Spearman $r_s = 0.58$, $P = 0.049$, $N = 12$).

We then looked whether dominance had an effect on the performance of the subjects. Overall, dominant individuals did not get more food than subordinates (Wilcoxon $T = 45.5$, $N = 12$, $P = 0.224$, see Fig. 2). Although subordinate subjects got food in more trials in the Shareable condition than in the Non-Shareable condition (Mann–Whitney $U = 0.0$, $n1 = 6$, $n2 = 6$, $P = 0.002$), condition did not matter for the dominant individuals (Mann–Whitney $U = 11.5$, $n1 = 6$, $n2 = 6$, $P = 0.310$). Figure 3 shows that the problem was solved significantly faster the more trials the dominant subject got food (number of trials the dominant got food versus latency: Kendall's partial $\tau = -0.576$, $P = 0.007$, $N = 12$), but this was not true for the subordinate (number of trials the subordinate got food versus latency: Kendall's partial $\tau = -0.120$, $P = 0.610$, $N = 12$). In addition, subordinates invested significantly more effort than dominants (Wilcoxon $T = 64.0$, $N = 12$, $P = 0.050$, see Fig. 2).

Finally, we looked at the correlations within individual pairs between latency to success and trial number; see Tables 4 and 5 for Spearman correlations for each pair. Interestingly, three pairs in the Shareable condition became significantly faster at solving the problem, whereas two pairs in the Non-Shareable condition became significantly slower. For the other pairs, there were no correlations. (Note that here we included trials in which the problem was not solved, in which case we scored 70 s latency.) Fisher's omnibus test ($\chi^2 = 69.37$, $df = 24$, $P < 0.001$) showed that the distribution of these correlations differed from the null hypothesis that all correlations were zero.

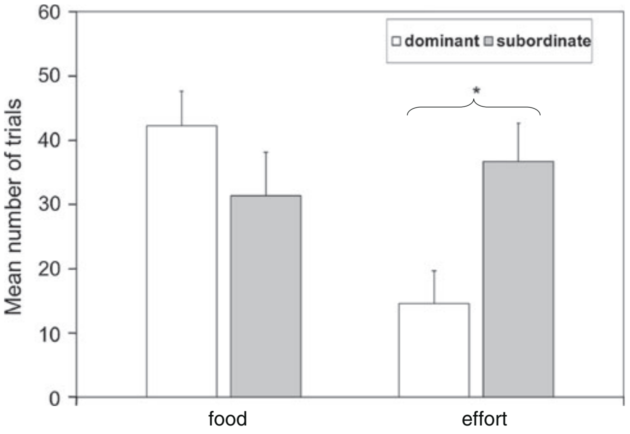


Fig. 2 Mean number of trials in which dominants and subordinates got food and invested effort in Experiment 2

Discussion

Again, all pairs were able to solve the problem in the majority of the trials. It turned out that the problem was solved faster the more trials the dominant subject got food. This indicates that at least dominant subjects' motivation to participate in the task may decrease when they have not been reinforced in previous trials. That is supported by the fact that two pairs in the Non-Shareable condition became slower at solving the problem over trials. In contrast, three pairs in the Shareable condition became faster at solving the problem, suggesting that the subjects learned to coordinate better over trials.

Interestingly, effort was not shared equally. In all pairs, it was usually the same partner that approached the open door so that the sliding door was moved and the partner could cross the fence. Oldfield-Box (1967) tested groups of rats that could feed themselves by pressing a lever. The lever and the tray were on different sides of the cage. So as in the current study, the animal that invested the most effort and took the initiative was less likely to get the reward. Similar to the dogs, rats did not share the effort: usually one animal pressed the lever and received less food than the others. Oldfield-Box (1967) raised the question of why one animal kept pressing the lever (i.e., approaches the open door in case of the dogs) despite receiving least food than its partners. In the current study, mainly the subordinates paid the effort. Indeed, pairs coordinated their actions better the more often subordinates invested the effort.

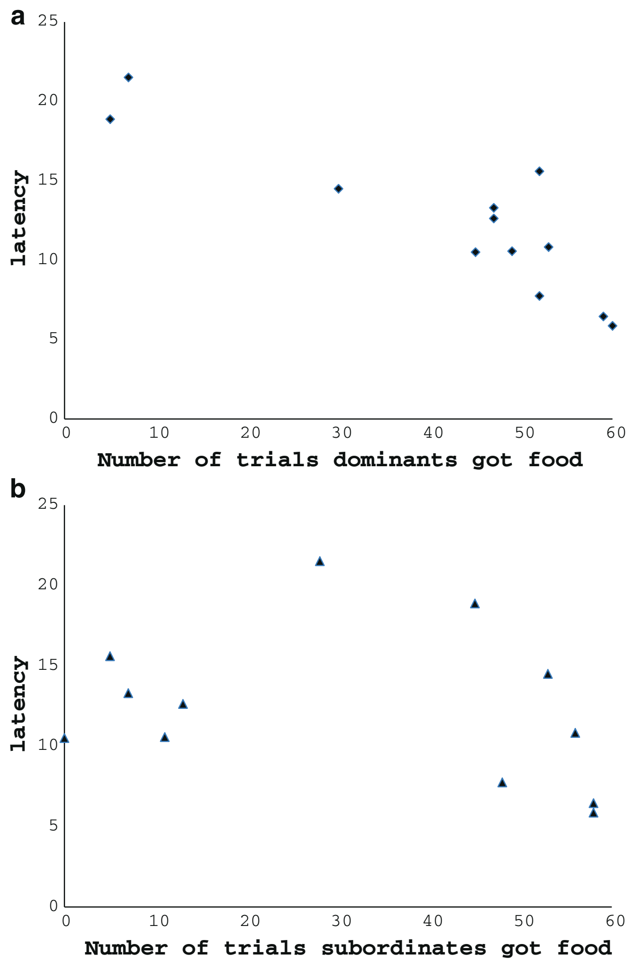


Fig. 3 Correlation of number of trials in which dominants and subordinates got food versus latency to solve the problem in Experiment 2

This finding raises several key questions: Do the subordinates understand that they invested more effort than their partners but could potentially receive less food than dominant dogs as they reached the food bowl later than them? What do dogs at all understand about the role of the other dog in this task? Do they understand that—in contrast to the rats in the studies of Oldfield-Box (1967)—they need their partner and that she/he is paying in effort when she/he is approaching the open door? Whether animals compare their own efforts and payoffs with those of others is a hotly debated topic (Bräuer and Hanus 2012; Bräuer et al. 2006, 2009; Brosnan and de Waal 2003; Brosnan et al. 2005; Dindo and de Waal 2007; Dubreuil et al. 2006; Jensen et al. 2006, 2007; Roma et al. 2006; Takimoto et al. 2010). Although there is conflicting evidence about whether animals react against inequity and are sensitive to the outcomes of others, there is no evidence that they are able to evaluate the relative effort committed by a partner (Fontenot et al. 2007; Range et al. 2009; van Wolkenten et al. 2007).

Range et al. (2009) have argued that dogs might lack the cognitive abilities to show sensitivity to the degree of effort in relation to the outcome of others. In the current study, there is again no evidence that the dogs compare their own efforts with those of their partner. Otherwise those dogs that invested the effort in opening the door in most of the trials should have stopped doing so and shared the work with the partner. One would also expect that pairs sharing the effort would solve the problem better. But the opposite was the case: pairs that did not share the effort were successful faster.

However, there is one—rather unlikely—alternative hypothesis. Subordinate dogs invested significantly more effort than dominants. Moreover, the problem was solved faster the higher the number of trials in which the dominants got the food. In a study of Bräuer et al. (2006), apes were less likely to accept low-quality food when they were dominant over a partner that was getting high-quality food than when they were subordinate. The authors have argued that subordinates may be more predisposed to accept any kind of food because they would always be displaced from a monopolizable food in competition with a dominant individual. In the same way, subordinate dogs might be similarly resigned to always contributing the effort. According to this hypothesis, dogs in the current study were able to compare their own increased effort with that of their partner, but they nevertheless accepted it. However, this explanation is not plausible as we found no behavior (such as aggressive displacement) that would indicate the dominant individuals were prepared to force the subordinate to approach the open door. Moreover, Bradshaw et al. (2009) have questioned the traditional concept of dominance in dogs as they could not detect an overall hierarchy in a group of domestic dogs.

General discussion

The current two experiments show that domestic dogs can coordinate their actions in a hunting-like paradigm. A crucial question is how dogs learned to coordinate their actions. One possibility is that dogs relied on knowledge about their partner's role. However, it is also possible that dogs simply learned to be in the right place at the right time without fully understanding the role of the partner. Regardless of the type of knowledge underlying dogs' responses, the result was coordinated behavior with a high success rate. It is conceivable that the group hunts of wolves and wild dogs (Coppinger and Coppinger 2001; Creel and Creel 2002; Mech 1970; Mech and Boitani 2003) may also consist of the independent actions of the individuals who have learned what it is best for them with little knowledge about their partners' roles (Tomasello et al. 2005).

This is supported by the fact that dogs' abilities to solve that problem do not depend on the divisibility of the reward (defined by the condition). Dogs could share within a trial only in the Shareable condition, but even in the Non-Shareable condition, they could share across trials, so that they got the food alternately. We found that dogs solve the problem faster the more food the dominant subject receives. Somewhat different results were found in other species that cooperated to pull a food platform. Pairs' ability to solve the pulling task was correlated with the possibility of sharing, and their tendency to share food (de Waal and Davis 2003; Melis et al. 2006a, b; Seed et al. 2008). This implies that animals decide to cooperate based on their chances of obtaining a reward. In the present study, especially the dominant individual dog is trying to cross the fence to get the reward. When the dominant dog fails to obtain reward over several trials because the partner gets everything, she/he stops participating and no longer approaches the doors. Interestingly, the motivation to continue participating without receiving a reward varies widely between individuals. Whereas Aimee approached the door 46 times without getting food, other dogs stopped doing so after a few trials.

One could argue that sharing might be a consequence of coordinated behavior. In other words, dogs might be better at sharing the food when they have solved the problem together faster. Boesch and Boesch (1989) reported that chimpanzee hunters get more of the prey meat than non-hunters and that good hunters receive most meat (but see Gilby et al. 2008). However, we did not find that dogs were better at sharing the food after they coordinated themselves better. It is unclear whether they understood the role of the partner at all. First, they usually did not share the effort. Second, we did not observe any intentional communication between dogs to coordinate their actions. Like chimpanzees, dogs did not produce communicative attempts to mobilize or reengage their partner (Bullinger et al. 2011; Melis et al. 2006a, b; Warneken et al. 2006). They did not force their partner to go to the other side of the central fence so that the problem could be solved.

Moreover, we did not find behavior that indicated that the dogs attended to each other. In contrast to chimpanzees and hyenas, the dogs seemed not to monitor the partner so as to promote coordination (Drea and Carter 2009; Melis et al. 2006a, b, 2009). Dogs seemed to show less sensitivity to their partner than another social carnivore, the hyena. There are three possible hypotheses for this. First, it is possible that the problem the dogs were trying to solve was too easy, and therefore, attending to each other was simply not necessary. Indeed, all pairs solved the problem in the majority of trials. The second hypothesis is that the dogs may have lost this skill during the domestication process. Indeed, some authors have considered dogs as omnivorous scavengers rather than carnivores (Serpell 1995; Miklosi 2007). Food is either provided by humans or dogs scavenge, so they do not have to hunt together in order to survive. In that case, one could argue that it is even disadvantageous for dogs to cooperate or to share food. So it is an interesting question, whether wolves, which are carnivores and dogs' closest relatives, would behave differently in an identical test situation. Third, dogs might attend to the partner and maybe even communicate with her when it is a human. A number of studies have shown that dogs prefer humans as social partners (Gacsi et al. 2005; Miklosi et al. 2003; Topal et al. 2005). This hypothesis is supported by the observation that dogs often approached the side of the apparatus from which the experimenter moved the sliding door and barked at her.

Further studies are needed to distinguish which of these three hypotheses is the best explanation for the dogs' behavior. Testing dogs with human partners, testing wolves and increasing the complexity of the task may help to answer the question of what dogs understand when they coordinate their action and how this skill may have evolved. Moreover, it would be interesting to compare the performance of familiar pairs with non-familiar ones. It is conceivable that—as in studies with other species—the kind of relationship between the two members of a pair might influence the performance of that pair.

In conclusion, we were able to show that dogs coordinate their actions in a new paradigm that models a possible situation during a cooperative hunt. They were faster at solving the problem the more food the dominant subject got. Moreover, dogs did not share the effort required to solve the problem—the subordinate invested the majority of effort. In contrast to other species, dogs did not monitor each other, suggesting that this coordination problem can be solved effectively without communication and without even attending to each other.

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Conflict of interest We declare that the experiments comply with the current laws of Germany. We also declare that we have no conflict of interest.

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Dogs (*Canis familiaris*) and Wolves (*Canis lupus*) Coordinate With Conspecifics in a Social Dilemma

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Cooperative hunting is generally considered to be a cognitively challenging activity, as individuals have to coordinate movements along with a partner and at the same time react to the prey. Wolves are said to engage in cooperative hunting regularly, whereas dogs could have maintained, improved, or reduced their cooperative skills during the domestication process. We compared the performance of individuals from two wolf packs and two dog groups with similar gender and rank structure. Members of these groups were tested in dyads with a problem-solving paradigm that involved aspects of a hunting-like situation. Subjects needed to coordinate their actions in order to get food. They were confronted with a social dilemma, in which an individual benefit from being selfish, unless the partner also chooses the selfish alternative, in which case the whole dyad loses. In the task, one partner was required to draw a barrier toward it by rushing forward, allowing the other partner to access the food, at which point both partners were allowed to access the food. Most dyads could solve the problem, with significant variation in their performance but no differences between species. However, the probability of taking the risk in a dyad depended on the species and rank of the individual and on cofeeding in the dyad. The results of this study show that wolves do not always outperform dogs when coordinating their actions, but that the cooperative behavior of *Canis* depends on many factors, including rank, type of task, and tolerance within the dyad.

Keywords: cooperation, coordination, canids

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Cooperation can be defined as any costly behavior that is beneficial to another individual or to all individuals involved in a task (Amici, 2015; Clutton-Brock, 2009; Melis & Semmann, 2010). Wolves breed cooperatively (Coppinger & Coppinger, 2001; Mech & Boitani, 2003) and also often hunt cooperatively in packs of two or more animals (MacNulty, Tallian, Stahler, & Smith, 2014; Mech, 2007; Mech & Boitani, 2003; Muro, Escobedo, Spector, & Coppinger, 2011). Similarly, domestic dogs also cooperate, but mainly with humans. Indeed, dogs are bred and kept by humans for various cooperative purposes including protection, hunting, and herding, and also for rescue, search, service, and guide purposes (Serpell, 2016; Svartberg & Forkman, 2002). In contrast, dogs' ability to cooperate with conspecifics is more controversial (Bräuer, Bös, Call, & Tomasello, 2013; Marshall-

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The research was initiated and designed by Juliane Bräuer, who wrote the manuscript. Katharina Stenglein helped to design the study and collected the data in Königswinter and Dörverden. F.A. did the statistical analysis and helped to improve the manuscript. All authors were based at the Max Planck Institute for Evolutionary Anthropology when data collection began, and later the work was supported by the Max Planck Institute for Evolutionary Anthropology. There are no competing interests. First, we want to thank our research assistant Katrin Schumann for her help in organizing and conducting the study, including collecting data in Petersberg and Greiz. We are very thankful to the staff at the two wolf parks (Tierpark Petersberg and Wolfcenter Dörverden) and to the dog owners—without them the study would not have been possible. We are also grateful to Michael Tomasello for financial support and to Josep Call for fruitful discussions about the idea of the project. We further thank Anika Rütz and Anna Pietschmann for practical help and Frauke Stenglein and Michael Brosch for coding as independent observers. Finally, we thank Juliane Kaminski and Alicia Perez Melis for very useful comments on an earlier version of this article and Anne Gibson for proof-reading.

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Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017; Ostojić & Clayton, 2014).

To date, little is known about the evolutionary origins of these cooperative behaviors. Dogs and wolves share a common ancestor (Serpell, 2016), and thus, if particular cooperative skills are found in both modern species, it is highly likely that this trait already existed in this common ancestor. However, if dogs show better cooperative skills, then it is plausible that they improved during the process of domestication, possibly because of their relevance to humans. In contrast, if wolves perform better than dogs, then either dogs' cooperative skills have declined during domestication (Lampe, Bräuer, Kaminski, & Virányi, 2017) or wolves' cooperative skills have increased. Indeed, recent studies on cooperation in hand-reared wolves socialized with humans provide some evidence that wolves outperform dogs, as they show high social attentiveness and tolerance and are highly cooperative (see Range & Virányi, 2015 for a review).

In a recent study, Marshall-Pescini, Schwarz, et al., 2017 investigated coordination, an important aspect of cooperation that is crucial for cooperative hunting (Bräuer, Bös, et al., 2013; Cronin, Kurian, & Snowdon, 2005; Noë, 2006). They compared the performance of similarly raised dogs and wolves in a string-pulling task, in which food was placed on an out-of-reach tray. A loose string was looped through rings on the tray, with the two ends of the string placed within the subjects' enclosure at such a distance that a single individual could not reach both ends. In test trials, two subjects were given access to the strings and had to coordinate their actions by simultaneously pulling on the two ends of the rope to pull the tray closer and access the food. Marshall-Pescini, Schwarz, et al. (2017) found that wolves outperformed dogs, despite comparable levels of interest in the task: Whereas wolves succeeded in pulling the rope ends at the same time, dogs never succeeded (Ostojić & Clayton, 2014). Marshall-Pescini, Schwarz, et al. (2017) concluded that dogs' and wolves' different conflict-management strategies were responsible for these results, as dogs might avoid potential competition over the apparatus, constraining their capacity to coordinate their actions.

Social tolerance is indeed a socioecological factor significantly differing between dogs and wolves living in packs. Dale, Quervel-Chaumette, Huber, Range, and Marshall-Pescini (2016) compared food sharing in the two species. When a carcass was presented to the group, dominant individuals of both species defended the carcass more than subordinates. However, subordinate wolves were more persistent and spent as much time as dominant individuals in proximity to, and feeding from, the carcass (Dale, Range, Stott, Kotrschal, and Marshall-Pescini, 2017, see also Range, Ritter, & Virányi, 2015). In contrast, subordinate dogs mostly stayed away from the resource so that the most dominant individual could monopolize the food (Melis, Hare, & Tomasello, 2006b).

Although the string-pulling task was successfully used for testing the cooperative capacities of a wide range of species, such as chimpanzees (Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2003; Melis et al., 2006a, 2006b), macaques (Molesti & Majolo, 2016), ravens (Massen, Ritter, & Bugnyar, 2015), gray parrots (Péron, Rat-Fischer, Lalot, Nagle, & Bovet, 2011), rooks (Seed, Clayton, & Emery, 2008), and keas (Schwing, Jocteur, Wein, Noë, & Massen, 2016), it might not be the perfect approach to test canids. First, it is known that both dogs and wolves have problems understanding means-end connections in string-pulling tasks (Osthaus, Lea, & Slater, 2005; Range, Möslinger, & Virányi, 2012). Second, wolves outperform dogs when using causal cues to locate hidden food, and thus, they might have a better general understanding of the physical world, which enables them to better understand the setup (Lampe et al., 2017). Third, wolves are more persistent in object manipulation than dogs (Marshall-Pescini, Virányi, Kubinyi, & Range, 2017; Miklósi et al., 2003; Udell, 2015). This implies that dogs may fail in the cooperative string-pulling task because of their limited understanding of the physical world and because they are less persistent in pulling the rope. Moreover, the string-pulling task is not intuitive for canids, and it requires intensive training. In fact, all animals in the referenced study had previous experience in pulling a string to obtain an attached piece of food (Marshall-Pescini, Schwarz, et al., 2017).

Here, we aimed to compare the cooperative abilities of dogs and wolves by using a more intuitive apparatus (using the setup of Bräuer et al., 2013). In our task, dyads of untrained subjects had to coordinate their actions to solve a problem and reach a reward behind a fence with two openings. A sliding door operated by the experimenter could block one opening but not both simultaneously. The intuitive behavior for subjects would be to approach the open side of the fence and try to retrieve food. However, to solve the problem, subjects needed to coordinate their actions, so that each individual had to approach a different opening, if one of them was to cross through and get food (Bräuer, Bös, et al., 2013). That means, subjects required natural behavioral sequences (i.e., approaching food) to solve the task, without specific training. The apparatus was reactive, in that the experimenter could react to the subjects' behavior, mimicking a natural situation (as prey is reactive to the subject; Noë, 2006). Although both subjects could coordinate by simultaneously accommodating their behavior to each other, the problem could also be solved also by one subject's unilateral actions, if the subject monitored the partner's behavior and coordinated his or her actions accordingly.

This task is a social dilemma (Allison, Beggan, & Midgley, 1996; Dawes, 1980; Sánchez-Amaro, Duguid, Call, & Tomasello, 2018) involving some aspects that are similar to a real hunting situation: One individual benefits from being selfish (so that the partner takes the risk, while the selfish individual obtains the food first), unless the partner also chooses the selfish alternative (so that nobody takes a risk, and food cannot be accessed), in which case the whole dyad loses. In our task, in particular, the subject that takes the risk and approaches the empty opening not only invests more energy but—more importantly—also runs the risk of receiving no share, as his or her partner gains access to the food first. This might be comparable to wolves hunting bison: The bison uses the horns for defense (i.e., MacNulty et al., 2014), so that the wolves in front of the horns are more at risk to be injured and may also receive less meat after the bison is killed. Thus, being selfish would be the most beneficial strategy for each subject: In our task, the selfish option is to wait in front of the fence and then eat both rewards, whereas in a real hunting situation, the selfish option would be to approach the bull from less dangerous sides. However, if both subjects behaved like this, neither of them would enter the fence (i.e., kill the bison), and the dyad would fail to solve the problem and obtain the food.

By mirroring a real social dilemma, our setup allowed us to assess (a) how individuals coordinate their actions to obtain a reward and (b) whether or not they cofeed on the reward so that each individual receives her/his share. We compared the performance of dog and wolf dyads to test three main hypotheses:

> *Hypothesis 1:* Wolves outperform dogs (Marshall-Pescini, Schwarz, et al., 2017), as they are cooperative hunters (Coppinger & Coppinger, 2001).
>
> *Hypothesis 2:* Dyads improve their performance over trials, as subjects learn to coordinate better over trials (Marshall-Pescini, Schwarz, et al., 2017).
>
> *Hypothesis 3:* Cofeeding in the dyad increases the probability of each individual taking the risk because individuals were rewarded for that in previous trials.

Method

Subjects

We tested nine wolves and nine dogs from four different locations. Five wolves originated from a pack in Wolfcenter Dörverden and four wolves from the Wildpark Petersberg. All wolves were individually recognizable and habituated to humans. Each dog group matched one of the wolf packs in size, gender ratio, and partially also in age (Königswinter matched to Dörverden and Greiz to Petersberg). The dogs were family dogs that either lived with each other (i.e., lived in one household) or knew each other very well (i.e., the whole group met once or twice daily or at least once a week). For more details about all subjects, see Table S1 in the online supplemental materials. This observational study adhered to the Guidelines for the Use of Animals in Research of Germany and was approved by the committee of the Max-Planck-Institute for Evolutionary Anthropology in Leipzig, Germany.

Apparatus

Figure 1 shows the apparatus (previously used by Bräuer, Bös, et al., 2013), consisting of a cage with a sliding door and two fences. Due to spatial limitations, the size of the cage varied slightly between groups (300 cm × 620 cm for Dörverden and Königswinter; 300 cm × 450 cm for Petersberg and Greiz), but we controlled for the cage size in our statistical models (see Statistical analyses and Results section). The entrance (ca. 50 × 80 cm) was located on one side of the cage and could be operated from outside the cage. The cage was divided into two parts by a central fence with two openings, and each of them could be blocked by the sliding door (but not both simultaneously). The sliding door was moved by the Experimenter E pushing or pulling a bar from outside the cage. An additional dividing fence (length = 200 cm), perpendicular to the sliding door, increased the distance the subjects needed to cover to go from one opening to the other. In the two corners behind the sliding fence, there were two containers. Each of them contained a food reward that could be monopolized (i.e., a whole chicken or a combination of a dog sausage and a chewing stick; see the online supplemental materials). To define a subject's approach to one opening, a line was marked on the ground, parallel to the central fence, circa 50 cm away from it. Whereas the walls of the cages were covered with opaque bamboo (to prevent distraction of the subjects), the fences, including the sliding door and the entrance door, were made of mesh or Plexiglas and were thus transparent (see Figure 1b for more details).

Pretest

All subjects were given the opportunity to explore the apparatus extensively and were encouraged with food to enter it (See in the online supplemental materials). Wolves required more time to become used to the cage and to the moving door, as they are neophobic (Moretti, Hentrup, Kotrschal, & Range, 2015; for details on habituation, see in the online supplemental materials). As soon as subjects were familiar with the apparatus, they were given a pretest to ensure that they understood the setup. Although the subject waited at the entrance, Experimenter E showed the food to the subject and put it into the food container that was closest to the opening of the sliding door and left the apparatus. Then the subject was released through the entrance and could approach the food, as the sliding door was not moved. To pass the pretest, the subject had to approach the food directly through the open sliding door four trials in a row (twice through each side).

Food Dominance Test

Before the test trial began, we assessed food dominance by identifying which member of each possible dyad monopolized food over the other. The food dominance test took place outside the apparatus—in a garden or open field (dogs) or in an enclosure (wolves). Experimenter E waited until both subjects were attentive and stood at least 3 m from each other. She then threw a piece of food between the two members of the dyad, so that the food was about equidistant to both subjects. We scored which subject ate the food. This procedure was repeated eight times in a row, and the response used to calculate the rank of each individual (see the following text).

Procedure

At the beginning of each trial, both members of the dyad were outside the apparatus on the entrance side and could watch Experimenter E (See in the online supplemental materials, for a clip with the procedure). The sliding door was either on the left or on the right side, with the side being counterbalanced over trials. Experimenter E entered the apparatus, went to the open side of the sliding fence, attracted the individuals' attention, and showed them the food rewards, before placing them into the containers. After Experimenter E left the apparatus to operate the sliding door, the entrance was opened so that the subjects could enter. As soon as one subject approached the opening by crossing the line on the floor, Experimenter E blocked it with the sliding fence, thus simultaneously leaving the other opening accessible. By moving the sliding door back and forth, Experimenter E tried to prevent the subjects from going through the central fence. If subjects simultaneously crossed the line on the opposite sides, the sliding door was moved once, so that the door was closed in front of the subject that had approached the open side, and the other subject could slip through the opening. Thus, dyads could only solve the problem by coordinating with each other, so that each individual approached the central fence on a particular side (see two video clips from two perspectives for each species).

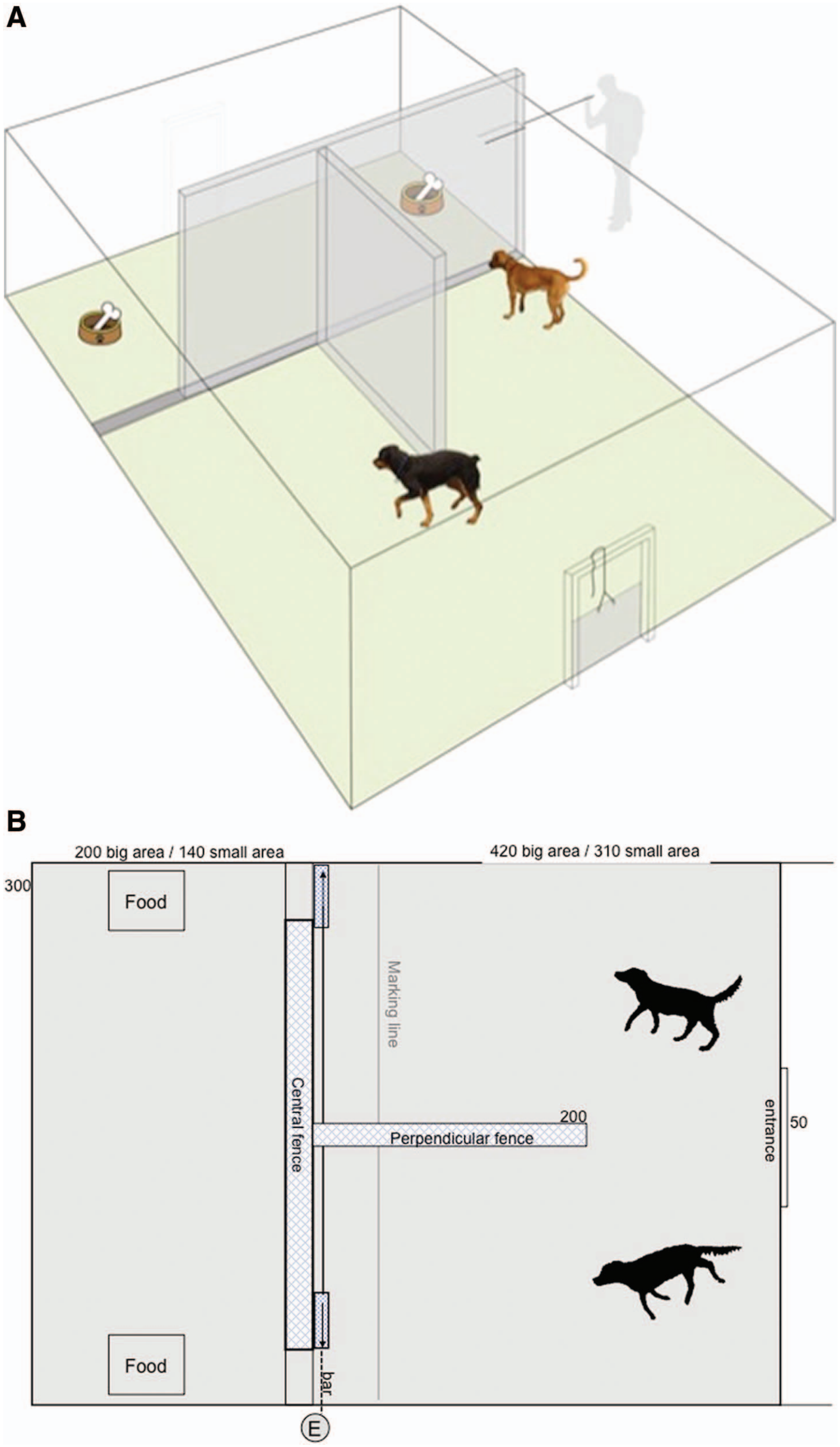

Figure 1. (A and B) General setup of the study. Food was presented behind the sliding door in two bowls left and right of the cage (as shown in Figure 1b; Copyright Animal Cognition). See the online article for the color version of this figure.

The problem was solved when one subject managed to pass through one opening of the central fence. The trial was then over, and Experimenter E stopped moving the sliding door, so that the other subject could also approach the reward. Trials were also ended if the subjects did not solve the problem within 70s.

Design and Coding

We tested all possible dyads within each pack, which resulted in 32 dyads (i.e., 16 dog dyads and 16 wolf dyads). Each dyad was tested in 60 trials, as we were interested in whether performance decreased over trials. Dyads received 20 to 40 trials per day with breaks of about 10 min (usually after 10 trials). One group of wolves and the matching group of dogs were tested in a larger area (Dörverden and Königswinter), and the other two groups were tested in a smaller area (Petersberg and Greiz).

All trials were video-recorded. From the video-tapes, we later coded the following measures: whether they succeeded in solving the task (i.e., success, as a binomial response); latency to solve the task (i.e., seconds elapsed from the opening of the subject entrance until the first subject managed to cross the fence); who moved toward the empty opened side, allowing the partner to first pass through the fence (i.e., risk); and who received the food (i.e., benefit). When both individuals received the food, we coded it as cofeeding. When food in both bowls was monopolized, subjects taking no risk were usually the only ones eating both food pieces, as individuals taking the risk by moving to the open door were too late to receive their share, and individuals usually did not replace each other at the food bowl. Because the food reward in each bowl was monopolizable, we never observed cofeeding in one bowl. We also looked for communicative exchanges between subjects, but we detected no behaviors that could be evaluated.

Two additional coders (who were unaware of the goal of the study) scored 20% of the trials to assess interobserver reliability (for practical reasons, we had one coder for Dörverden and Königswinter and one for Petersberg and Greiz). Reliability was excellent (Dörverden/Königswinter: $N = 108$; success: Cohen's $\kappa = 1.00$; Latency: Spearman Correlation $r = .96$; food received: Cohen's $\kappa = 1.00$; risk by dominant: Cohen's $\kappa = 1.00$; risk by subordinate: Cohen's $\kappa = 0.98$; Petersberg/Greiz: $N = 149$; success: Cohen's $\kappa = 1.00$; latency: Spearman Correlation $r = .91$; food received: Cohen's $\kappa = 0.97$; risk: Cohen's $\kappa = 0.96$).

Statistical Analyses

For each of the four study groups, we determined the dominance hierarchy with the epitaxial lateral overgrowth Elo method, based on the order of access to food in dyadic tasks. In contrast to other methods, the Elo method is based on the sequence of the interactions, not on an interaction matrix. After each interaction, the ratings of both individuals are updated, based on the outcome of the interaction (Neumann et al., 2011). In the absence of any knowledge of previous dominance relationships, an initial burn-in period is usually included when calculating the Elo rank (Newton-Fisher, 2017). In this period, all individuals are assigned the same initial Elo rating score, which is updated as interactions are added during the observation period. Therefore, during the initial burn-in period, the Elo rating trajectories have not yet reached stability, and the model is less reliable. Often, these initial burn-in periods are omitted from data analyses, but as we only included eight interactions per dyad, over a short time frame, our Elo rating was calculated on the whole dataset, including the initial burn-in period. Analyses over 32 dyads provided the Elo rank for all individuals, which varied from relatively stable for the wolves in Dörverden (0.647) to more stable for the other groups (wolves in Petersberg: 0.845; dogs in Greiz: 0.907; dogs in Königswinter: 0.998).

Analyses were conducted using generalized linear mixed models (Baayen, Davidson, & Bates, 2008) with the lme4 package in R (Version 3.5.0; Bates, 2010). Continuous variables (i.e., trial number) were z transformed as commonly done in literature to facilitate model convergence. We used a likelihood ratio test (Chatfield, Zidek, & Lindsey, 2002) to compare full models with null models. When full models differed significantly from null models, likelihood ratio tests were conducted to obtain the p values for each test predictor via single-term deletion (Barr, Levy, Scheepers, & Tily, 2013). Post hoc comparisons were then conducted using Tukey's tests and only reported if significant. No convergence or stability issues were detected. To rule out collinearity, we used variance inflation factors (Field, 2005), which were very good (maximum variance inflation factors across all models = 1.11).

Model 1 investigated whether the probability of solving the task varied across species, through time. As test predictors we therefore entered species (i.e., wolf or dog) and trial number (i.e., from 1 to 60). Here and in the next models, we opted to include trial number within each dyad (rather than trial number for each subject, regardless of the partner) as test predictor because the cooperative nature of the task requires both individuals to coordinate their actions to solve the task, and a learning process should be based on dyads and not on individuals. This choice was corroborated by the individual results (Table S3 in the online supplemental materials), showing that the number of trials solved by each dyad strongly varied even between dyads in which one of the two individuals was the same. As control predictors, we entered the side of the opened door when the trial started (i.e., right or left) and the cage size (i.e., small or large), and as random effect, the subject and partner identity (to account for the nonindependence of data points), including trial number as random slopes. In Model 2, we only included successful trials to investigate whether the latency to solve the task varied depending on species and trial number. Control predictors, random effects, and random slopes were entered as in Model 1. In Model 3, we only included successful trials to analyze whether the probability of sharing food varied across species, depending on who takes the risk (i.e., subordinate or dominant in the dyad). Control predictors, random effects, and random slopes were entered as in Model 1, with the further inclusion of trial number as control predictor. Model 4 investigated whether the probability that dominants took the risk in the dyad was affected by the two-way interaction of species with the probability of having already cofed within that dyad (i.e., number of previous trials in which the dyad cofed, out of the total number of trials already made by that dyad). As control predictors we entered the cage size, trial number, and side of the opened door, including dominant and subordinate identity as random factors and trial number as random slopes. The probability that subordinates took the risk was inverse to the probability that dominants took it, so a further model was not needed. When the dependent variable was

Table 1

Results of Models 1 to 4, Including Estimates, Standard Errors, χ^2, Degrees of Freedom, and p Values for Each Test and Control Predictor (in Parentheses, the Reference Category Is Included)

Models	Estimate	*SE*	χ^2	*df*	*P*
Model 1: Probability of solving the task					
Intercept	4.31	2.29	—	—	—
Species (wolf)	−2.24	2.76	0.637	1	.425
Cage size (small)	1.41	2.80	0.270	1	.603
Trial number	0.29	0.40	0.522	1	.470
Door opened (right)	−0.08	0.19	0.196	1	.658
Model 2: Latency to solve the task					
Intercept	9.76	2.96	—	—	—
Species (wolf)	−0.76	3.63	0.055	1	.815
Cage size (small)	5.50	3.64	2.510	1	.113
Trial number	−0.42	0.79	0.281	1	.596
Door opened (right)	−0.09	0.49	0.040	1	.842
Model 3: Probability of cofeeding					
Intercept	2.44	1.90	—	—	—
Species (wolf)	1.41	2.35	0.369	1	.543
Cage size (small)	−2.25	2.36	0.901	1	.342
Taking the risk	**−2.28**	**0.29**	**70.879**	**1**	**<.001**
Trial number	0.03	0.49	0.005	1	.944
Door opened (right)	*0.44*	*0.20*	*4.448*	*1*	*.035*
Model 4: Probability that dominants took the risk					
Intercept	−0.533	2.136	—	—	—
Species (wolf) × Previous cofeeding	**3.892**	**1.366**	**7.76**	**1**	**.005**
Cage size (small)	−1.870	2.599	0.52	1	.472
Trial number	−0.362	0.335	1.11	1	.292
Door opened (right)	*0.791*	*0.156*	*25.61*	*1*	*<.001*

Note. Significant test predictors are in bold, significant control predictors in italics. Trial number had been previously *z*-transformed.

binary, models were run with a binomial structure (Models 1, 3–4). More complex models including more test and control predictors could unfortunately not be run, to avoid convergence and/or stability issues. For details, see also Table 1.

Results

Task Solution

Overall, subjects were successful in solving the task in 77% of the trials (see Table S3 in the online supplemental materials for detailed results of each dyad). In Model 1, the comparison between the full and null model was not significant (generalized linear mixed model [GLMM]: $\chi^2 = 1.17$, $df = 2$, $p = .557$). On average, it took subjects 11 s to solve the task. Model 2 was also not significant (generalized linear mixed model: $\chi^2 = 0.33$, $df = 2$, $p = .847$).

Cofeeding

In Model 3, the comparison between the full and null model was significant (GLMM: $\chi^2 = 71.40$, $df = 2$, $p < .001$; Table 1, Figure 2). In particular, the probability of cofeeding was affected by who took the risk ($p < .001$), with the probability of cofeeding being higher when the dominants took the risk. No other test predictor was significant.

Risk

In Model 4, the comparison between the full and null model was significant (GLMM: $\chi^2 = 11.07$, $df = 3$, $p = .011$; Table 1, Figure 3). In particular, the probability that dominants took the risk was affected by the two-way interaction of species and previous cofeeding in the dyad ($p = 0.005$). Post hoc tests revealed that dominant wolves had a higher probability to take the risk than dominant dogs, and in dominant wolves, this probability also increased when the proportion of previous cofeeding was higher (i.e., the more they cofed, the more the dominant wolves took the risk). In dogs, in contrast, previous cofeeding decreased the probability that dominants took the risk.

Discussion

In contrast to our first hypothesis, dogs were not outperformed by wolves in coordinating their actions when approaching food behind a sliding door. In particular, neither the probability (Model 1) nor the latency to solve the task (Model 2) varied across species. This is somewhat surprising, as it contradicts the recent findings by Marshall-Pescini, Schwarz, et al. (2017). It is possible that the dogs in our study performed similarly to wolves because our task was ecologically more relevant and involved no intensive training. Coordinating behavior by simultaneously approaching two sides of a sliding door is indeed much more intuitive for a dog than pulling a rope, as dogs are unable to use causal cues reliably to locate hidden food and do not perform well in string-pulling tasks

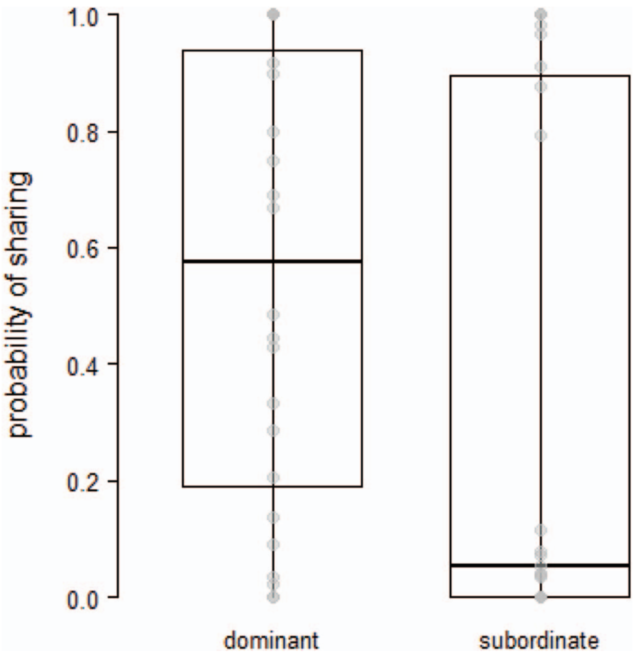

Figure 2. Box plot representing the data distribution for the probability of cofeeding, separately for trials in which dominants took the risk, and trials in which subordinates took the risk, from a generalized linear mixed model. The horizontal ends of the box represent the 75% and 25% quartiles, and the ends of the vertical bars represent the 97.5% and 2.5% quartile, respectively. The ticker line inside the box plots represent the model estimates. Gray dots represent data points.

(Lampe et al., 2017; Osthaus et al., 2005; Range et al., 2012). Another possibility is that our task was less demanding; that is, it did not require the same level or kind of coordination as the string-pulling task (see the following), and that is why dogs performed similarly to wolves. Indeed, one aspect that could have played a role here is that to coordinate their actions, subjects had to be in two different locations. It was argued that tolerance is an important limitation when coordinating actions, so that tolerant pairs perform better (Massen et al., 2015; Melis et al., 2006b). Our task may actually have minimized tolerance requirements, as successful partners had to keep their distance from one another. This could have made the task easier for less tolerant individuals. When retrieving food, however, tolerance between partners was crucial again. In the paradigm of the current study, we could not precisely measure food sharing defined as a joint use of a monopolizable food source (Stevens & Stephens, 2002), but we measured cofeeding, that is, feeding together around a source of food that could be monopolized (Scheid, Schmidt, & Noë, 2008). In particular, this measure quantified whether a subject was able to monopolize both food sources, which depends on the tolerance within the dyad.

Another potential reason why our results on dog performance contradict those by Marshall-Pescini, Schwarz, et al. (2017) could be explained by the living conditions of the tested dogs. In their study, the dogs lived in packs in an enclosure with no owner, whereas the dogs in our study lived with their owners. By being exposed to different socioecological stimuli during their development, they might have developed different cognitive skills. In another study using the string-pulling apparatus, for instance, all five tested dyads of family dogs succeeded in coordinating their actions (Ostojić & Clayton, 2014), possibly because they lived in the same household, where typically owners train their dogs not to engage in conflicts over resources, promoting a level of tolerance that may facilitate cooperation (Marshall-Pescini, Schwarz, et al., 2017). The dogs in our study might also have more experience with an intervening owner, although dyads did not all live in the same household. Thus, there might be a large variability across different dog populations and probably also within wolf populations, emphasizing the high behavioral plasticity of the genus *Canis*.

Our experimental manipulation created a social dilemma in which the subject that moved to the opposite door ran the risk of getting no share of the reward. In line with this, the probability of cofeeding during successful trials was higher when dominants took the risk (Model 3), because their higher rank gave them a higher chance to nonetheless get their share, even if they accessed the food reward a few seconds after the subordinate. However, note that rank in our study was assessed with the ELO-rank procedure (Neumann et al., 2011), but only based on a limited number of interactions over a short time frame, so that these results must be taken with caution. Contrary to our second hypothesis, neither wolves nor dogs improved their performance over trials. Given the high percentage of successful trials, this is likely to reflect the intuitiveness of our setup, with subjects spontaneously solving the task from the very first trials.

Regarding our third hypothesis, we found that the probability of taking the risk in a dyad depended on the species and rank of the individual and on the previous occurrence of cofeeding in the dyad. In general, dominant wolves took the risk more often than dominant dogs. This might imply that dominant wolves are either more willing to cooperate than dominant dogs or that they were more certain that they would receive their share as they live in more stable groups. For subordinates, the opposite pattern is true (as only one individual could take the risk in each trial). Subordinate dogs took the risk more often than subordinate wolves. This might be explained by the fact that dominant dogs more often monopolize food resources (Dale et al., 2016). Therefore, subordinate dogs may be more used to situations in which food is not shared, and they may nonetheless be motivated to take the risk, even if they do not get their share in every trial.

Moreover, in dominant wolves and subordinate dogs the probability of taking the risk increased when the proportion of previous cofeeding was higher. This can be easily explained by motivational changes, as these individuals were probably more willing to take a risk after receiving their share in previous trials. The finding that subordinate wolves and dominant dogs took fewer risks if there had been more cofeeding in previous trials is more difficult to explain, but it may be just the consequence of how their partners were performing—and that the risk could only be taken by one member in each pair. In other words, previous cofeeding might have been essential to motivate dominant wolves and subordinate dogs to take the risk, as they were not willing to abandon their share, whereas their partners' strategy simply followed as a consequence. Thus, our findings suggest that species differences between wolves and dogs in their hierarchy structure and food-sharing habits (Dale et al., 2016) may influence the way individuals coordinate their actions in this social dilemma (Melis et al., 2006b; Suchak et al., 2016).

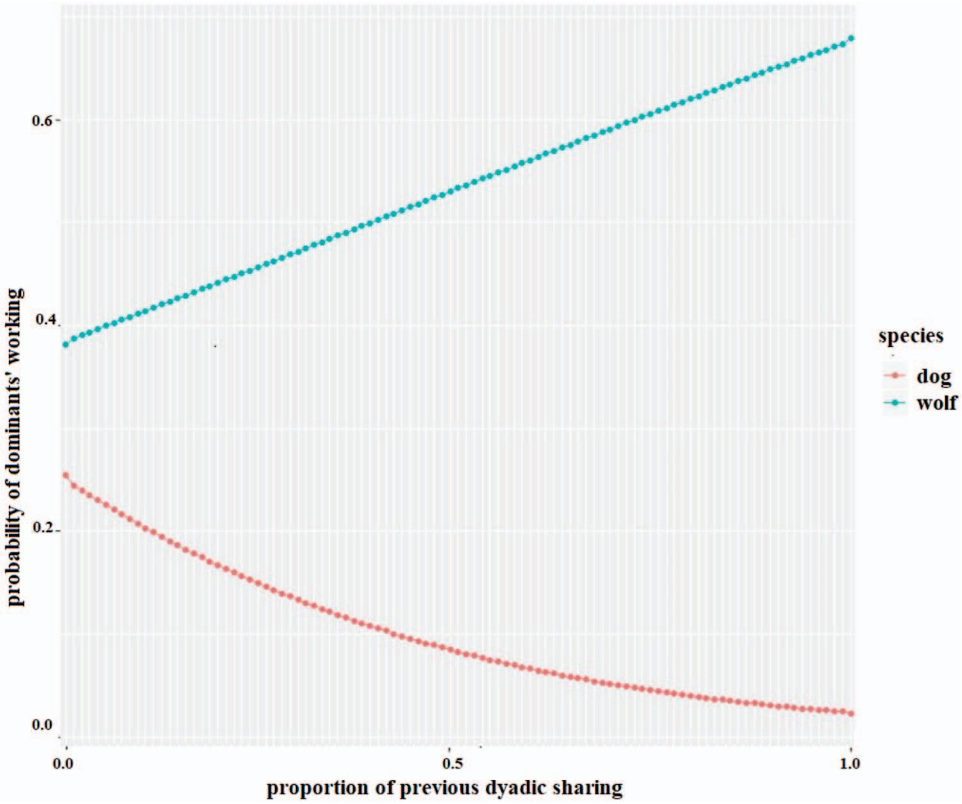

Figure 3. For each species, probability of dominants' taking the risk as a function of the proportion of previous cofeeding in the dyad. See the online article for the color version of this figure.

One question that arises is about the cognitive aspects of the behavior displayed. As Brosnan, Salwiczek, and Bshary (2010) pointed out, coordination of individuals might be achieved without individuals realizing the situation and without monitoring their partners, similar to social spiders (*Stegodyphus*) that pull their prey victim to their communal nest as they all pull in the same homeward direction (Enders & Ward, 1985; Muro et al., 2011; Wickler & Seibt, 1993). In a previous study using exactly the same setup (Bräuer, Bös, et al., 2013), it was shown that dogs understood how the apparatus worked. In a condition when the sliding fence was moved only once, subjects sometimes opened the door by themselves when the partner refused to participate. Moreover, in the current study, after a few trials, some subjects hesitated to cross the marking line in front of the open door. They approached the open door slowly and often stopped before the marking line and ran back to the still closed door. This suggests that subjects understood that when they crossed the marking line, the door would be closed and the other door would open (see also in the online supplemental materials, clips Cooperation_Dog2 and Cooperation_Wolf2).

Overall, this study provides clear evidence that dogs and wolves can successfully coordinate their behavior, although we found no evidence that the two partners monitor each other. Actually, to solve the task, it was sufficient that one animal adjusted her/his behavior to the partner's one. However, this is also true for other cooperative tasks—including the string-pulling task—that are labeled as collaborative coordinated actions (see Melis & Semmann, 2010 for a review). It is possible that paying attention to each other is simply not necessary to solve an easy problem (Bullinger, Wyman, Melis, & Tomasello, 2011; Muro et al., 2011). However, in the string-pulling task, wolves were able to learn to pay attention to each other over trials so that they were able to solve the task even when they had to wait for the partner for 10 s (Marshall-Pescini, Schwarz, et al., 2017).

Therefore, the results of the current study do not allow us to distinguish between the following possibilities: (a) subjects coordinate their action with full understanding of the partner's role, (b) subjects monitor each other, (c) only one subject monitors the other, or (d) subjects simply learn to be in the right place at the right time (Bräuer, Bös, et al., 2013; Muro et al., 2011). Possibly, group hunting in wolves and wild dogs (Coppinger & Coppinger, 2001; Creel & Creel, 2002; Mech, 2007; Mech & Boitani, 2003) mainly consists of the independent actions of multiple individuals who have learned to master their individual role during the hunt and only attend to their partners when it is necessary (Tomasello, Carpenter, Call, Behne, & Moll, 2005).

What can these results tell us about how cooperative behavior has evolved during the domestication process? Clearly, the kind of coordination we have evidenced in our study may rely on more simple mechanisms than cognitively complex forms of cooperation in which subjects monitor their partners and have a full understanding of their roles (mentioned earlier). However, these forms of more basic coordination are likely essential prerequisites for the evolution of more complex forms of cooperation. According to our results, wolves do not outperform dogs when tasks require coordination, which is an essential component of cooperation. This suggests that the abilities needed to coordinate their actions were already present in the dog-wolf ancestor. However, given that dogs prefer humans to other dogs as social partners (Gácsi et al., 2005; Miklósi et al., 2003; Prato Previde & Valsecchi, 2014; Topál et al., 2005), it is likely that dogs might coordinate better with a human partner than with another dog. In other words, dogs and wolves may show similar cooperative skills with their conspecifics, but dogs might cooperate better with humans, as they have been selected to cooperate *specifically with humans* (Bräuer, 2015; Bräuer, Schönefeld, & Call, 2013). In a recent study by Range, Marshall-Pescini, Kratz, and Virányi (2019), both dogs and wolves, which had been highly socialized with humans, were very successful with a human partner in a string-pulling task. However, the study also revealed remarkable interspecific differences: Whereas hand-reared wolves were more inclined to initiate behavior and take the lead, dogs were more likely to wait for the human partner. Moreover, there is some evidence for prosocial behavior in dogs toward humans, with dogs being highly motivated to help humans but having problems inferring the human's goal if this is not clearly communicated (Bräuer, 2015; Bräuer, Schönefeld, et al., 2013; Kaminski, Neumann, Bräuer, Call, & Tomasello, 2011; Quervel-Chaumette, Dale, Marshall-Pescini, & Range, 2015; Quervel-Chaumette, Mainix, Range, & Marshall-Pescini, 2016).

In conclusion, it is likely that cooperative skills were already present in the dog-wolf ancestor, as the genus *Canis* shows high behavioral plasticity in cooperative tasks. Future studies should focus on the question of how exactly factors like social dynamics, living conditions, the type of task, and maybe also breed differences influence the cooperative behavior of dogs and wolves. Furthermore, future studies should take into account that cooperative endeavors (such as cooperative hunting) often create social dilemmas in which the ratio between individual costs and benefits may vary strongly across subjects depending on their characteristics, significantly affecting their response.

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A Ball Is Not a Kong: Odor Representation and Search Behavior in Domestic Dogs (*Canis familiaris*) of Different Education

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There has been a growing interest in the cognitive skills of domestic dogs, but most current knowledge about dogs' understanding of their environment is limited to the visual or auditory modality. Although it is well known that dogs have an excellent olfactory sense and that they rely on olfaction heavily when exploring the environment or recognizing individuals, it remains unclear whether dogs perceive odors as representing specific objects. In the current study, we examined this aspect of dogs' perception of the world. Dogs were presented with a violation-of-expectation paradigm in which they could track the odor trail of one target (Target A), but at the end of the trail, they found another target (Target B). We explored (a) what dogs expect when they smell the trail of an object, (b) how they search for an object, and (c) how their educational background influences their ability to find a hidden object, by comparing family dogs and working dogs that had passed exams for police or rescue dogs. We found that all subjects showed a flexible searching behavior, with the working dogs being more effective but the family dogs learning to be effective over trials. In the first trial, dogs showed measurable signs of "surprise" (i.e., further searching for Target A) when they found Target B, which did not correspond to the odor of Target A from the trail. We conclude that dogs represent what they smell and search flexibly, which is independent from their educational background.

Keywords: olfaction, representation, search behavior, domestic dog, working dog

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In recent years, there has been a growing interest in how animals perceive their environment and what they understand about it. Domestic dogs, *Canis familiaris*, are especially interesting, as they have evolved various skills for functioning effectively in human societies. Indeed, dogs show outstanding skills in the social–cognitive domain (for reviews, see Huber, 2016; Kaminski & Marshall-Pescini, 2014; Miklosi, 2007). Besides their communicative skills, dogs might also have evolved their motivation to cooperate and their perspective-taking abilities during domestication (Bräuer, 2014, 2015; Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016). In contrast, regarding their physical cognitive skills (i.e., what dogs understand about their physical environment), dogs seem to perform similarly to other nonprimate mammals and birds (Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Erdõhegyi, Topál, Virányi, & Miklósi, 2007; Osthaus, Lea, & Slater, 2005; Miletto Petrazzini, & Wynne, 2016; Rooijakkers, Kaminski, & Call, 2009).

However, until now, studies of dogs mostly took an anthropocentric view, mainly looking for skills and modalities that are important for humans. Thus, most current knowledge about dogs' understanding of their social and physical environment is limited to the visual or auditory modality (Bräuer et al., 2013; Kaminski, Call, & Fischer, 2004; Kundey et al., 2010), even though olfaction is an important sense that dogs use to explore their environment (Gazit & Terkel, 2003; but see also Horowitz, Hecht, & Dedrick, 2013; Szetei, Miklósi, Topál, & Csányi, 2003).

Olfactory cues play an important role in individual recognition and communication and also for the detection and selection of food (Brown & Johnston, 1983; Cafazzo, Natoli, & Valsecchi, 2012; Köhler, 2004; Lisberg & Snowdon, 2009; Wells & Hepper, 2006). Similar to wolves, dogs possess a large olfactory epithelium, expanded respiratory turbinates, and a huge number of olfactory neurons and receptors (Green et al., 2012; Köhler, 2004; Zhang, Wei, Zhang, & Chen, 2011). Dogs' olfactory acuity, that is, their ability to sense chemicals by smell at low concentrations, is excellent (Köhler, 2004; Miklosi, 2007; Vonk & Leete, 2017; Walker et al., 2006 but see also Horowitz et al., 2013), and they

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can learn to recognize various odors (Hall, Glenn, Smith, & Wynne, 2015; Williams & Johnston, 2002). In detection tasks, they indicate the presence of specific trained odors. Dogs can be trained to discriminate and indicate the presence of odors of narcotics, explosives, plants, parasites, and various diseases, such as cancer and diabetes (Alasaad et al., 2012; Browne, Stafford, & Fordham, 2006; Dalziel, Uthman, McGorray, & Reep, 2003; Furton & Myers, 2001; Gazit, Goldblatt, & Terkel, 2005; Lim, Fisher, & Burns-Cox, 1992; Lippi & Cervellin, 2012). In addition, dogs are also able to match odors (Marchal, Bregeras, Puaux, Gervais, & Ferry, 2016), that is, they can confirm or deny that two odors come from the same source (Brisbin & Austad, 1991; Schoon, 1996).

Interestingly, there are some contradictory findings about breed differences in odor detection. Polgár, Kinnunen, Újváry, Miklósi, and Gácsi (2016) used a natural detection task and compared dog breeds selected for their scenting ability, dog breeds bred for other purposes, dog breeds with exaggerated short-nosed features, and hand-reared gray wolves. As one would expect, it was found that wolves and scent breeds outperformed the other two groups. In contrast, in a study by Hall et al. (2015), pugs outperformed German shepherds in acquiring odor discrimination and maintaining performance when the odor concentration was decreased. Moreover, Jezierski et al. (2014) tested the efficacy of drug detection by police dogs of various breeds and found that German shepherds outperformed the other breeds, whereas terriers showed relatively poorest detection performance. This suggests that performance in an odor task not only depends on olfactory abilities but also on trainability, education, motivation, and the type of test (Polgár et al., 2016).

One further question is how dogs use their olfactory sense to find a target. A study by Hepper and Wells (2005) investigated how dogs determine the direction of an odor trail left by a human. The authors found that dogs trained in tracking humans are able to determine the direction of an odor trail after 1 hr by using only five footsteps (see also Wells & Hepper, 2003). In contrast, Polgár, Miklósi, and Gácsi (2015) used untrained dogs and investigated their strategies to find either their owner or food in one of three locations. Surprisingly, dogs did not perform above chance when the target was more than 1 m away, indicating that dogs could not gather olfactory cues at this distance. Subjects often used a win–stay strategy in that task, that is, they went to the place where the target was located in the trial before. Interestingly, dogs often first attempted to solve the problems based on the little visual information they had, rather than on the available olfactory cues. The authors concluded that despite their ability to successfully collect information through olfaction, family dogs often prioritize other strategies, such as a win–stay strategy, to solve such tasks (Polgár et al., 2015).

However, it remains completely unclear whether and how dogs *represent* objects via odors, that is, whether they have an expectation of something specific when smelling an odor trail. Bräuer and Call (2011) investigated how dogs represent objects. They used a classical violation-of-expectation paradigm with a container with a double bottom ("magic cup") that allowed them to change the type of food that subjects had seen being placed in the container. Whether subjects received a generally preferred or less preferred food and whether the food was substituted varied. It was found that when dogs were introduced to the so-called "surprise condition"—when food was substituted—their search behavior increased and they stayed in proximity to the experimenter. Thus, subjects did not search for just any reward but for exactly that reward that was placed in the container. Bräuer and Call (2011) concluded that dogs were indeed able to individuate objects according to their properties or type, in the same way as apes (and humans) do, and that this ability is, contrary to previous claims, neither uniquely human nor essentially language dependent (Xu, 2002). Although dogs used their sense of smell in the study, the relevant information (i.e., what food was placed) was also given in the visual modality.

Thus, although we know much about cognitive skills and olfaction in dogs, there is a lack of knowledge of how the two are linked together or how olfaction influences cognitive processes in dogs. Hence, the aim of the current study was to investigate whether dogs represent what they smell. We explored (a) what dogs expect when they smell the trail of an object, (b) how they search for an object, and (c) how their educational background influences their ability to find a hidden object. Overall, we expected dogs to not only have excellent olfaction but also represent specific objects from their odors and be able to search flexibly, that is, to use reasonable strategies to adapt to the challenges of the novel search task.

To test this, we adopted the classical violation-of-expectation paradigm of Bräuer and Call (2011). In the critical condition, subjects could track the odor trail of one object (Target A), but at the end of the trail, they found another object (Target B). If subjects represented what they smelled, we predicted that they would show measurable signs of "surprise" by searching (for Target A) when they find Target B, which does not correspond to the odor of Target A from the trail. In contrast, if subjects showed no change in behavior in the critical "surprise" condition compared with a baseline condition in which odor trail and target corresponded, it is likely that they perceive odors as positive (or aversive or neutral) stimuli without the expectation of the object/individual that they smell. In other words, this pattern of response would show that dogs do not associate the smell of an object with the object itself. Because dogs individuate objects according to their kind (Bräuer & Call, 2011), and because dogs have an excellent olfactory sense, our hypothesis was that they indeed have a representation of someone or something when they sense a smell.

In addition, we investigated dogs' search strategies, which was measured by how often they use sniffing to find the object, how long it takes them to find the object, and how they potentially improve over trials. Finally, we compared the performance of the two groups of dogs with or without special training in odor tracking, hypothesizing that dogs with special training would outperform family dogs.

Method

Subjects

In total, 48 dogs (21 male and 27 female) of various breeds and ages (ranging from 1 to 12 years) participated successfully in this study (Table 1). The dogs were divided into two groups. The first group consisted of 25 specially trained working dogs (11 male and 14 female, ranging in age from 1 to 12 years, with an average age of 5.3 years) that had passed the exams for either rescue dogs or police dogs and were part of the K9 unit of the Thuringia state

Table 1
Subjects Participating Successfully in the Experiment (i.e., Met the Two Preconditions for Participating)

Subject	Breed	Gender	Age (years)	Educational background
Aaron	Belgian shepherd	Male	3	Working
Agent	Belgian shepherd	Male	3	Working
Akela	Belgian shepherd	Female	6	Working
Alice	Belgian shepherd	Female	4	Working
Angel	German shepherd	Female	1	Family
Angus	Labrador retriever	Male	2	Family
Azana	Golden retriever	Female	1	Family
Bella	Mongrel (Belgian shepherd and unknown)	Female	8	Working
Bill	Golden retriever	Male	6	Family
Bruno	Belgian shepherd	Male	1	Working
Cero	German shepherd	Male	7	Working
Cora	Golden retriever	Female	1	Family
Darwin	Labrador retriever	Male	5	Family
Dina	Lagotto Romagnolo	Female	5	Family
Duke	German shepherd	Male	6	Working
Ella	Nova Scotia duck tolling retriever	Female	3	Working
Fero	Mongrel (Belgian shepherd and unknown)	Male	8	Working
Finja	Tervueren	Female	4	Working
Frau Buber	Briard	Female	7	Family
Godin	Belgian shepherd	Male	9	Working
Isie	Belgian shepherd	Female	4	Working
Jack	Mongrel (German shepherd and schnauzer)	Male	2	Family
Joran	Collie	Male	3	Family
Kiba	Border collie	Female	1	Working
Kilo	German shepherd	Male	4	Family
Lina	Labrador retriever	Female	4	Family
Lotte	Mongrel (poodle and schnauzer)	Female	8	Working
Luna	Old German shepherd	Female	4	Working
Maja	Mongrel (border collie and Labrador retriever)	Female	6	Family
Mephisto	Standard poodle	Male	10	Family
Michel	German shepherd	Male	4	Working
Mira	Mongrel (Labrador and unknown)	Female	5	Working
Mira	Mongrel (Podenco and unknown)	Female	9	Family
Pearl	Australian shepherd	Female	12	Working
Pepsi	Belgian shepherd	Female	3	Working
Polly	Golden retriever	Female	4	Family
Prinz	German shepherd	Male	4	Working
Quino	Groenendael	Male	5	Working
Reni	Belgian shepherd	Female	6	Working
Rudy	Mongrel (Belgian shepherd and unknown)	Male	6	Working
Shari	Mongrel (Berger Blanc Suisse and golden retriever)	Female	6	Family
Tiffany	Mongrel (border collie and fox terrier)	Female	7	Family
Toni	Muensterlaender	Female	1	Family
Unique	German shepherd	Female	1	Family
Uschi	Mongrel (German shepherd and unknown)	Female	9	Working
Victor	Mongrel (Great Dane and Labrador)	Male	4	Family
Willy	Golden retriever	Male	4	Family
Yoshi	Mongrel	Male	8	Family

police at that time. The second group (referred to as family dogs) included 23 family dogs (13 male and 10 female, ranging in age from 1 to 12 years, with an average age of 4.6 years) that had received no special training. For both groups, the owners were only informed about the research question, and the specifics of their dogs' tasks in the study, after the test was completed to avoid potential training or influence by the owners.

All subjects lived with their owners and were registered in our database. The dogs' owners decided voluntarily to take part in this study. Dogs were tested individually and were motivated to participate with toys. The dogs were encouraged to explore all testing rooms before the test. The study adhered to the *Guidelines for the Use of Animals in Research* of Germany.

Preconditions

There were two preconditions for participating in this study. The first precondition was that every participating dog would be generally interested in playing with two different toys, which was ensured by the pretest. Subsequently, two toys of similar size were chosen that had to be equally interesting to the dog. To make sure that both toys were equally interesting, each dog was individually tested in a small test room. The dog was held by the collar by the first experimenter E1, who was seated about 1.5 m away from the second experimenter E2. Two toys were placed on the floor 1 m apart by E2, who sat on a small stool. Then, E2 pointed at one object and said, “Fetch this!” (in German: *Hol’s dir!*) to the dog, who was released in that moment to fetch the toy. E2 and the dog then played with the toy for a short period. In total, there were 10 trials presented according to a predetermined counterbalanced order, five for each object, including a short break after five trials. The decisive criterion was that the dog should bring each object at least four times. If the objects, however, were not equally interesting or were completely ignored, another toy combination was chosen and the pretest was repeated. If subjects could not be motivated to play with any toy (i.e., ignoring the toy when the experimenter was throwing it), they were listed as dropouts and could not take part in the experiment. Eight dogs did not meet this precondition, either because they did not fetch any toy or because they always had a stronger preference for one of two objects.

The second precondition to participate successfully in the test was that dogs entered the target room (with E1 and E2, but also alone) in a short familiarization phase before the experiment without showing fearful behavior and fetched the toy at least once in the test (see procedure). Two dogs did not meet this precondition.

Materials

All tests were performed in the testing facilities of the dog lab at the Max Planck Institute for the Science of Human History in Jena. The pretest took place in the small test room (4.0 × 4.0 m), whereas the main test took place in Compartments 1 and 2 that were interconnected as depicted in Figure 1a. Compartment 1 consisted of two large rooms (13.0 × 5.0 m and 7.0 × 5.0 m) with a connecting double door. Compartment 2 was the target room where the target was hidden (3.5 × 3.5 m; this room was a former kitchen that had not been used for 1.5 years before the experiment started). The shortest distance between the starting point in Compartment 1 and the target in Compartment 2 was about 18 m.

Dogs were tested by two experimenters, E1 and E2. E1 was a member of the dog lab and was unfamiliar to the dog. For practical

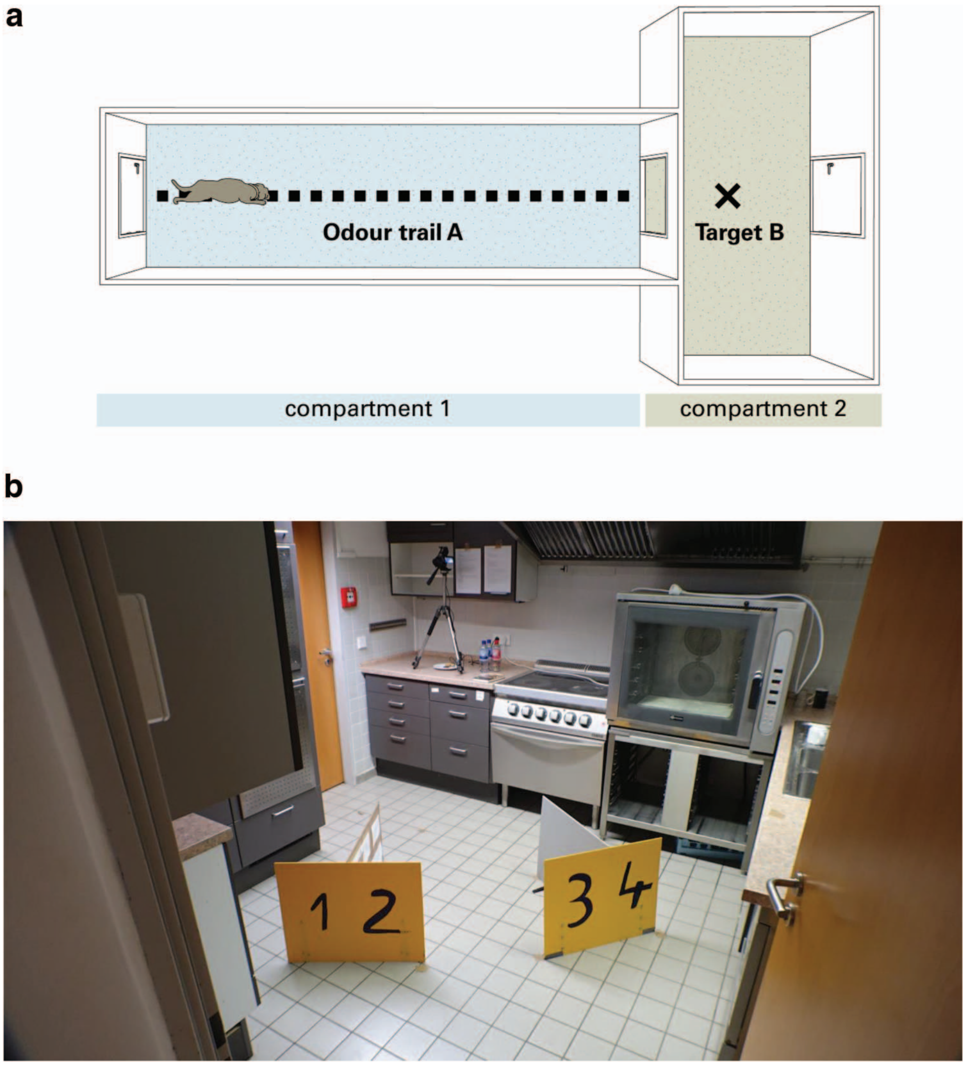

Figure 1. (a) Schematic setup of the experiment. (b) Target room with barriers. See the online article for the color version of this figure.

reasons, E2 could be either the dog's owner/handler (for 20 working and 14 family dogs) or a member of the dog lab (for five working and nine family dogs). The material for this experiment included toys such as balls, kongs, and ropes made out of rubber, leather, or cloth. Depending on her/his preferences, each dog was tested with a particular combination of two toys (usually consisting of similar materials, e.g., ball and kong), which had the same value for the tested dog. These toys were not new, dogs had played with them before, either in the dog lab or in their homes. Moreover, both toys were handled by E1 and E2 before and during the test; thus, the toys contained odors of E1, E2, and the subject dog and were not cleaned between trials. E1 regularly walked through both compartments, and E2 did so at least once during the familiarization phase. Care was taken that the toys were only carried through the compartments in plastic bags, except when they were slid on the floor and when the dog fetched one of them to E2. If the toys were not needed in the test, they were placed separately into plastic ziplock bags, then into a plastic box, and finally in the storage room located close to Compartment 2.

Before the experiment started in Compartment 1, little color markers (1 × 4 cm) were taped to the floor at a distance of about 2 m. These markers indicated four different routes in red, yellow, blue, and green that did not cross each other, so that the toy was not always slid on the same route (see below) and E1 could clean the predetermined route after each trial. In the target room (Compartment 2), two t-shaped barriers made of plastic were located 55 cm apart and about 2 m away from the entrance of the target room. Each barrier had a size of 60 × 50 cm with a dividing barrier of 60 × 50 cm in the perpendicular direction, so that two hiding places were formed. These four spots behind the two barriers, which were labeled with numbers from 1 to 4, served as hiding places for the toy and, thus, blocked visual access when the dogs entered the room (Figure 1b). All trials, including the pretest, were video-recorded. There were two cameras installed in the target room, Camera 1 that filmed the whole Compartment 2 and Camera 2 that filmed in the direction of Compartment 1.

Procedure

After a short familiarization phase in the compartments and after passing the pretest, the subject waited in the small test room. Both objects, which were successfully evaluated as equally interesting in the pretest, were put separately into ziplock plastic bags, which were then closed. Depending on the condition, E1 took one of the toys out of the plastic bag and slid it with pressure on the starting point in Compartment 1. Then, E1 continued sliding the object on the floor through Compartment 1 following one of the four routes indicated by the color markers. When she entered Compartment 2, she slid the object on a direct path that ended at one of the four hiding places. Both the color of the route and the hiding place were predetermined. Then, the toy was put back into the plastic bag and taken out of the test rooms into the box in the storage room. Immediately after that, E1 either carried the same toy back, took it out of the plastic bag, and placed it in the hiding place (baseline condition) or carried another toy back, took it out of the plastic bag, and placed it in the hiding place (surprise condition).

Then, E1 left Compartments 1 and 2 and the subject was brought to Compartment 1 by E2. Once they had entered, E2 drew the dog's attention to the starting point of the odor trail by pointing at it, released the dog from the leash, and gave the command "Search for it! Fetch it!" (in German: "Such‘s! Bring‘s her!"). E2 did not know which toy was hidden and whether it had been replaced.

While the dog explored the room, E2 motivated him/her by talking to him/her and repeating the command. E2 usually stayed close to the starting point, but in cases where the dog had problems finding the toy, she was allowed to follow the dog halfway into Compartment 1, but not so far that she was able to see the toy in the hiding places. After fetching the toy, the dog was praised and allowed to play with the toy for a while in an additional room before the next trial started. If the dog, however, did not fetch the toy within 120 s, the trial was over, E1 entered through Compartment 2 and showed the toy to the dog, but the dog was not allowed to play with it. Between each trial, there was a break of at least 10 min. During that time, the dogs stayed in the small test room and the floors of the two compartments were cleaned with a mild detergent (Frosch® Neutral Reiniger; Erdal Rex, 55120 Mainz, Germany), in particular at the color marks of the previous trial.

Design

We used a within-subjects design, and dogs were presented with four conditions. We manipulated the colored routes where the toys were slid on the ground, the hiding places in Compartment 2, and whether there was an agreement between Toy A (toy slid on the ground) and Toy B (toy found behind the cupboard), resulting in two baseline and two surprise conditions. Every dog was confronted with each of the following four conditions (counterbalanced):

(1) *Baseline AA*: Toy A was slid on the floor to produce an Odor Trail A. Toy A was also present/hidden behind one of the hiding places in Compartment 2.

(2) *Baseline BB:* Same as Baseline AA with the alternative in the toy being used. In this condition, Toy B was slid on the floor and also found behind one of the hiding places in Compartment 2.

(3) *Surprise AB*: Contrary to the baseline conditions, the surprise condition varied in the toy slid on the floor and the toy found in Compartment 2. In this condition, Toy A was slid on the floor and Toy B was found behind one of the hiding places.

(4) *Surprise BA*: Likewise, as in Surprise AB, there is a difference in the odor trail that is produced by a toy and the toy found. More precisely, Toy B was slid on the floor and Toy A was found behind one of the hiding places.

The hiding places, which were labeled with numbers from 1 to 4, were also assigned in randomized order. Each dog was tested once in each of the conditions, resulting in a total of four trials. Half of the dogs started with the baseline condition and half of the dogs started with the surprise condition (i.e., 12 dogs started with one of the four conditions, so the order of each condition was *Baseline AA, Baseline BB, Surprise AB, Surprise BA*). The subsequent three trials were counterbalanced in the 24 possible orders, so that each order of conditions was experienced by two dogs. The total duration of the experiment was about 60 to 90 min.

Data Scoring and Analysis

The behavior of the subjects was coded from the videos of Camera 1 in the target room (as the angle of Camera 2 was too narrow for useful coding of the behavior in Compartment 1). We coded the latency until subjects fetched the toy, the occurrence and the kind of sniffing behavior, hesitation before fetching the toy, whether dogs approached the toy directly, and what hiding places the dogs visited before finding the toy.

(1) For latency, the time was measured from the closing of the door of Compartment 1 until the dog took the toy into his or her mouth before immediately carrying it back through the door of the target room to bring it to E2.

(2) The occurrence of sniffing was defined as (a) dog performed an audible sniffing noise, (b) dog moved his or her nose to within 3 cm of the floor or toward an object (such as barrier) while mouth was closed, or (c) dog held closed mouth in the air. When sniffing occurred, we distinguished between two kinds of sniffing: ground-scenting (all sniffing occurred within 3 cm of the floor/an object) and air-scenting (all sniffing occurred with head in the air), so that in a given trial, dogs could either show air-scenting only, ground-scenting only, or air- and ground-scenting.

(3) Hesitation was defined as either not immediately approaching and fetching the toy, even though the dog obviously detected it (as her/his muzzle was directed at it within a distance of less than a meter), or approaching and grabbing it but dropping it again (see online supplemental materials for an example video clip). This was easy to distinguish from trials with no hesitation, as dogs usually approached and fetched the toy immediately using the shortest approach after detecting it.

(4) Direct approach was coded when dogs directly went to the object after entering the target room using the same route as the object when it was slid on the floor.

(5) Visiting a hiding place was coded when subjects approached an empty hiding place and sniffed there with their nose on the floor.

A coder who was unaware of the goal of the study scored 20% of the trials to assess interobserver reliability. Interobserver agreement was above 0.9 for all measures (Spearman $r = .97$, $N = 38$ for latency; Cohen's $\kappa = 1.00$, $N = 40$ for sniffing; Cohen's $\kappa = 0.91$, $N = 39$ for hesitation; Cohen's $\kappa = 0.93$, $N = 37$ for direct approach; Cohen's $\kappa = 0.95$, $N = 40$ for visiting an empty hiding place).

All statistical tests were nonparametric two-tailed and the alpha level was set to 0.05: We used Friedman's test, Cochran's Q test, Wilcoxon's signed-rank test, and McNemar's test for comparisons between conditions; Mann–Whitney U test and Fisher's exact test for comparisons between groups and trials; and binominal test to test whether a hiding place was revisited. We analyzed the differences between the conditions, evaluated search strategies, and compared the performance of two groups of dogs with or without special training in odor tracking. The color of the routes did not influence the performance of the subjects (latency: Friedman $= 2.68$, $N = 37$, $df = 3$, $p = .344$; sniffing: Cochran's Q test $= 2.47$, $df = 3$, $N = 48$, $p = .515$; hesitation to fetch the toy: Cochran's Q test $= 2.79$, $df = 3$, $N = 39$, $p = .452$; direct approach: Cochran's Q test $= 0.379$, $df = 3$, $N = 37$, $p = .976$).

Results

All dogs solved the problem and fetched the toy within 120 s in nearly all trials. Only 11 out of 48 dogs did not fetch the toy in all trials (nine of these dogs failed in the first trial). This was independent from condition (dogs failed to fetch the toy in nine trials in the baseline and five trials in the surprise condition, Wilcoxon's test: $t = 27.00$, $N = 8$, $p = .289$), but working dogs tended to perform better than family dogs (eight family and three working dogs failed once or twice; Mann–Whitney U $= 217.50$; n1 $= 23$; n2 $= 25$; $r = .30$; $p = .056$). See Table 2 for the mean values of the coded behavior and online supplemental materials for a detailed data file of all behaviors.

Surprise Versus Baseline

Overall, dogs did not hesitate more in the surprise compared with the baseline condition (Wilcoxon's test: $t = 44.00$, $N = 12$, $p = .724$), and they did not fetch the toy faster in the baseline condition compared with the surprise condition (Wilcoxon's test: $t = 606.00$, $N = 47$, $p = .639$).

However, when only considering the first trial, significantly more dogs hesitated to fetch the toy when it was replaced (surprise condition) compared with the baseline condition (Fisher's exact test: $p = .026$, $N = 41$; Figure 2). Regarding the latency to fetch the toy, there was no significant difference between conditions in the first trial (Mann–Whitney U $= 172.50$; n1 $= 21$; n2 $= 18$; $r = .064$; $p = .651$).

Table 2

Mean Values for the Coded Behaviors of the Working Dogs and Family Dogs (Values for the First Trials in Brackets)

Educational background	*M* % of trials fetching the toy within trial	*M* latency until fetching the toy in seconds	*M* % of trials sniffing behaviour	*M* % of trials hesitation	*M* % of trials direct approach
Family	88 (69)	35 (60)	72 (85)	20 (41)	21 (19)
Working	97 (92)	38 (43)	78 (79)	12 (13)	28 (22)

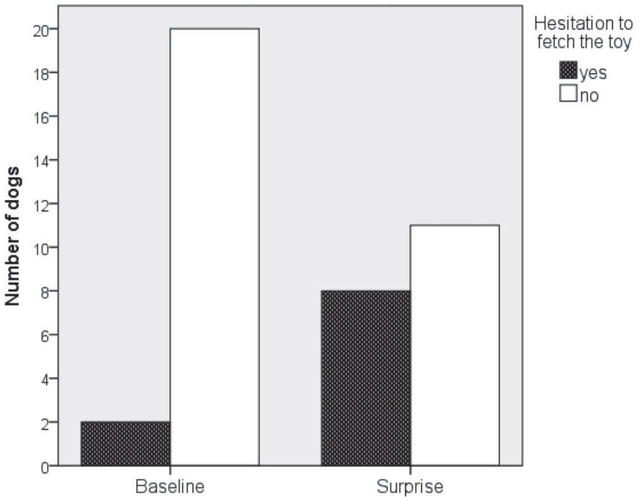

Figure 2. The numbers of dogs that did and did not hesitate in the baseline and the surprise condition in the first trial.

Search Strategies

Dogs showed sniffing behavior in 75% of the trials, indicating that they often used their sense of smell to find the object in the target room. In some of these trials, dogs showed air-scenting only (21% of all trials) or ground-scenting only (15% of all trials) but usually both (38% of all trials). It is not surprising that it took dogs longer to fetch the toy in trials when they sniffed compared with when they did not sniff (Wilcoxon's test: $t = 355.50$, $N = 29$, $p = .002$). Similarly, they took more indirect approaches when they sniffed than when they did not sniff (Wilcoxon's test: $t = 276.00$, $N = 23$, $p < .001$).

Interestingly, dogs showed a different search behavior depending on the place where the toy was hidden, although all four hiding places were easily approachable and did not differ much in their distance from the door of Compartment 2 (see also Dumas & Dorais Pagé, 2006). There was a significant difference in sniffing behavior depending on hiding place (Cochran's $Q = 28.06$, $N = 43$, $df = 3$, $p < .001$). In particular, dogs sniffed in more trials when the toy was hidden in Hiding Place 1 or 4 compared with Hiding Place 2 or 3 (McNemar's test: 1 vs. 2, $N = 45$, $p < .001$; 1 vs. 3, $N = 47$, $p < .001$; 1 vs. 4, $N = 45$, $p = .625$; 2 vs. 3, $N = 46$, $p = 1.000$; 3 vs. 4, $N = 46$, $p = .002$). Similarly, there was a difference in the kind of approach (Cochran's $Q = 29.62$, $N = 37$, $df = 3$, $p < .001$). Dogs never or rarely approached Hiding Places 1 and 4 directly but approached Hiding Places 2 and 3 significantly more often directly (McNemar's test: 1 vs. 2, $N = 42$, $p < .001$; 1 vs. 3, $N = 43$, $p < .001$; 1 vs. 4, $N = 38$, $p = .125$; 2 vs. 3, $N = 45$, $p = 1.000$; 2 vs. 4, $N = 40$, $p = .003$; 3 vs. 4, $N = 41$, $p = .003$). However, there was no difference between hiding places in the latency to fetch the toy (Friedman = 3.36, $N = 35$, $df = 3$, $p = .366$) and in hesitation to fetch the toy (Cochran's Q test = 2.36, $df = 3$, $N = 37$, $p = .547$).

During their search, 39 out of 48 dogs went in some trials to a hiding place in which the toy was not hidden. It turned out that in 36 out of 61 cases (62%), dogs revisited the hiding place in which the toy was hidden in the trial before (note that for this analysis, the first trial was excluded). Assuming that the probability that dogs visit one of the four hiding places is 25%, there was a significant effect for dogs revisiting the correct place of the previous trial (binominal test: $N = 61$, $p < .001$). This suggests that dogs used a win–stay strategy. Dogs also became much faster at fetching the toy between the first trial and the fourth trial (Wilcoxon's test: $t = 614.00$, $N = 38$, $p < .001$), but they did not change their behavior over time in the other measures (McNemar's test: sniffing: $N = 44$, $p = .727$; hesitating to fetch the toy: $N = 41$, $p = .146$; direct approach: $N = 38$, $p = 1.000$).

Difference Between Groups

Surprisingly, in the comparison of all trials, there was no significant difference in all measures between the two dog groups of different educational background. Considering only the first trial, however, the working dogs were significantly faster to fetch the toy than family dogs (Mann–Whitney U = 102.50; n1 = 16; n2 = 23; $r = .30$; $p = .019$), but this effect was not there in the fourth trial (Mann–Whitney U = 268.50; n1 = 22; n2 = 25; $r = .08$; $p = .895$). Figure 3 shows that family dogs were slower to fetch the toy in the first trial but improved their searching behavior, so that they became as fast as working dogs. For the direct approach, there was no difference in the behavior of the working and the family dogs in the first trial (Fisher's exact test: $p = 1.000$, $N = 39$) but a significant difference for the fourth trial (Fisher's exact test: $p = .025$, $N = 47$), indicating that working dogs approach the toy more often directly in the last trial than family dogs. For the other measures, there was no difference.

Finally, we tested whether E2's identity, as either the owner of the dog or not, influenced the dog's behavior. Whereas there was no difference in fetching the toy (21% of dogs tested with E2 as owner and 29% of dogs with E2 as stranger did not fetch the toy in all trials), dogs hesitated less often when E2 was the owner (Mann–Whitney U = 134.00; n1 = 14; n2 = 34; $r = .41$; $p = .006$). Moreover, when E2 was the owner, dogs were significantly faster to fetch the toy in the first trial (Mann–Whitney U = 82.00;

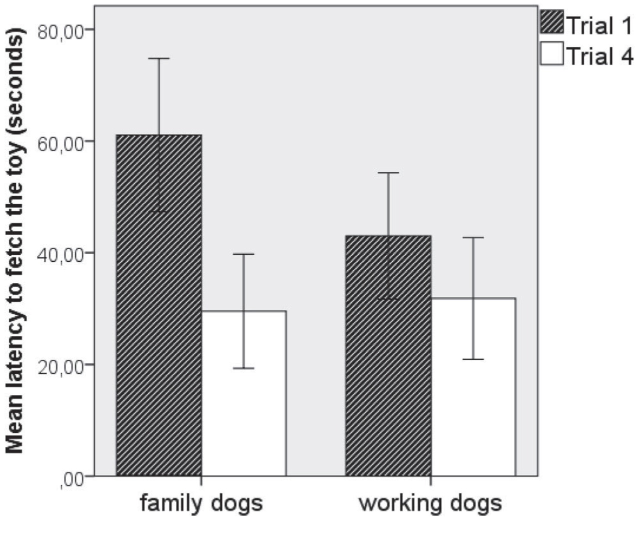

Figure 3. The mean latency to fetch the toy in the first and the last trial for the family dogs and the working dogs (error bars represent 95% confidence intervals).

n1 = 11; n2 = 28; r = .41; p = .023) but not in the fourth trial (Mann–Whitney U = 215.50; n1 = 13; n2 = 34; r = .06; p = .883). For all the other measures, there was no difference. More importantly, the whole analysis with only the dogs tested with E2 as owner (N = 34) revealed exactly the same result patterns as for all dogs (see online supplemental material), indicating that—although dogs tested with owners hesitated less and were faster in the first trial—there was no interaction between owner identity and performance in the two conditions or over trials or between the two groups.

Discussion

Dogs in the current study successfully found and fetched a toy that was hidden in another room. In the first trial, significantly more dogs hesitated to fetch the toy when it was replaced, that is, when the odor trail of the toy was not identical with the hidden toy (surprise condition) than when it was not replaced (baseline condition). Our results suggest that dogs (a) could distinguish between the two toys by odor, (b) tried to localize the identified toy, (c) represented what they smelled—that is, they had an expectation of what they would find at the end of the trail and did not simply perceive the odors of the given toy as positive stimuli, and (d) hesitated less in general when they were tested with their owner.

However, the effect of hesitation was only present in the first trial. In subsequent trials, dogs did not hesitate more often when the object was replaced. It is highly unlikely that dogs no longer had an olfactory expectation in subsequent trials, but there are two possible explanations for that finding that are not mutually exclusive. First, due to their excellent olfactory sense, it is not unlikely that dogs still perceived the smell of previous trials. We tried to avoid this by using different routes (that we marked with color stripes so that the experimenters could find them) for each trial and by cleaning the track after each trial with a mild detergent that does not prevent dogs from using their nose. Moreover, according to dog professionals, even naïve dogs have a tendency to follow the most recent track, which has ecological implications, as in a variable environment, the most recent information should be weighted more because it is more certain (Devenport & Devenport, 1993).

Second, it was also possible that, as dogs were always rewarded with playing as long as they fetched an object, they learned rapidly (a) that it did not matter whether they fetched the toy that corresponded with the odor trail and (b) to search for the toy determinedly in the target room. It is possible that from the second trial on, the dogs relied more on the visual prompts like the barriers than on the olfactory trail, as they now knew the task. However, there was no decrease in sniffing behavior over the trials, indicating that the dogs still used olfaction in Trials 2 through 4.

That leads to the question of how the dogs understood what they were searching for. Gadbois and Reeve (2014) referred to three processes to localize olfactory stimuli: searching, trailing, and tracking. "Searching" requires subjects to have an identified target. The only cue the dogs in the current study received was that E2 pointed at the starting point of the odor trail and said to the dog "Look for it! Bring it!" These cues were obviously sufficient for all dogs to fetch the toy in most trials. The dogs then "trailed," that is, tried to localize the identified target by sniffing. What odors dogs used to trail (i.e., what volatiles of the toy) and how the airflow influenced the scent remain unclear but were not the questions of the current study.

Interestingly, dogs rarely "tracked" by following the exact path of the target by sniffing only the floor (Gadbois & Reeve, 2014; Miklosi, 2007; Thesen, Steen, & Døving, 1993). This is illustrated by the fact that dogs in the current study hardly ever approached the outer hiding places (1 and 4, respectively) directly. Thus, they did not follow the track exactly in the way that the object was slid to the baited hiding place. Indeed, even police dogs trained for man-trailing do not exactly follow the track of the target person but take shortcuts (personal observation during training sessions of the K9 unit of the Thuringia state police).

Remarkably, dogs in the current study sniffed more often when the object was hidden in the outer hiding places, but they were not slower in fetching the toy in those cases. In accordance with previous studies, in which dogs searched for their owners or food (Polgár et al., 2015), this may suggest that dogs search for the object by vision and learned strategies, using their nose merely in cases when it is necessary (see also below). Indeed Gagnon and Doré (1992) found that dogs sniffed more in difficult than in simple object permanence tasks and concluded that dogs might gather information from other sensory modalities when one was not sufficient. Indeed, in the current study, dogs either found the object on their direct approach or sniffed on the indirect approach, also suggesting that they sniffed in particular when they did not find the toy by vision. Both strategies were obviously effective, as dogs were equally successful (i.e., equally fast) in fetching the toy in all four hiding places, indicating that they either found the toy during their—often direct—approach to the inner hiding places or sniffed and then found the toy in the outer hiding places.

It is not surprising that dogs also improved their searching behavior over time and fetched the toy much faster in the last trial compared with the first trial. Probably their familiarity with the visual setup and task helped them fetch the toy faster, but they still used their nose for sniffing, which did not decrease over the trials.

The dogs also often revisited the hiding place in which the toy was hidden in the previous trial. This win–stay strategy is in line with previous findings (Polgár et al., 2015, see above). In a study by Claude Dumas (1998), dogs had to retrieve a hidden object on the basis of the place (or the feature) of the hiding location. Dogs associated spatial cues (but not feature information) and followed egocentric search criteria (see also Fiset, Gagnon, & Beaulieu, 2000; Fiset, Landry, & Ouellette, 2006). Kaminski, Fischer, and Call (2008) tested two specially trained dogs that had to fetch two sets of objects that were placed in two rooms. Subjects were asked to retrieve the objects that were called by name, one after the other. Both dogs successfully retrieved the correct objects. One dog was even able to integrate information about the object's location, as from the second trial on, he chose the correct location in which the object had been placed. Similar to these findings, dogs in the present study took into account what they had experienced in the trial before.

One further aim of the current study was to compare the two groups of dogs with or without special training in odor tracking. As expected, working dogs were significantly faster to fetch the toy than normal family dogs in the first trial, and they also approached the toy often more directly in the last trial. One also might speculate that the working dogs would not search for the toy but for the targets they were trained for (drugs, explosives, corpses, and living humans). However, that the dog handler pointed to the starting point of the odor trail was obviously sufficient enough for the working dogs to adapt to the new task.

Surprisingly, the working dogs were not faster in the fourth trial, and overall, working dogs did not outperform family dogs. Thus, family dogs learned within four trials to be as effective as working dogs. These results could reflect a ceiling effect, that is, the task was so simple that the working dogs were unable to show further improvement. However, as it still took working dogs about 30 s on average to fetch the toy from a distance of about 18 m (see Figure 3), it is also possible that they always performed the strategic search they were trained for. Other studies that compare the performance of working and nonworking dogs have produced mixed results. Whereas dogs with special training outperformed family dogs in understanding the communicative intent of a human (Kaminski, Tempelmann, Call, & Tomasello, 2009), working dogs were not better than family dogs in using communicative cues to locate hidden food (Gácsi, Kara, Belényi, Topál, & Miklósi, 2009). Furthermore, in a study by Topál, Miklosi, and Csanyi (1997), in which dogs were observed in a simple problem-solving task, working dogs did not outperform nonworking dogs. Instead, dogs' problem-solving abilities depended on their kind of relationship to their owner/handler. Indeed, also in the current study, dogs showed more hesitation to fetch the toy and were slower (in the first trial) when the person asking for the toy was unfamiliar to them, suggesting that it was less obvious to these dogs what to do.[1] Thus, it is likely that education per se—that is, training for a specific duty, including an exam—does not improve the performance of dogs in a given task, but many other factors play a role here, that is, the kind of training, the kind of task, and the relationship to the dog handler (Polgár et al., 2016).

In conclusion, our results confirm that dogs can use olfactory information in an adaptable way: Their hesitation in the first trial indicates that dogs indeed represented what they smelled—that is, had an expectation about which toy they would find in the end of the trail. We also found that family dogs improved their searching behavior quickly and that dogs do not always use their nose but also search for the object using their vision and the win–stay strategy. It is an open question how these issues are linked together, that is, what factors play a role (such as the target, education, previous experience, and relationship to the handler) so that dogs use their nose or other search strategies.

As for dogs, for other macrosmatic animals, we currently lack knowledge about how exactly olfaction and cognition are linked. Plotnik, Shaw, Brubaker, Tiller, and Clayton (2014) found that Asian elephants relied on olfaction to locate food and to exclude nonrewarding food locations but failed to use auditory information. Likewise, in rodents, olfaction seems to be the main sense used to explore the environment (Lavenex & Schenk, 1998; Maruniak, Darney, & Bronson, 1975), and olfactory cues play an important role in kin recognition and individual recognition (Drickamer, 2001; Hurst, 1993; Klemme, Eccard, Gerlach, Horne, & Yloenen, 2006; Solomon & Rumbaugh, 1997). The question is whether other macrosmatic animals besides domestic dogs represent what they smell and, thus, have a clear expectation when they smell something—or whether they perceive the smell as a positive or aversive stimulus. For rodents, the latter could be hypothesized, as captive rodents that have no experience with predators also react to odors of their predators (Ylönen, 2001). It is also possible, however, that olfaction is linked with cognition in a similar way in such distinct macrosmatic animals as carnivores (Green et al., 2012), rodents, and elephants.

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[1] Note also that the two dogs that showed hesitation to fetch the toy in the baseline condition in the first trial were tested by an unfamiliar person.

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Metacognition in dogs: Do dogs know they could be wrong?

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Abstract
In the current study, we investigated the question of whether dogs were sensitive to the information that they themselves had or had not acquired. For this purpose, we conducted three consecutive experiments in which dogs had to find a reward that was hidden behind one of two V-shaped fences with a gap at the point of the V. This setup allowed us to distinguish between selecting one of the fences by walking around it and seeking additional information by checking through the gap in the fence. We varied whether dogs had visual access to the baiting procedure or not. In addition, we manipulated the type and quality of reward as well as the time delay between baiting and choosing to analyze if the dogs' searching behavior was affected. Our results were partly consistent with the findings of Call (Animal Cognition, 13 (5)*,* 689–700, 2010) with great apes, on whose findings we based our experiments. We found that dogs checked more often through the corner of the V-shaped fence when they had not seen where the reward was hidden. Interestingly, dogs rewarded with toys selected the correct fence more often than dogs rewarded with food. Even though dogs' performance was not affected by the food quality condition, dogs were significantly faster in fetching a high-quality food reward as opposed to a low-quality food reward. When testing whether forgetting and checking would increase as a function of delay, we found that although dogs slightly decreased in their success in finding the food when time delays were longer, they were not more likely to check before choosing. We show that – similar to apes – dogs seek additional information in uncertain situations, but their behavior in uncertain situations is less flexible compared to great apes.

Keywords Metacognition · Domestic dog · Seeking information · Comparative psychology

General introduction

While in recent years much attention has been given to what animals understand about each other, only little is known about what animals understand about their own mental processes. Moreover, the evolutionary origins of metacognition – the ability to access, monitor, and control one's own perceptual and cognitive processes and, thus, know about one's own cognitive potentials as well as limitations (Flavell, 1979; Hertzog & Hultsch, 2000; Smith, Shields, & Washburn, 2003; Zohar, 1999) – are still widely debated (Rosati & Santos, 2016). The question therefore arises whether human-like forms of metacognition exist in other species (Carruthers, 2008; Crystal & Foote, 2011; Hampton, 2009; Kornell, 2009; Smith, Beran, Couchman, & Coutinho, 2008). Thus, the general issue we raise here is whether animals have access to what they have seen and what they know, and whether they seek additional information in situations of uncertainty.

However, the question is not only whether animals share humans' capacity for metacognition (Foote & Crystal, 2007; Smith, Shields, & Washburn, 2003; Smith, 2009), but also what the best methods are for studying non-linguistic behavior for evidence of metacognition in animals. Comparative psychologists have conducted cognitive tests on non-human animals to determine whether they possess knowledge of their own cognitive states by using memory and food concealment as well as perceptual and information-seeking paradigms (Kornell, 2014). It seems that some animals make certain judgments in similar ways to humans, although not by directly

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accessing their memories but rather by drawing inferences based on cues like ease of processing and reaction time (Kornell, 2014).

Griffin (2004) has emphasized that all animals regularly face uncertain situations, not only when they have to read social signals but also when they have to make a determination about the presence of a predator or available food. It is essential for survival to evaluate ambiguous information. Therefore, it is clearly advantageous to differentiate between certain and uncertain situations, paying the cost of seeking extra information only when it is really necessary (Griffin, 2004). In a number of different experiments, it has been shown that humans, dolphins, monkeys, and rats refuse to complete trials that are difficult, such as at a threshold in an auditory discrimination task. In other words, when the task is difficult, the risk of failing at a task, and therefore not receiving a reward, is so high that it might not be worth the cost of trying. In some cases, a wrong choice could, additionally, result in a time-out (rhesus macaques: Hampton, 2001; Smith et al., 2006; rats: Foote & Crystal, 2007; orangutans: Suda-King, 2008; also, see Smith et al., 2003 and Smith, 2009 for reviews). Additionally, it has been argued that subjects perform better in tests when they have the option to decline trials as compared to when they are forced to make a decision (Foote & Crystal, 2007; Hampton, 2001). These results can be interpreted as evidence for the fact that these species know what they remember (but see Browne, 2004 and Carruthers, 2008 for different interpretations).

Several researchers have criticized such methods by arguing that the results of these tests could be interpreted in an associative-behaviorist way (Smith, Zakrzewski, & Church, 2016). More precisely, in a more difficult trial an uncertainty state is created when a perceptual threshold is exceeded. By using the uncertainty response, the animal will know about knowing or not know whether it will successfully pass trials that are at the perceptual threshold (Smith, Beran, Couchman, Coutinho, & Boomer, 2009). However, studies using uncertainty responses have been criticized because the animals' behavior might solely be based on learned responses to a specific stimulus (Carruthers, 2008; Crystal & Foote, 2009).

Call and Carpenter (2001) introduced a novel and different approach to the question of metacognition: the information-seeking paradigm that does not require extensive training or prior knowledge. The key features of this more naturalistic approach are that animals can seek additional information when needed, which enables them to respond accordingly as soon as they have gathered the relevant information (Call & Carpenter, 2001). The experimental set-up in Call and Carpenter's study consisted of two parallel tubes that chimpanzees, orangutans, and 2.5-year-old children observed. The tubes were placed on a platform with their openings oriented towards the subjects. Then the experimenter placed a piece of food inside one of the tubes while ensuring that the subject was aware of the baiting procedure. In order to receive the reward, they had to touch the baited tube containing the bait on the first attempt. They introduced two conditions: in one condition, the subjects witnessed the baiting process (Seen condition), while in the other condition, baiting took place behind an opaque occlude that blocked the subjects' visual access to the bait (Unseen condition). All subject groups spontaneously bent down more often to look inside the tubes before making a decision during the Unseen condition. The authors concluded that subjects had access to their own mental states (Call & Carpenter, 2001).

The information-seeking paradigm has been subject to criticism on the grounds that animals could just engage in a routine by looking for information instead of applying metacognitive abilities (Call, 2010). Call (2012) pointed out two sorts of alternative explanations of a non-metacognitive nature. One alternative non-metacognitive approach is the broad-beam explanation, which states that a non-metacognitive construct actually accounts for the observed results in studies on animal metacognition and not on monitoring processes of knowledge states. The second approach is the narrow-beam hypothesis (see Call, 2012), which claims that subjects who lack information about a reward's location engage in search behavior until they find it. Many animals are presumably engaged in this so-called "search, locate, retrieve routine," which might be an alternative explanation for the results in the hidden and visible trials. To address this issue, Call (2010) introduced five conditions to test the flexibility of the information-seeking behavior in great apes. He referred to the so-called "Passport Effect," i.e., that in humans as well as in other animals, whether an individual will search for extra information depends on various factors, such as the value of the "reward" (i.e., a passport is more valuable than a tram ticket) and the time delay between hiding and searching (i.e., re-checking for the passport when it was packed yesterday, but not 5 min ago).

In his study, Call (2010) introduced five conditions, manipulating (1) whether subjects had visual access to the baiting, (2) costs associated with seeking information, (3) food quality, (4) additional information offered regarding the food's location, and (5) the time delay between baiting and selecting one of the hiding places. Call concluded that his ape subjects knew that they could be wrong and that "the looking response appears to be a function of at least three factors: the cost of looking inside the tube, the value of the reward and the state of the information" (p. 699).

The domestic dog (*Canis familiaris*) represents an interesting model to study animal cognition as during the long domestication process dogs have evolved special skills to function effectively in the human environment, such as reading human social and communicative skills (Marshall-Pescini & Kaminski, 2014), in which they even outperform great apes (i.e., Bräuer et al., 2006; Hare et al., 2002). However, the literature has no consensus on metacognition in dogs, i.e., whether they have knowledge of their own cognitive states (Bräuer, Call, & Tomasello, 2004).

McMahon, Macpherson, and Roberts (2010) applied an information-seeking paradigm, where subjects needed to fetch a reward without immediately available information. To fetch the hidden reward, dogs had to seek additional information. More precisely, the experimental set-up was comprised of four boxes, all of which were completely black, except for one box, which had a white side. In an extensive training, dogs learned that the reward was always hidden under the box with the white side. In the experimental manipulation, the boxes were rotated (45°, 90°, and 135°) and, thus, the one white side gradually rotated out of the dogs' view. Their findings show that the dogs' accuracy progressively declined. The authors concluded that if dogs could use additional information, as stated in the information-seeking paradigm, they should have walked around the boxes in order to choose the correct one. In a follow-up experiment, the authors again applied an information-seeking paradigm, but this time in a human-oriented context, to examine whether dogs would seek further information. The reward could be hidden underneath one of three boxes. Before being able to select one of the boxes, dogs had to choose one of two human experimenters, where one was the informant (i.e., person who would point to a location) and the other was the non-informant (i.e., person who would not provide any information by turning his or her back to the dog). Dogs chose the informant significantly more often than the non-informant, which suggests that dogs seek additional information in an information-seeking task when the information source is a human (McMahon, Macpherson, & Roberts, 2010).

Similarly, Bräuer, Call, and Tomasello (2004) investigated whether dogs are sensitive to the information they themselves have acquired. In an object-choice task, dogs were presented with two identical wooden boxes, of which only one contained a baited reward. On one side of each box was a transparent window of glass with holes through which dogs could seek extra information about whether the food was placed in that box, such as by looking or smelling through the window. On the other side of that box there was a lever, and dogs were trained to select one of the boxes by pressing this lever with their paw. In the Seen condition, the location of the reward was shown to the dogs and therefore the dogs had information about the location of the food. In the Unseen condition they were prevented from seeing the baiting procedure by two occluding barriers. Before selecting, the dogs had the opportunity to seek extra information regarding the location of the hidden reward, which would be especially useful in the Unseen condition. The results showed that the dogs selected the correct box in the Seen condition, but performed only at chance level when they were prevented from seeing the reward's location. Most importantly, dogs rarely showed checking behavior before selecting one of the boxes and they did not check more often, as assumed, in the Unseen condition compared to the Seen condition. The authors concluded that their findings might indicate that dogs do not have access to their own perceptual and knowledge states (Bräuer, Call, & Tomasello, 2004).

However, both of these studies about metacognitive abilities in dogs had some constraints. First, training was involved (i.e., pressing the lever in Bräuer et al., 2004, and learning that the food is in the box with the white side in McMahon et al., 2010), and second, dogs were rewarded with food. It is possible that dogs would show a more flexible searching behavior when they searched for their favorite toy – a precise object they "personally" know and that they fetch and that does not "disappear" as they consume it. (Note that in dog studies about object permanence and memory, toys are often used as a reward; see Collier-Baker et al., 2004; Fiset et al., 2003; Miller et al., 2009; Müller et al., 2014.)

More importantly, training could have led to an automatic response in the dogs. Thus, dogs chose a box because they had learned to do so and could not inhibit this response despite their lack of information about the contents of the boxes (Bräuer et al., 2004). Therefore, in the current study we investigated metacognition in dogs using a new set-up in which dogs did not have to learn new behaviors in order to check or to make their decision. As it is clearly adaptive to differentiate between certain and uncertain situations (see above, Griffin, 2004), and as dogs show special social cognitive skills (Marshall-Pescini & Kaminski, 2014), we hypothesized that dogs would show flexible metacognitive skills – comparable to those of apes and human children – when tested in an appropriate set-up.

On the basis of Call's experimental set-up and procedure, we conducted three consecutive experiments in which dogs had to find a reward that was hidden behind one of two V-shaped fences in order to test whether dogs were sensitive to the information that they themselves have or have not acquired and whether they seek extra information in situations of uncertainty. We manipulated the type (Experiment 1) and quality of reward (Experiment 2), as well as the time delay (Experiment 3) between baiting and choosing to analyze if the dogs' searching behavior was affected.

Dogs were presented with a Seen and an Unseen condition. They could make their decision by walking around the V-shaped fence, and they could check before choosing through the corner of the V to see or smell whether the reward was there. Based on the study of Call (2010), we predicted that the dogs would check more frequently before choosing when they had not seen where the reward was baited (Unseen condition) than in cases when they had. We further predicted that dogs would show more flexibility when searching for a toy (being a concrete object they often search for) than when searching for food pieces (Experiment 1); that dogs would be more likely to check when high-quality food was hidden as opposed to low-quality food (Experiment 2); and that for higher time delays between baiting and choosing, dogs would check more or have a reduced accuracy in finding the reward (Experiment 3).

Experiment 1: Does the type of reward impact dogs' accuracy in an information-seeking task?

In the first experiment, we wanted to investigate if the witnessing of baiting (Seen and Unseen conditions) and the type of reward (toy or food) had an impact on dogs' accuracy to find the baited reward. Therefore, we tested subjects in the Seen and Unseen conditions, and half of the dogs searched for food as a reward whereas the other half searched for their favorite toy. We predicted that if dogs did not know what they had seen, they would seek extra information. For the type of reward, we expected the dogs to show more flexibility when searching for a toy (which they often do in their daily life) than searching for food pieces, as the favorite toy is a concrete object that the subjects know.

Methods

Subjects

In total, 48 dogs (22 males and 26 females) of various breeds and ages (range 1.5–11 years, mean 4.6 years) participated successfully in the experiment. All subjects lived as pets with their owners and received the normal obedience training typical for domestic dogs. The dog owners were not present during the test and they were informed about the precise research question as well as about the specifics of their dogs' tasks in the study only after the completion of the test, in order to avoid potential training (by the owners).

The owners decided voluntarily to participate in this study, and if they were interested they were provided with the video material of the performance of their dog after the test was completed. All of the dogs were naïve to the information-seeking task and did not have any prior knowledge of the experiment. They were all healthy individuals with no known sight or hearing impairments and no known history of aggression towards humans. Another precondition for this experiment was that dogs had to be interested in food or toys in order to participate in this study. For the toy condition, owners were asked to bring their dogs' favorite toy to the testing sessions. In total, 24 dogs were rewarded with food and 24 other dogs were rewarded by playing with their favorite toy. Females were not tested during estrous.

Materials

The test took place in a quiet room (8.5 m × 4 m) at Alte Messe in Leipzig, Germany. The experimental set-up (Fig. 1) was comprised of a two-part apparatus. Each side consisted of two V-shaped wooden fence structures (1.20 m × 1.00 m) that were connected with a flexible hinge at the upper end to form a V-shape with a 45° angle. At the lower end of each V-construction was a gap of approximately 2 cm in width, through which the first experimenter (E1) placed the reward as bait on a small plate. Subjects could check whether the reward was actually hidden there or not and make their decision based on this information by walking around the fences. The distance between the corners of both barriers was 1.55 m. A centerline indicated both the exact middle of the room as well as the exact middle of the apparatus. Another marking, 1.60 m away from the corners, indicated the exact position (i.e., the nearest point) at which the dog had to wait at the beginning of each trial. E1 sat in the middle between the two fences and was responsible for baiting the reward, and the second experimenter (E2) was located next to the centerline at the starting position to hold the dog, both facing E1. The dogs had to choose one side and move around the V-shaped fences, which was only possible by walking around the outer sides. Two additional barriers prevented the subjects from passing E1 and going around the inside to fetch the reward. The dogs were rewarded with either food or their favorite toy. In the Unseen condition, a curtain was installed to prevent dogs from witnessing the baiting. All trials, including the pretest, were video-recorded by one camera that was installed directly across from the apparatus.

Procedure and design

All experiments in this study consisted of three consecutive units: familiarization, pretest, and experimental phase. First, each dog received a familiarization to become familiar with the testing room and to understand how to properly find the reward at the corner of the fence. Accordingly, this was followed by a pretest, which had to be successfully passed in order to make sure that all participating subjects understood the experimental set-up. Only dogs that passed the pretest took part in the experiment.

We varied whether subjects received food or their favorite toy as a reward. Therefore, one fundamental assumption was that dogs that participated in this study had either a high degree of interest in food or their favorite toy, and were furthermore motivated to fetch the reward after being released. This was confirmed in the pretest and during the familiarization sessions. As dogs have trouble obtaining a reward that is placed at the inner corner of a V-shaped fence, even if the fence is transparent (Pongracz, Miklosi, Vida, & Csanyi, 2005), we gave subjects the opportunity to investigate the

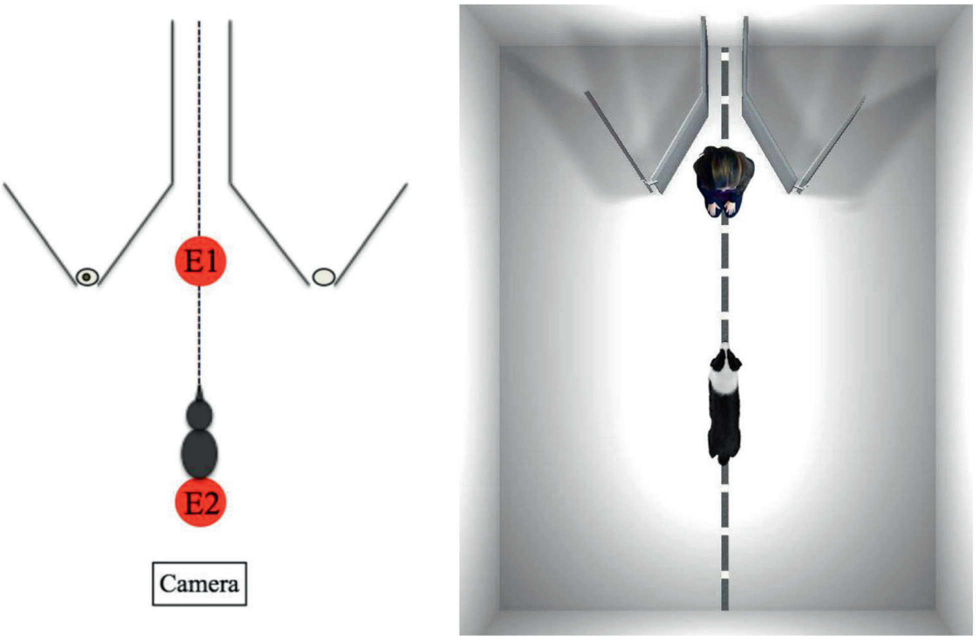

Fig. 1 Basic set-up for Experiments 1, 2, and 3

testing room with the two V-shaped fences before the actual experimental phase (Pongrácz, Vida, Banhegyi, & Miklósi, 2008). Before the final experimental phase began, three dogs were tested in a pilot study. None of these subjects was included in this study. In the following section, we will explain the experimental procedure in more detail.

Familiarization

Before the actual test, we introduced the dogs to the testing room to ensure that they understood the apparatus and were able to find the reward without checking. The familiarization was conducted successively, meaning that the subjects became familiar with the task step-by-step. During the familiarization sessions many breaks were given. Depending on the condition, the dog was either rewarded with food or his or her favorite toy. Similar to the tests, familiarization was always conducted by the same experimenter E1, who baited the reward, and an arbitrary second experimenter E2, who held the dog at the starting position. E1 used a certain command to motivate the dogs to find the baited reward (e.g., German "Ok," "Such!" ("Look!"), "Wo ist es?" ("Where is it?")). When the dog approached the reward he or she was rewarded either by eating the food or by playing with the toy with E1.

At first, E1 led the way and showed the dogs where the treat was placed by walking around the fence and hiding the reward behind the corner. E1 used nonverbal cues, such as pointing, showing, and eye gaze to further assist the dog in finding the treat. After the baiting was finished, the dog was released to search for the reward. In subsequent trials E1 placed the reward through the gap. The procedure was repeated until the subject approached the reward by going around the fence without trying to get the reward through the gap.

The speed of familiarization always depended on the dog's individual learning progress and motivation to find the reward. Dogs were given a break from familiarization either when they performed the action successfully, or when their willingness, motivation, or attention was significantly decreased.

Pretest

In order to pass the pretest, the dogs had to be able to walk around the fence where the reward was placed, without checking. The subjects passed the pretest when they found the reward in four consecutive trials or four out of six trials without checking through the gap. In the pretest, we did not apply any manipulation and therefore subjects witnessed the baiting procedure completely and had no delay between baiting and choosing. Only subjects that passed the pretest could take part in the actual experimental phase in the second and third sessions. However, if dogs showed no interest in participating, if they did not learn to find the food behind the fence within 120 min, or showed no interest in the reward, they were excluded from this study and marked as dropouts. For this reason, we had to exclude six dogs from the study.

Experimental phase

After becoming familiar with the testing room and passing the pretest, the subjects were tested in two consecutive sessions. The general procedure in the experimental trials was the same for all dogs: Two experimenters, E1 and E2, tested all subjects individually. One experimenter (E1) had to be the same person for all trials, as in the pretest. The second experimenter (E2), however, could be any person. At the beginning of each trial the dog was held by E2 at the starting position while E1 knelt between the two fences. E1 then held up the reward to show it to the dog while calling his or her name to get the dog's attention. The baiting process differed according to two conditions:

1) In the Seen condition, E1 baited the reward while allowing the dog to see the baiting process. E1 leaned over one fence and put the reward through the gap onto the plate behind of the fence. E1 then returned to the middle of the fences, placing her arms parallel to her body.
2) In the Unseen condition, E2 closed the curtain so that the dog could not see the baiting process. E1 touched first the left and then the right gap of the two fences while placing the reward through one of them. After that, E1 again touched both gaps simultaneously in order to make sure that the subject could not hear where the reward was baited. Then she went back into the middle of the two fences, placed her arms parallel to her body, and told E2 to open the curtain.

After the baiting process was complete, E2 released the dog and E1 called his or her name and encouraged him or her to find the reward. In both conditions, E1 did not move and avoided giving any cues to the dog. She waited until the dog had made his or her choice by walking around one fence. If the dog chose the correct fence he or she was allowed to eat the food or to fetch the toy, and E1 played with him or her by throwing the toy. If the dog chose the wrong fence, i.e., where the reward was not hidden, E1 took him or her by the collar and led him or her behind the correct fence. E1 showed the reward to the dog but the dog was not allowed to eat it or play with it. After the dogs had eaten the food or played with the toy, or the reward was shown to them (when they were wrong), the trial was over and a new one began.

The reward was placed behind one of the barriers in the Seen condition only when the dog looked and paid attention to E1. The dog's attention was essential for the continuation of the experiment as the dog needed to witness the whole baiting process. After placing the reward, E2 leaned back to the middle and placed his or her arms parallel to his or her body without looking at the dog. It was important that both E1 and E2 did not give any accidental cues (e.g., gaze, pointing, non-verbal cues) and, thus, they looked down at the floor while waiting.

Half of the dogs were tested with the food reward and half of the dogs were tested with the toy reward. They were presented in two sessions on 2 days, so that each dog received the Seen condition 12 times per day and the Unseen condition 12 times per day. Within a session, there was a break after half of the trails. The order of the conditions and the location of the food were randomized, with the stipulation that a condition occurred no more than two trials in a row, and that the food was not hidden on the same side in more than two consecutive trials. Each dog received 24 trials of each of the two conditions, totaling 48 trials (see Online Supplementary Materials for details).

Data scoring and analysis

All trials were analyzed from the videotapes. We scored the following three variables for each trial: success (correct choice), checking, and latency. For success we scored whether the dogs selected the correct fence, having at least the front paws and shoulder behind the outer side of the fence where the reward was baited. For checking behavior we coded whether and where the dogs checked before choosing by approaching the gap, having the mouth less than 10 cm from the gap while hesitating for at least a half a second. Finally, we scored the latency to select a fence in the trials when subjects did *not* check. Therefore, we recorded the time from E1's first call of the dog's name until his or her front paws and shoulder had crossed the outer part of the V-shaped fence.

To assess inter-observer reliability, one independent observer scored a randomly selected sample of 20% of the trials where the dogs were rewarded with food and the trials where the dogs were rewarded with a toy. Reliability was excellent for correct selection (food: Cohen's Kappa=0.98, N=240; toy: Cohen's Kappa=0.98, N=239), for checking behavior (food: Cohen's Kappa=0.95, N=240; toy: Cohen's Kappa=0.77, N=239), and for the latency to select (food: Pearson Correlation r=0.80, N=182; toy: Pearson Correlation r=0.77, N=153).

For the analysis, we used repeated measures 2 × 2 ANOVAS with the within-subject-factor condition (Seen vs. Unseen) and the between-subject-factor reward (food vs. toy). To test for learning over trials, we used repeated measures 2 × 2 × 2 ANOVAS with the within-subject-factors condition (Seen vs. Unseen) and session (first vs. second session) and the between-subject-factor reward (food vs. toy). For comparisons against chance within one condition, one-sample t-tests were used, as indicated.

Results

Success

The dogs selected the correct fence in 94% of the trials in the Seen condition and in 57% of the trials in the Unseen conditio,n and were above chance in both conditions (Seen: t(47)=31.09, p<0.001; Unseen: t(47)=3.90, p<0.001, one-sample t-tests). They performed better in the Seen than in the Unseen condition (F(1.46)=282.04, p<0.001), and they showed increased accuracy when they were rewarded with the toy (F(1.46)=5.95, p=0.019), but there was no interaction between Condition × Reward (F(1.46)=1.77, p=0.190).

Checking

Figure 2 presents the mean percentage of trials in which the dogs checked for the different rewards in the two conditions. The dogs checked more frequently in the Unseen condition than in the Seen condition (F(1.46)=35.69, p<0.001), and they tended to check more when they were rewarded with the toy (F(1.46)=3.91, p=0.054). There was no interaction of Condition × Reward (F(1.46)=0.28, p=0.601).

Checking and success

If subjects checked in the Seen condition, they then selected the correct fence above chance in 95% of the cases (t(37)=20.32, p<0.001, one-sample t-test). Similarly, if they checked in the Unseen condition they were correct above chance in 68% of the cases (t(44)=4.41, p<0.001, one-sample t-test). Thus, the dogs' success rate was higher when they checked in the Seen condition than in the Unseen condition (F(1.35)=40.47, p<0.001). There was no effect of reward (F(1.35)=2.65, p=0.112) and there was no interaction between Condition × Reward (F(1.35)=1.47, p=0.234). Figure 3 illustrates the checking behavior of the two groups of dogs in the Unseen condition.

Latency

Food-rewarded dogs selected a fence faster than toy-rewarded dogs in the cases when they did not check (F(1.45)=12.20, p=0.001), but there was no effect for condition (F(1.45)=2.18, p=0.147) and no interaction effect (F(1.45)=0.06, p=0.816).

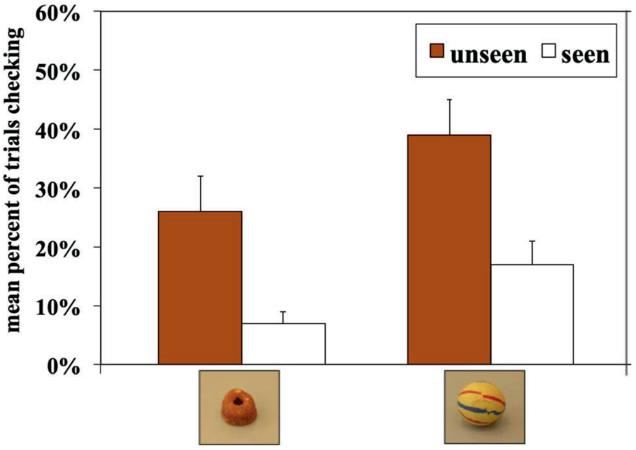

Fig. 2 Mean percent of trials in which the dogs checked for the different rewards in the conditions (+/-SE) in Experiment 1

Learning

Regarding success, we found no learning over trials in this experiment. Subjects did not select the correct fence more often in the second session compared to the first session (F(1.46)=0.008, p=0.930). However, there was a significant interaction effect (Condition × session × reward: F(1.46)=4.429, p=0.041). In contrast, subjects checked more in the first session than in the second session. There was a significant effect for session (F(1.46)=8.099, p=0.007), but no interaction effect.

Individual performance

Individuals were above chance when they selected the correct fence in 18 (75%) out of 24 trials or more (binomial test p=0.5, N=24, P=0.02). Forty-five dogs were above chance in the Seen condition (21 food rewarded and all 24 toy rewarded dogs). Eight dogs were above chance in the Unseen condition (two food-rewarded and six toy-rewarded dogs). Two food-rewarded dogs never checked whereas all toy-rewarded dogs checked at least twice.

Discussion

The dogs checked more often before selecting the correct fence when they did not see where the reward was hidden. They showed a flexible checking behavior, indicating that dogs may have access to their own visual perception. Similar to primates (Call, 2005; Call & Carpenter, 2001; Hampton et al., 2004; Marsh & MacDonald, 2012; Perdue, Evans, & Beran, 2018), they sought extra information when they did not know the reward's location. When dogs did not witness the baiting, they were able to adapt their behavior by gathering additional information that might have led to success; by checking, they could select the correct fence where the reward was hidden. Moreover, they were able to revise their choice when they began their inspection at the wrong fence.

Overall, the dogs showed similar checking and searching patterns to primates. However, there were three differences compared to primates.

First, dogs in general checked less than the apes tested by Call (2010) and Call and Carpenter (2001), and were therefore less likely to be successful in the Unseen condition (they only performed slightly above chance level). Second, having begun checking the contents of the containers before choosing, the apes continued to do so throughout the remaining trials (Call & Carpenter, 2001). For the dogs, we did not find such an effect. Dogs either

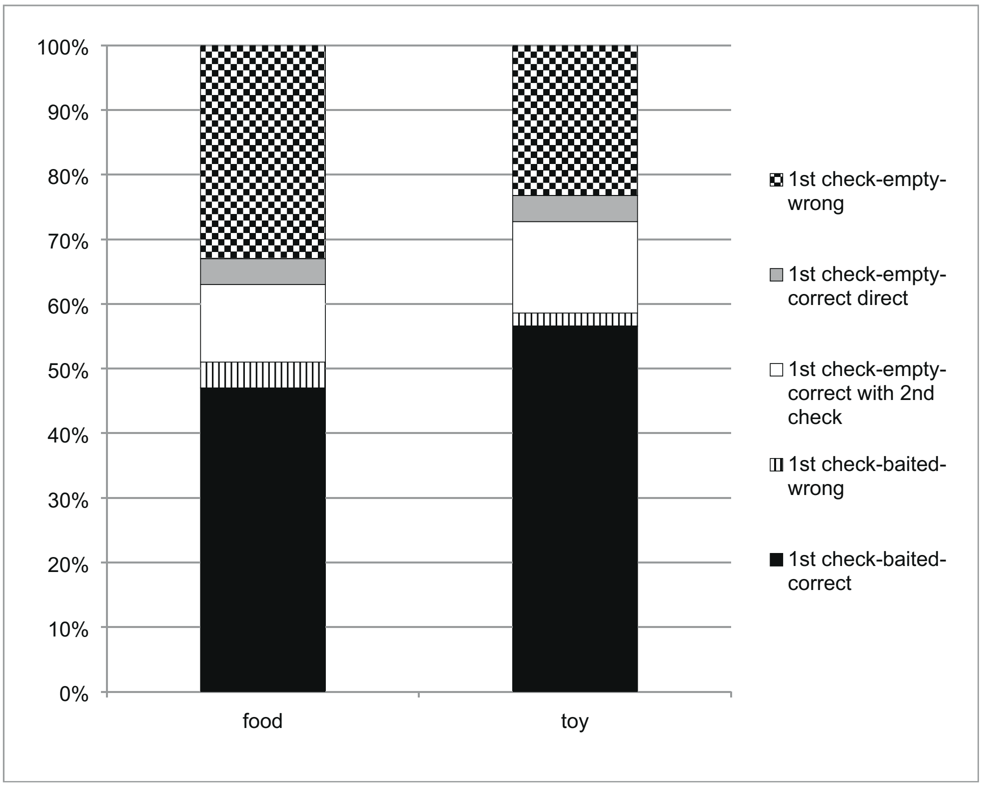

Fig. 3 Percentage of dogs' performance regarding checking behavior followed by their decision for one side depicted for food and toy in the Unseen condition in Experiment 1. Depicted are all five possibilities of dogs' checking behavior with food and toy rewards, i.e., which fence they attempted first when they check and which side they selected. By chance dogs can first check the baited side, then they can either go to the correct side (first check-baited-correct) or – wrongly – to the fence where the reward is not hidden (first check-baited-wrong). When dogs check the wrong side on their first attempt, they can either then select the wrong side (first check-empty-wrong), or they can do a second check at the baited side and select the correct fence (first check-empty-correct with second check), or they can choose the baited side without further checking (first check-empty-correct direct)

checked very often or rarely. Moreover, there was a decrease in checking behavior between the first session and the second session. Thus, although the dogs checked less in the second session, they did not learn the most effective strategy over trials, i.e., checking more when they had not seen and less when they had seen where the reward was hidden. This means that their flexible checking behavior was not learned during the experiment.

The third difference was that the dogs – in contrast to the apes – were not always accurate when they checked. This might be due to the set-up, as looking and smelling through the narrow gap might lead to less accuracy than looking inside a tube. But still dogs as a group were able select the correct fence above chance level in the Unseen condition.

Can we conclude from these results that dogs have access to what they have seen? Studies using the information-seeking paradigm have been criticized because subjects may simply engage in a search for information routinely without any metacognitive involvement. According to this hypothesis, individuals engage in a variety of exploratory responses until they detect the reward (Hampton et al., 2004; Kornell et al., 2007).

However, as Call (2010) pointed out, this is unlikely for two reasons: the tested primates selected the correct tube in about 20% of the trials after only having looked inside the empty tube (Call & Carpenter, 2001; Call, 2005; Marsh & MacDonald, 2012; Perdue, Evans, & Beran, 2018). Dogs in the current study were also able to make this inference by exclusion (as was also shown in other studies, see, e.g., Aust et al., 2008; Erdohegyi et al., 2007; Wallis et al., 2016), although less than the primates, in about 5% of the cases. This means that subjects did not need to smell or see the reward to select the correct alternative. The second reason why it is unlikely that subjects simply engaged in a search for information routinely is that the dogs, like the primates, also checked when they had seen where the reward was hidden (in more than 10% of the trials). However, it is unlikely that they had forgotten the location of the reward because the delays were very short and subjects were correct in nearly 100% of the trials even when they did not check.

Our results are in contrast to previous findings of Bräuer et al. (2004) and McMahon et al. (2010), Experiment 1. The dogs in these studies were apparently influenced by the fact that they were trained before the test in how to select the correct box. In the current study the dogs also had some previous experience with the apparatus but they did not have to learn to press a lever or a cue to locate the reward. Thus, with the current paradigm dogs could search naturally for the reward and it was shown that they are able to distinguish between a situation in which they had and had not seen where the reward was hidden. Our results are supported by Experiments 2 and 3 of McMahon et al. (2010), in which dogs had a choice between an informant and a non-informant. The dogs preferred to approach the informative human who then pointed to the location of the reward. This again suggests that dogs are seeking extra information when they do not know where the reward is hidden.

Interestingly, dogs selected the correct fence more often when they were rewarded with the toy, and they then also tended to check more often. Thus, it is possible that dogs search in a more flexible way when they are rewarded with a toy. Dogs also showed flexible searching strategies when they searched for a toy in a number of other studies (Erdohegyi et al., 2007; Fiset, 2009; Fiset et al., 2000, 2003, 2006). Why were dogs more successful with the toy? One possibility is that they were able to perceive the toy better when they were checking through the gap, as it is bigger. The second possibility is that the dogs rewarded with food were less motivated to search for their reward than the dogs that searched for the toy. That is very unlikely because the dogs actually approached the food reward even faster than the toy reward. It could, however, be the case that the dogs were too motivated to get the food reward, so that it was more difficult to be patient enough to check before choosing. In other words, dogs may have been more impulsive, and therefore less likely to show metacognitive abilities, when the reward was food. A third possibility is that the dogs perceived the two rewards in different modalities. It is not clear how the dogs perceived the reward behind the gap, whether they saw or whether they smelled it. It is possible that the dogs used smell to check for the food and vision to check for the toy, and that the visual modality makes them more flexible (see also Szetei et al., 2003). In an information-seeking experiment with capuchin monkeys conducted by Vining and Marsh (2015), subjects were either shown where the food was hidden, they could infer its location, or they were not given information about the location of the food. Monkeys also had the opportunity to search for extra information, and similar to our dogs they used this opportunity especially in the Unseen condition but less in the Seen condition. But when the monkeys potentially could infer the reward's location, they were more likely to search for further information. The authors conclude that capuchins only metacognitively control their information seeking in situations in which information is presented in the visual domain (Vining & Marsh, 2015).

The fourth possibility lies in the nature of the rewards. The favorite toy is a concrete object that the subjects know. Thus, it is a focused search, as subjects know exactly what they are looking for. In contrast, searching for food is more diffuse, as there could potentially be more pieces around (although subjects probably perceived that the test is about one piece). Moreover, the dogs in their daily life probably have much more experience with searching for a toy, and especially their favorite toy, than searching for food.

Experiment 2: Do subjects check more when a high-quality reward is involved?

In Experiment 1, we demonstrated that dogs seek out extra information when they have not seen where a reward was hidden and that they were more accurate when their favorite toy was hidden. Following Call (2010), we were interested in the question whether the location of a high-quality reward was better remembered than the location of a low-quality reward. We predicted that dogs would check more often when a high-quality reward was baited as opposed to a low-quality reward. In this experiment, new subjects that were unfamiliar with the task were presented with two types of reward in Seen and Unseen trials.

Methods

Subjects

We tested 24 dogs that did not take part in the previous experiment but were chosen based on the same selection criteria. As food was given as a reward, it was crucial for the experiment that dogs were motivated by food. There were 12 females and 12 males ranging from 1 to 6 years of age. As in Experiment 1, all subjects lived as normal family dogs and were individually tested at the Alte Messe in Leipzig, Germany.

Materials

The same experimental set-up was used, including the apparatus with the aforementioned two V-shaped wooden fence structures as in Experiment 1. Again, a gap of approximately 2 cm in width was used to hide the reward. For high-quality food, dogs were given meat sausages ("Hundewürstchen"), while dry dog food served as low-quality food.

Procedure and design

The basic procedure was the same as in Experiment 1: While E1 kneeled between the two barriers facing the dog, E2 held him or her at the starting position. The two experimenters tested all subjects individually, whereby one experimenter (E1) placed a piece of food behind one of the fences, as was the procedure in Experiment 1.

After the familiarization and the pretest, a classical food preference test was conducted before each session to ensure that dogs had a preference for one type of food. We assumed that dogs would prefer meat sausages as high-quality food as opposed to dry dog food, which was seen as low-quality food. The preference test was conducted in another part of the room, where dogs were presented with a wooden table. To ensure that dogs really preferred the meat sausages (the high-quality food) over the low-quality reward, E1 sat behind the table across from the dog and fed him or her with a piece of high-quality and a piece of low-quality food. E1 moved towards the dog, holding a piece of food in each hand close to the dog's nose, and then placed simultaneously a piece of each type of food at the end of the board. Dogs were included if they showed a clear preference for the high-quality reward (sausages), i.e., chose the high-quality reward above chance level in the four food preference tests. Overall, dogs chose the preferred food in 89% of trials (t(23)=16.31, p<0.001, one-sample t-test).

Only if the pretest and food preference test were successfully passed, were the Seen and Unseen conditions, which were similar to Experiment 1, introduced. It was also varied whether high-quality food (sausage) or low-qualify food (dry food) was hidden, resulting in four conditions: Seen-high / Seen-low / Unseen-high / Unseen-low. Dogs were tested in four sessions (two sessions per day). Each session consisted of 16 trials: the food preference test has four trials and each of the four main conditions contained three trials. All trials were presented randomly with the requirement that a condition occurred in no more than two trials in a row. Moreover, the food was not hidden on the same side in more than two consecutive trials.[1]

Data scoring and analysis

All trials were videotaped and scored in the same way as in Experiment 1. Thus, we scored success (correct choice), checking, and latency. The inter-rater reliability, which was based on 20% of the trials, was very good for correct selection (Cohen's Kappa=0.988, N=24), for checking behavior (Cohen's Kappa=0.792, N=24), and for the latency to select (Pearson Correlation r=0.936, N=24). For the main analysis we used a 2 × 2 ANOVA with the within-subject factor condition (Seen vs. Unseen) and the between-subject factor reward (high- vs. low-quality reward).

Results

Success

The dogs selected the correct fence in 94% of the trials in the Seen condition and in 52% of the trials in the Unseen condition, and were above chance in the Seen condition (t(23)=22.20, p<0.001), but not in the Unseen condition (t(23)=1.12, p=0.274, one-sample t-tests). They were more accurate in the Seen than in the Unseen condition (F(1.23)=239.74, p<0.001), but there was no effect for the type of food (F(1.23)=0.64, p=0.429), and no interaction effect (F(1.23)=0.89, p=0.354).

Checking

Figure 4 presents the mean percentage of trials in which the dogs checked for the two different food rewards in the two conditions. The dogs checked more frequently in the Unseen condition than in the Seen condition (F(1.23)=8.32, p=0.008), but there was no effect for the type of food (F(1.23)=0.74, p=0.400) and no interaction effect (F(1.23)=1.00, p=0.328).

Checking and success

If subjects checked in the Seen condition they then selected the correct fence above chance in 98% of the cases (t(18)=23.82, p<0.001, one-sample t-test). However, if they checked in the Unseen condition they were correct only in 60% of the cases, which was not above chance (t(21)=1.44, p=0.165, one-sample t-test). The dogs' success rate was higher when they checked in the Seen condition than in the Unseen condition (F(1.9)=18.76, p=0.002). These results suggest that dogs in the Seen condition simply might have re-assured themselves that the food was still there, but did not use checking successfully in the Unseen condition. Moreover, there was no effect of type of food (F(1.9)=1.01, p=0.342)

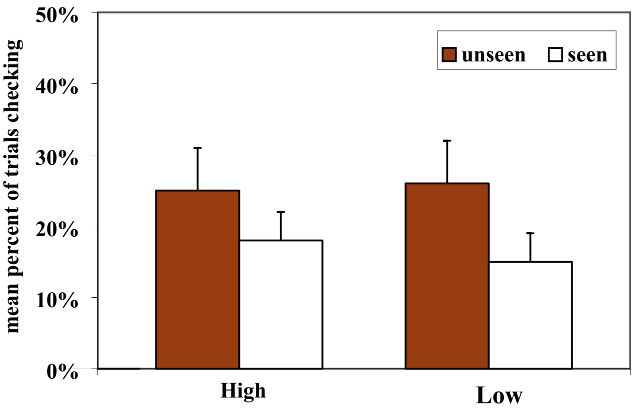

Fig. 4 The mean percentage of trials in which dogs checked for the two different food rewards in the two conditions in Experiment 2

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[1] Similar to Call (2011), we implemented 12 trials of a control condition at the end of each test to make sure that the dogs remembered where the food was hidden. None of the tested dogs made a mistake.

and there was no interaction between Condition × Type of food (F(1.9)=0.91, p=0.365).

Latency

On average it took subjects 2.8 s to select a fence in the cases when they did not check before choosing. Dogs selected a baited fence faster when the food was preferred than when it was not preferred (F(1.22)=6.59, p=0.018), but there was no effect for condition (F(1.22)=0.69, p=0.414) and no interaction effect (F(1.22)=0.20, p=0.659).

Learning

There was no learning over trials. Subjects did not select the correct fence more often in the second session compared to the first session: although there was a significant effect for condition (F(1.23)=239,60, p<0.001), there was no interaction effect (Condition × Session F(1.23)=2.38, p=0.137) and for session (F(1.23)=0.03, p=0.863). Similarly, subjects did not check more in the first session compared to the second session (F(1.23)=0.27, p=0.608), and there was no interaction effect (Condition × Session F(1.23)=1.28, p=0.270), but again there was an effect for condition (F(1.23)=8.30, p=0.008).

Individual performance

Again, individuals were above chance when they selected the correct fence in 18 (75%) out of 24 trials or more (binomial test p=0.5, N=24, P=0.02). Whereas 23 dogs were above chance in the Seen condition, only one dog was above chance in the Unseen condition. Two dogs never checked at all, 22 dogs checked at least once in the Unseen condition and 19 dogs checked at least once in the Seen condition.

Discussion

As in Experiment 1, dogs checked more frequently in the Unseen condition than in the Seen condition, but there was no effect for type of reward. Dogs remembered the locations of both food types equally well, and did not remember the location of a high-quality reward better. We predicted that dogs would check more often when a high-quality reward was baited as opposed to a low-quality reward, independent of whether subjects had or had not witnessed the baiting. However, that was not the case as dogs showed the same patterns for checking, no matter whether the food was preferred or not.

One could argue that dogs did not perceive or forgot which type of food was hidden. However, dogs selected the baited fence faster when a high-quality reward was hidden compared to a low-quality reward, indicating that they did indeed know which food was hidden. This increased selection of preferred food could indicate some evidence for the response competition hypothesis (Hampton, Zivin, & Murray, 2004). It predicts that if a higher value reward is available, the subject will be more motivated to go for it, i.e., in our case to go faster. However, as we did not find *decreased* checking for the high-value reward, the evidence remains weak.

In sum, in contrast to apes and humans, dogs' checking response was independent of the value of the reward, although they were aware of the type of food that was hidden.

Experiment 3: Does forgetting predict checking?

In this experiment, we raised the question whether time delay had an impact on dogs' accuracy and checking responses. The delay between baiting the reward and selecting one of the fences was manipulated to foster forgetting and examine whether checking would increase accordingly. Thus, we adapted the previously used information-seeking paradigm and varied the time delay (5, 20, 60, 120 s) between baiting the fences and letting dogs choose one side (similar to Call, 2010). Longer time delays are associated with a higher degree of difficulty to locate a baited reward (Call, 2010). Because forgetting would predict an increase in checking, we proposed that longer time delays lead to greater forgetting and, thus, foster checking.

Methods

Subjects

The selection criteria for the subjects were the same as in the previous two experiments, i.e., dogs had to be interested in food and to be able to pass the pretest. All subjects were normal family dogs that lived as pets with their owners in Jena and surroundings. In total, 25 privately owned dogs (11 males and 14 females; mean age = 5.21 years) of various breeds and ages (range 1–12 years) participated for the first time in this kind of experiment. All 25 dogs were rewarded with food – either Frolic or, in case of food allergies, equally preferred food.

Materials

All tests were conducted in a test room (7.20 m × 5.50 m) at the Dog Lab of the Max Planck Institute for the Science of Human History in Jena from April to August 2017. The experimental set-up was exactly the same as in the previous experiments. Additionally, we used two thick blue mats that were placed in front of the gaps and served to block visual access to the fences' contents (see below). All trials, including the pretest, were video-recorded by one camera that was installed directly across from the apparatus.

Procedure and design

In this experiment, the general procedure was the same as in the Seen condition of Experiments 1 and 2, but we varied the time delay between baiting and the dog's release. We used time delays of 5, 20, 60, and 120 s. E1 measured the exact time delays with a stopwatch, starting right after the reward was baited and E1 was in the initial position.

Similar to Call (2010), we also wanted to implement a "Blocked" condition in which dogs were prevented from checking by placing two thick blue mats in front of the gaps. However, as dogs did not show any difference in their behavior between the conditions "Blocked" and Unblocked" for success, checking, or latency, we concluded that we could not prevent them from checking as they used their nose to check. Thus, as this manipulation did not work, we treat the "Blocked" and "Unblocked" trials as one condition.

In total, each subject received two administered 24-trial blocks (one block for Seen and one block for Unseen trials), resulting in a total of 48 trials. The order of the time delays (5, 20, 60, and 120 s) was randomized for all dogs within eight trials and repeated in the exact same order afterwards. Food was placed an equal number of times on each side with the only restriction that the reward was hidden not more than twice in a row in the same place in a session.

Data scoring and analysis

All trials were analyzed and scored from the video material in the same way as in Experiments 1 and 2. Thus, we used the three measures checking, success, and latency.

In order to assess inter-rater reliability, a second observer unfamiliar with the task scored a randomly selected sample of 20% of the trials, which equaled a total of five dogs. Subjects were chosen randomly. For all measures, the inter-rater reliability was excellent and similar to Experiments 1 and 2 (Correct choice: kappa = 1.0, Checking: kappa = 0.80, Latency: Pearson Correlation r=0.78, N=25). For the main analysis we used a 1 × 4 ANOVA with the within-subject factor time delay.

Results

Success

On average, dogs selected the correct fence in 93% of the trials.[2] For a time delay of 5 s, they chose the correct side in 94% of trials, for 20 s in 95% of trials, and for both 60 and 120 s in 91% of trials (see Fig. 5). We found a significant effect for time delay (F(3.72)=3.21, p=0.028). A paired-sample t-test revealed that dogs were significantly more accurate in 5 s compared to 60 s (t(24)=2.681, p=0.013), 20 s compared to 60 s (t(24)=2.071, p=0.049, and 20 s compared to 120 s (t(24)=2.089, p=0.047).

Checking

On average, dogs checked in 28% of trials with a time delay of 5 s, in 27% of 20 s, in 31% of 60 s, and in 35% of 120 s (see Fig. 5). We had assumed that dogs would check more when the task is more difficult, e.g., when the time delay between hiding and the possibility of searching for the food is longer. However, the statistical analysis revealed that there were no significant differences between the four time delays. Dogs did not check more often depending on time delay (F(3.72)=2.086, p=0.11).

Latency

Subjects took on average 3.1 s to select a fence in the cases when they did not check. There was no effect for latency (F(3.69)=2.038, p=0.12), thus, subjects did not take significantly longer to retrieve the reward as a function of delay when they did not check.

Learning

In this experiment, there was no learning over trials. Subjects did not select the correct fence more often in the last session compared to the first session: Although there was a significant effect for delay (F(3.72)=3.21, p=0.028), there was no interaction effect (delay × session F(3.72)=1.21, p=0.31) and for session (F(1.24)=1.81, p=0.19). Similarly, subjects did not check less in the first session as opposed to the second session (F(1.23)=0.104, p=0.75), there was no interaction effect (delay × session F(3.69)=0.79, p=0.5), and no effect for delay (F(3.69)=1.97, p=0.13).

Discussion

In this experiment, we investigated metacognition in dogs by assessing the impact of time delay in an information-seeking task. We found that the dogs' overall retrieval accuracy was significantly higher for shorter time delays, i.e., dogs were less accurate when the delay was longer. However, in contrast to the apes tested by Call (2010), dogs did not check more often in situations in which the task was more difficult. Thus, dogs did not search for extra information when they were uncertain, which might suggest that they did not have access to their own knowledge in that situation.

Similar to Call (2010), we also wanted to implement a "Blocked" condition in which dogs were prevented from

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[2] As mentioned above we did not find any significant difference between blocked and unblocked trials, and therefore analyzed the data regardless of this manipulation.

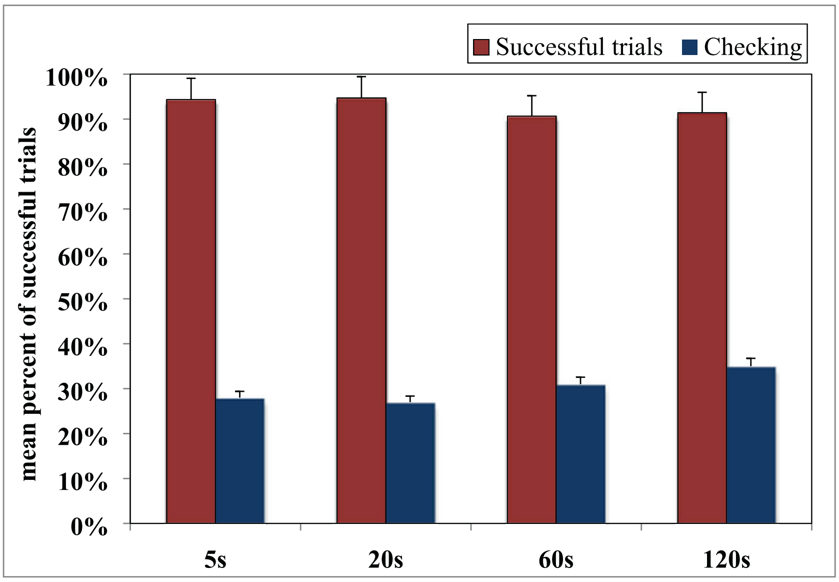

Fig. 5 The mean percent of trials in which dogs retrieved the reward successfully in Experiment 3. Dogs showed higher accuracy in trials with shorter time delays compared to trials with longer delays between baiting and choosing

checking by using an occlude in front of the gap. However, that manipulation did not work, as dogs did not show any difference in their behavior between the "Blocked" and "Unblocked" trials. Thus, dogs checked and were equally successful in "Blocked" trials, meaning that they were able to check through the occlude. This indicates that dogs used their olfactory sense to check whether the reward was present or absent, which is not so surprising as dogs very much rely on their nose when they search for a reward (Gazit & Terkel, 2003; Miklosi, 2007; see also Bräuer & Belger, 2018).

General discussion

Similar to apes, monkeys, and 2.5-year-old children (Call & Carpenter, 2001; Hampton et al., 2004), dogs tend to actively seek extra information when they have not seen where a reward is hidden. Although subjects checked more often before selecting the correct fence when they did not see where the reward was hidden (Experiments 1 and 2), their searching behavior was not affected by their preference for a type of food (Experiment 2). Manipulating the time delay between baiting and choosing slightly affected dogs' performance: subjects were significantly less accurate, but they did not check more often for higher time delays (Experiment 3). In contrast to previous studies (Bräuer et al., 2004) we were able to demonstrate that dogs showed some aspects of information-seeking behavior related to metacognition, but less flexibly than apes.

The main objective was to examine whether dogs were sensitive to the information that they themselves have or have not seen and whether they seek extra information in situations of uncertainty. As shown in Experiments 1 and 2, dogs checked more when they did not witness the baiting procedure. This suggests that they expected the bait was hidden behind one of the fences and, additionally, they grasped that they did not have enough information about where exactly it was hidden. Therefore, dogs must have adapted their searching behavior to increase their chance of success. We showed that dogs checked more in the Unseen condition, although they were not as successful as in the Seen condition when they checked. We were able to replicate this effect in two experiments with two independent cohorts of dogs.

However, we found one major difference between Experiment 1 and Experiment 2 regarding the performance of the two cohorts of dogs (probably due to the fact that a toy reward was easy to follow, see discussion of Experiment 1 and below). While checking in the Unseen condition in Experiment 1 indeed helped dogs to increase their accuracy above chance level, increased checking behavior in Experiment 2 did not lead to a higher accuracy. In other words, although dogs checked more often in the situation of uncertainty (i.e., when they did not witness the baiting process) in Experiment 2, they did not find the food more often than what was expected by chance. Thus, although this did not lead necessarily to increased success, dogs looked for extra information. They sometimes checked, but not until they were certain where the food actually was. This might indicate that dogs sometimes have a problem inhibiting the approach to the reward, even when they perceive that they need to gather extra information. Apes in the study of Call (2010) did not have that problem. They could get the information with a glance into the tube. However, overall, dogs were potentially able to gather enough information through the gap in order to get enough information to find the reward (as proven in Experiment 1).

All dogs that passed the pretest indicated that they understood the experimental set-up and they also knew that a reward was hidden behind one of the fences. Similar to the tip-of-the-tongue phenomenon – I know that I know something but cannot retrieve the information – checking in the Seen condition could be seen as some kind of verification process to maximize the chance of reward. The fact that dogs checked more when they had no knowledge of the reward's location (Unseen condition) could suggest that dogs show metacognitive abilities, as they meet one of the assumptions of knowing about knowing (Beran, Brandl, Perner, & Proust, 2012; Fleming, Dolan, & Frith, 2012; Hofer & Pintrich, 1997; Metcalfe & Shimamura, 1994; Nelson & Narens, 1994).

From our results we can furthermore conclude that dogs not only showed increased accuracy but also checked more when the reward was their favorite toy as opposed to food. One possible reason for this is that the dogs' motivation was higher when a toy was at stake (see also above). Another possibility is that they smelled the food and therefore checked less often. However, dogs were faster in approaching food than approaching the toy behind the fence (when not checking), suggesting that their motivation for food was higher. Hence, one might argue that dogs had an inhibition problem for food, which is furthermore confirmed by the food quality condition: dogs retrieved the preferred food faster than the less preferred food, although there were no effects for success as well as for checking. Thus, we speculate that the latency to approach the food might be correlated with motivation. The higher the motivation, the less dogs are able to inhibit a direct approach without checking. Consequently, dogs' greater performance with a toy reward might not only be explained by their experience with searching for a toy but also by the fact that they are not as over-motivated as with food. Indeed, in an inhibition task with food, dogs were shown to commit a number of seek errors, simply induced by ostensive-communicative cues (Topál et al., 2009).

As pointed out by Hampton (2009), several studies on non-human animal metacognition showed that difficult trials in memory or perception tests were avoided while the searching behavior could be adapted by gathering more information to maximize the reward. The dog's overall performance may be the result of response competition theory (Hampton, Zivin, & Murray, 2004), as an alternative explanation. Knowing the location of the food may have predisposed the dogs to select a side while excluding all other options, such as searching for the reward. According to this interpretation, dogs had two competing options in our experimental design: retrieving food or searching for further information. In the Seen trials the drive to retrieve the reward was dominant, and so the dogs went directly to the location where the reward was hidden. In Unseen trials, however, the dogs did not know where the food was located and therefore the drive to search for information was more dominant (Hampton, 2009). Thus, one could even argue that searching for the food is the default behavior of foraging dogs, and this default behavior is inhibited by knowing where food is.

While Call (2010) defined the looking responses (i.e., bending down to look into the tubes) as crucial features for seeking additional information for the apes, we introduced *checking* through the gap of the V-shaped fence as an equivalent measure. Dogs did not show any differences in their performance between situations in which the gap was and was not blocked by an occlude. That means that they were able to successfully check through the occlude, indicating that they mainly used their olfactory sense to check whether the reward was present or absent. This is not as surprising as dogs very much rely on their nose when they search for a reward (see Bräuer & Belger, 2018), and their olfactory perception is proven to be excellent (Vonk & Leete, 2017). Thus, it is likely that dogs and apes used different senses for checking. Indeed, other studies have also shown that apes and dogs use different strategies to deal with the same task. For example, Bräuer and Call (2011) investigated object individuation in dogs and apes by implementing a classical violation-of-expectation paradigm. Their findings revealed that while apes showed increased begging and looking behaviors, dogs showed increased smelling when their expectation was violated (Bräuer & Call, 2011). Moreover, other studies have shown that dogs sniff more with increasing difficulty of the task, be it when searching for a toy (Bräuer & Belger, 2018) or in object permanence tasks (Gagnon & Dore, 1992), thus gathering information from other sensory modalities when one was not sufficient. Future studies investigating metacognition in dogs should therefore consider that dogs will mainly use their sense of smell when searching for extra information in situations of uncertainty.

So far, our results have only been interpreted in the light of humanlike metacognitive abilities while other alternative non-metacognitive explanations could also apply. According to the non-metacognitive anxiety model by Carruthers (2008), the subjects react to their anxiety produced by their knowledge states and not to their knowledge states, which are opaque to the individual. This alternative explanation could also offer an alternative explanation for the passport effect (Call & Carpenter, 2001; Call, 2010). Subsequently, this would imply that not receiving the high-quality reward generates a higher state of anxiety as opposed to not receiving the low-quality reward. Therefore, dogs may be more likely to seek information even though they already know where the reward is baited, since the costs of failing to locate the high-quality reward would be higher. The same anxiety model can be applied to our Seen and Unseen condition in which dogs checked more often when they had not seen where the reward was hidden: while in the Unseen condition more anxiety should result in an increase in checking, less anxiety entails less checking in the Seen condition. According to the response competition hypothesis (Hampton, Zivin, & Murray, 2004), which potentially explains behavior without evoking a metacognitive decision, checking in the Seen condition should, contrary to our results, be reduced for high-quality rewards, because the strength of the motivation to reach the food would be much higher. This, however, does not match with our results, which show that dogs checked more in the Unseen condition.

In contrast to Call's (2010) study with apes, we did not find evidence that the dogs' searching for extra information depended on the value of the food reward (i.e., food quality) and the time delay between hiding and searching. As for the time delays, we found that although dogs' accuracy was better for shorter delays, they did not adapt their searching strategy to compensate their lack of knowledge by checking. In contrast to the apes, dogs checked in fewer trials, and more importantly they did not check more for longer time delays. One could argue that this was due to a ceiling effect, as dogs overall selected the correct fence in 93% of trials, and the pressure for seeking extra information was low. However, apes showed a similar accuracy (see Call, 2010, Fig. 3) but showed increased looking for longer delays. It might, however, be that dogs would show increased checking when the pressure is higher, i.e., when their accuracy gets much lower as the delays are longer. However, from the current data we can conclude that dogs do not have the flexibility that is described in the passport effect, and thus their search for extra information does not depend on the value of the reward or on the time delay between hiding and searching.

In sum, we tested in three experiments whether dogs know that they could be wrong. Our hypotheses that dogs show flexible metacognitive skills were not fully confirmed and our results were only partly consistent with Call's (2010) results. Dogs checked significantly more in the Seen than in the Unseen condition, indicating that they may have metacognitive abilities to some extent. Checking was voluntarily used to reduce the probability of being wrong and to maximize the possible reward. However, dogs' searching behavior for extra information did not depend on the value of the food reward or the time delay between hiding and seeking, which according to Call (2010) would be clear evidence that they knew that they could be wrong. Dogs are able to adapt their searching behavior by looking for extra information in a flexible way, indicating that they have access to what they have seen. However, further work is needed to determine which specific monitoring processes related to metacognition are involved.

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ARTICLE

An attempt to test whether dogs (*Canis familiaris*) show increased preference towards humans who match their behaviour

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Abstract

Studies suggest that being mimicked can positively affect human social interactions, not only in adults but also in children and even in individuals with atypical social competences. Outside of the human species, however, little is still known about this so-called 'social glue function' of mimicry; with only two studies—both on primates—testing whether other animals can show increased affiliation towards humans who mimic them. The present paper provides two pioneer studies on whether dogs—a domesticated species strongly attached to humans—show increased preference toward humans who display matching behaviour (walking). Results from both studies, including several tests, evidenced no preference of dogs for the human experimenter who matched the dogs' walk. Methodological issues are discussed and a number of new routes of experimentation are proposed that we hope will prove valuable for future studies.

Keywords Behavioural matching · Affiliation · Domestic dogs · Mimicry

Introduction

Behavioural matching (also called behavioural synchrony, allelomimicry or behavioural mimicry; Duranton and Gaunet 2015) is recognized as an adaptive "default behavioural tendency" widespread among animals for enhancing chances of survival (Dijksterhuis and Bargh 2001). In humans, behavioural matching serves an additional 'social glue' function: promoting harmonious relationships (Lakin et al. 2003). During social interactions, people reflexively mimic others to communicate affinity (Bavelas et al. 1986) and even more so to create rapport (Lakin et al. 2003), leading to increased feelings of affiliation (Lakin et al. 2003), empathy (de Coster et al. 2013), and trust (Stel et al. 2013) in the mimicked. Being mimicked also activates brain areas associated with reward processing (Kühn et al. 2010) and motivates pro-social behaviour (Cirelli, 2018). In contrast, lack of mimicry can enhance salivary cortisol levels (Kouzakova et al. 2010).

Though most research on the social effects of mimicry has been done with adults, there are some relevant findings on children. For example, it has been shown that infants are particularly sensitive to the 'imitative quality' of the behaviour of caregivers, apparently preferring mimickers over other people (Agnetta and Rochat 2004). Being mimicked

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Karine Silva and Juliane Bräuer contributed equally to this work.

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also seems to trigger a general prosocial orientation towards others. In a study testing 18-month-old infants, Carpenter et al. (2013) showed that infants helped an adult more often and more quickly and spontaneously if that adult had just mimicked them than if that adult had played with them contingently without mimicking them. Some studies suggest that being mimicked can positively affect social interactions also in children with impaired social competence, such as children with Autism Spectrum Disorders (Contaldo et al. 2016).

Of notice, behavioural matching in humans takes several different forms (e.g., mimicry of mothers' conspicuous emotional expressions during early infant–mother face-to-face interactions (Isomura and Nakano 2016); mimicry of transitive, object-related behaviour, also occurring in face-to-face contexts (Agnetta and Rochat 2004); movement synchrony encompassing activities like walking in synchrony (Wiltermuth and Heath 2009). Not all forms of behavioural matching, however, appear to similarly impact on affiliation. For example, while the conspicuous nature of mimicry during early infant–mother face-to-face promotes affiliation (Agnetta and Rochat 2004), the "social glue effect" of mimicked facial or postural mannerisms is hindered when mimicry is obvious to the interaction partner (e.g., Leander et al. 2012).

Not only human social interactions are affected by behavioural matching. Paukner et al. (2009) investigated whether the positive social consequences of a particular form of behaviour matching—mimicry of transitive, object-related, behaviour in face to face settings—may extend beyond the human species. These authors adapted for capuchin monkeys (*Sapajus apella*) research designs previously used on infants (e.g., Agnetta and Rochat 2004), and tested if these animals could differentiate between an experimenter mimicking them while manipulating a ball and an experimenter performing temporally contingent but structurally nonmatching actions. They found that the monkeys were more likely to affiliate with the experimenter mimicking them: they looked longer at the mimicker human, spent more time in proximity, and chose to interact more frequently with this human in a token exchange task (Paukner et al. 2009). More recently, Sclafani et al. (2015) used nursery-reared infant monkeys—which are believed to be at increased risk for developing aberrant social behaviours—as models to test the effect of mimicry on early social interactions. Specifically, they tested if obvious mirroring of the infant monkeys' facial gestures could promote their visual engagement and affiliation towards a human model. Results showed that the monkeys were not only sensitive and more responsive to caregivers matching their behaviours but also showed a significant increase in social interest, looking more at those caregivers and also displaying more affiliative gestures towards them (Sclafani et al. 2015).

Following from the above, the question arises of whether non-primates may also show increased social interest and affiliation towards humans who match their behaviour. In this context of inter-specific interactions, domestic dogs (*Canis familiaris*) may be a particularly interesting study species. Palagi et al. (2015) showed that rapid mimicry within dog–dog dyads leads to longer and more successful play sessions suggesting an evolutionary explanation for mimicry in dogs associated with group cohesion. An intra-species role for mimicry seems also likely. Dogs show remarkable skills for attending to, and reading human social behaviour, outperforming other animals more closely related to humans (e.g., Call et al. 2003; Hare and Tomasello 2005, see Kaminski and Marshall-Pescini (2014) for a review). Also, dogs seem to have the capacity to synchronize behaviourally with humans (reviewed in Durandon and Gaunet 2015), which suggest they may also be able to recognize when humans' behaviour is matching their own (for example during dog walking and other shared activities).

Following from Paukner et al. (2009) work, the present investigation describes two tests aimed at assessing whether domestic dogs display affiliation towards humans matching their behaviour in some form. The major challenge in adapting Paukner et al. (2009) methodology for dogs related to the mismatching body plans between humans and dogs. Two basic criteria were defined for selecting this target behaviour: (1) it had to be a common behaviour in both dogs and humans, (2) it should not require dogs to recognize the matching or not-matching of sophisticated details—which is prevented inherently by dogs' and humans' different body types. In light of these criteria, a simple, straightforward and common behaviour was selected for this study: walking behaviour. Thus, in this study, we specifically tested for movement synchrony.

Although largely anecdotal, the notion that dog walking increases rapport and strengthens the dog–human relationship is widely held, particularly among dog trainers. In light of this, if walking your dog does have an effective relationship-building effect then one should expect to find increased affiliation of dogs towards humans who walked in unison with them. Such prediction matches previous results on human interactions showing that walking in step does increase feelings of connection with counterparts (Webb et al. 2017). Two studies are here presented aiming at exploring whether a similar observation can be found in the particular case of the dog–human interaction.

Methods

Study 1

Subjects

Thirty-four domestic dogs of different breeds were tested and included in the analysis (16 females and 18 males; ages range 1–11 years, mean age 5 years). Six additional dogs participated but were excluded from the analysis as they did not move during the Mimicry phase of the experimental procedure (see below for details on this phase). Dogs were recruited from a database of dog-owners. All dogs were healthy with no known sight or hearing problems and no known aggression towards humans.

Testing was conducted by three experimenters (E1, E2 and E3). E1 and E2 were unfamiliar to the dog but E3 was allowed to be familiar as E3 was not visible to the dog during testing. No owner was present in the room during either the habituation phase or the testing phase. This eliminated potential effects of the owner on the positioning of the animals during testing. The experimenter playing the role of E1, E2 and E3 varied so that each experimenter played each role for some dogs (see above).

Setup

Testing took place in a room (7.20 m × 5.50 m) with a cabinet (5.50 m × 1 m × 1 m) on one side. During the experimental procedure, dogs were put on an extended leash (ca. 6 m long) fixed on a drawer down of the cabinet and in the middle of it (see Fig. 1). The tested dogs could approach the experimenters but the length of the leash was chosen so that it did not allow for physical contact. For the Ball Test phase of the experimental procedure three identical red-yellow tennis balls were used (see also below).

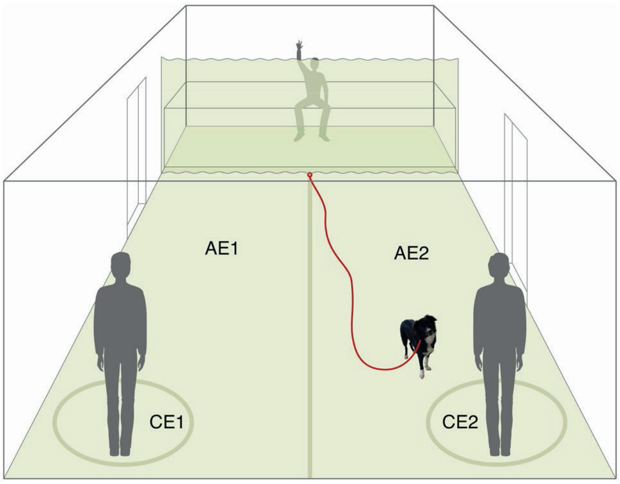

Fig. 1 Experimental set up from the view of the camera. A_{E1} and A_{E2} represent proximity areas and C_{E1} and C_{E2} represent close proximity areas of the experimenters (E_1 and E_2). [Dog, on a leash, is in A_{E2}]

During trials, E3 sat on the cabinet behind an opaque curtain, whereas E1 and E2 stood on two predetermined points opposite to the cabinet, 2.50 m away from each other. E3 could look through very small holes in the curtain. The dogs' walking zone was divided into two equal areas (A_{E1} and A_{E2}; approximately 17 m^2 each), representing proximity areas of E1 and E2,respectively. Close proximity areas were also (C_{E1} and C_{E2}; diameter 1.5 m each; see Fig. 1).

All trials were videotaped with one camera from the moment E1, E2 and the dog entered the testing room for Preference Test 1 (see below).

Experimental procedure

Each dog was given one trial. Before testing, the dog was assigned randomly to one of the two conditions: "Preferred" or "Non-preferred". Half of the dogs were mimicked by their "Preferred" experimenter and the other half by their "Non-preferred" experimenter (see below on procedure). Which human was preferred by the dog was assessed by E3, who coded life whether the dog preferred E1 or E2 during the phases before the preference test (see also below on procedure). Such grouping was done so as to control for the possibility that dogs might initially have tended to approach one of the Experimenters over the other, not because of a direct effect of the behaviour of the experimenter on dogs' level of affiliation but rather because of the animals' predisposition to approach that experimenter.

Also before testing, the dog was allowed to freely explore the experimental room and get used to the settings, the experimenters as well as to the owner's absence. During the habituation phase, E1 and E2 avoided any kind of interactions. Testing only started when E1 and E2 agreed on the fact that the dog looked calm and relaxed.

After the habituation phase, both E1 and E2 left the testing room with the dog, while E3 stayed there hidden behind the curtain. In the adjoining room each of E1 and E2 threw a ball once and asked the dog to bring it back. This was to make the dog familiar with the ball.

The trial started after E1 and E2 entered the testing room with the dog. Both experimenters then called or lead the dog to the middle line on the floor close to the curtain to put him/her on the leash. Once one experimenter succeeded in that, the other experimenter touched the dog in the same way and for the same amount of time. Then both experimenters walked backwards to their predetermined places while looking at the dog.

During testing, E1 and E2 behaved identically (except for the Mimicry phase, see below) according to a predetermined

Table 1 Details of the experimental procedure

Test phase	Duration (in s)	Procedure
Preference Test 1	30	Test for spontaneous predispositions to approach E1 or E2 E1 stood right and E2 stood left from the camera at their predetermined positions
Calling Test 1	30	E1 and E2 at once: called name of the dog, clapped hands at knees twice, called name of the dog, clapped hands at knees twice and stood silently again. The tone and pitch of the two experimenters' calls were trained prior to the experimental procedure so to be as similar as possible
Exchange	10	E1 and E2 exchanged places
Preference Test 2	30	E2 stood right and E1 stood left from the camera at their predetermined positions
Mimicry	90	One E mimicked the walking behaviour of the dog (the "mimicker") and the other E did not mimic it (the "non-mimicker")—so that the first E was stepping on the spot when the dog was walking Stepping meant lifting the knees in a walking fashion on the predetermined position but without actually moving in any direction and trying to remain in-step with the dog: left foot with left front paw, right foot with right front paw. In Study 1, the "non-mimicker" also stepped on spot but did so only when the dog was not walking. In Study 2, whenever the dog walked (and the "Mimicker" experimenter stepped on spot), the "Non-mimicker" experimenter, instead of remaining still, performed a *contingent* but *non-matching* behaviour: a "flying movement" by moving both arms right and left from the body up and down (both at the same time) Which of the two Es was mimicking was determined by the condition ("Preferred" or "Non-Preferred") and by the preference of the dog for E1 or E2. This was judged by E3 depending on the presence of the dog in A_{E1} and A_{E2} during Preference Test 1 and 2 and Calling Test 1
Exchange	10	E1 and E2 exchanged places
Preference Test 3	30	E1 stood right and E2 stood left from the camera at their predetermined positions (like Preference Test 1)
Calling Test 2	30	E1 and E2 at once: called name of the dog, clapped hands at knees twice, called name of the dog, clapped hands at knees twice and stood silently again (like Calling Test 1)
Exchange	10	E1 and E2 exchanged places
Preference Test 4	30	E2 stood right and E1 stood left from the camera at their predetermined positions (like Preference Test 2)
Ball Test	40	Both, E1 and E2 took a ball at once from the window sill behind them, called the name of the dog, clapped hand and ball twice at their knees, threw ball down once and caught it again, faked throwing the ball in direction at the curtain. At the same time E3 threw her ball down from behind the curtain. When this ball hit the ground E1 and E2 then put both hands behind their backs and said, "Bring it!"

schedule including with eleven phases in the following order: Preference Test 1; Calling Test 1; Exchange; Preference Test 2; Mimicry; Exchange; Preference Test 3; Calling Test 2; Exchange; Preference Test 4; Ball Test (details in Table 1). Unless otherwise indicated, E1 and E2 stood silently on their places with arms straight down left and right of their bodies. They kept looking at the dog but did not react to the behaviour of the dog and avoided any communicative gestures.

In the Mimicry Phase, one experimenter (the "Mimicker") mimicked any walking behaviour of the dog. That is, whenever the dog walked, this experimenter stepped on spot while the other experimenter remained still (the "Non-mimicker"). Importantly, as opposed to actual walking, stepping allowed the experimenters to keep their position throughout the demonstration, thus ruling out potential effects of moving either towards or away from the dogs. This stepping-on-spot seemed not to have caused awkwardness in the dogs nor precluded approach behaviour, as evidenced by the fact that no stress-related behaviours nor fearful postures were ever observed during this phase. Instead, the motor patterns resembling walking were likely familiar to the dogs.

Following the Mimicry Phase, tests were conducted in three different contexts to assess whether the mimicry had an effect on dogs' affiliation towards the experimenters: a spontaneous context approach (Preference Test 3 and 4), a calling context (Calling Test 2) and a play context (Ball Test).

During the whole trial, E3 timed with a stopwatch and gave inconspicuous silent signs with her hand over the curtain so that E1 and E2 knew when a new phase started and who had to mimic. Testing ended after the Ball Test.

Measures

Three different measures were considered here as dogs' affiliation indicators towards E1 and E2. For each dog, the cumulative times spent in proximity (A_{E1} and A_{E2}) and close proximity (C_{E1} and C_{E2}) areas were measured (see below). A dog was considered to be in one of the referred areas when it had at least one paw and its snout in it. In addition, we coded dog's attention paid to E_1 and E_2 (as measured by cumulative time gazing at E_1 and E_2), and whether the dog took the ball to C_{E1} or C_{E2}.

Study 2

In order to increase the comparability of our results with results from previous studies on infants (e.g., Agnetta and Rochat 2004) and monkeys (Paukner et al. 2009), a second study was run, upon reviewer suggestion, involving a different group of dogs.

In Study 1, E1 and E2 differed in contingency but not in mimicry: the "Mimicker" stepped on spot whenever the dog walked, and the "Non-mimicker" also stepped on spot—but only when the dog was not walking. This contrasts to previous studies in which two experimenters performed contingent behaviours but only the "Mimicker" matched the participant's behaviour (the "Non-mimicker" contingently performed a *different* behaviour). This was also implemented in Study 2 here, thus serving to control for the possibility that obtained results in Study 1 might be traced back to the alteration of the established procedures in infants and monkeys.

Subjects

Thirty-three domestic dogs of different breeds were tested in Study 2 and were also included in the analysis (14 females and 19 males; ages range 7 months–9 years, mean age 3 years). 16 additional dogs participated but were excluded from the analysis, as they did not move during the Mimicry phase.

Setup

The setup was exactly the same as in Study 1.

Experimental procedure

The experimental procedure of Study 2 followed that described for Study 1 in all respects, except for the following: In Study 2, during the Mimicry Phase, whenever the dog walked (and the "Mimicker" experimenter stepped on spot), the "Non-mimicker" experimenter, instead of remaining still, performed a *contingent* but *non-matching* behaviour: a "flying movement" by moving both arms right and left from the body up and down (both at the same time).

Measures

The same measures assessed in Study 1 were considered in Study 2 (proximity, gazing, and ball).

Data analysis (Study 1 and Study 2)

All phases of Study 1 and Study 2 were video recorded. Scoring was performed from video by two of the Experimenters. An independent and naïve observer scored a randomly selected sample of 20% of the trials in Study 1 to assess inter-observer reliability. For Study 2, a non-naïve observer coded 20% of the trials (also selected randomly). Pearson correlation coefficients (r) were calculated to estimate inter-observer agreement in both studies. The values obtained in Study 1 were above 0.9 for all measures. In Study 2 the values were above 0.88 for all measures. Whether dogs fetched the ball into C_{E1} and C_{E2} was unambiguous; thus, very high inter-observer agreements were achieved.

Data from both studies were analsed together, after separate analyses showed almost no difference between the experiments. Data analysis was planned so as to test the hypothesis that dogs' baseline levels of affiliation towards the experimenters (estimated by proximity and attention measures from Preference Test 1, Calling Test 1, and Preference Test 2) could be modified by the experimenters' behaviour during the mimicry phase. For both studies, data from the post-mimicry tests (Preference Test 3, Calling test 2, Preference Test 4 and Ball Test) were thus considered as the sum of the baseline levels of affiliation and the effect of the experimenters' behaviour during the mimicry phase. We predicted that dogs who were mimicked by their preferred experimenter would intensify their initial levels of affiliation, while dogs who were mimicked by their non-preferred experimenter would weaken their initial preferences—or even switch their preferences.

Most of the responses were expressed as a proportion of times (e.g. the proportion of time the dog was in proximity to the preferred experimenter). These measures were transformed to the log odds scale (Warton and Hui 2011), with zeroes set to 1/120 (i.e. half a second), so they were continuous and not bounded: the model could then assume that these had normally distributed errors.

Data from both studies were analysed together in a single model. Close proximity was not used in the analysis, because half of the observations were zero, i.e. the dog did not come into close proximity with the experimenter (and in a quarter of tests the dog did not move into close proximity to either experimenter).

The log odds of Proximity was modeled assuming normally distributed errors, whilst gazing and wagging at each experimenter was modelled as a Bernoulli variable, with a probit link (the probit and more common logit links typically give indistinguishable models, but using the probit link makes the interpretation of repeatability slightly easier).

The same model structure was used for Proximity and for Gazing at the preferred experimenter. The covariates are the dog's preference for the mimicker, which experimenter mimicked the dog ("Group"), the Test (preference, ball, etc.), and whether the test was before or after the mimicking test (mimicking was considered before, although this has no effect on the inference). Using the notation of Wilkinson and Rogers (1973) the model for proximity was the following:

$$\text{Proximity} \sim \text{Preference} \times (1 + \text{Group} \times \text{Test} + \text{Before After} \times \text{Test}). \tag{1}$$

The notation $Y{\sim}A$ says that Y is the response (i.e., proportion of time in proximity), and A is the covariate. $Y{\sim}A+B$ means that the model has main effects of A and B; $Y{\sim}A \times B$ means that an interaction is also included (e.g. the effect of Test depends on whether it was before or after the mimicking).

Thus, before the mimicry phase, the model assumes that the proportion of time in proximity to the preferred experimenter is affected by a preference for that experimenter, and this is modulated by the different Test type. After the mimicry phase, this effect is modulated by which experimenter mimicked the dog (Group variable). Thus, if a dog has a positive preference for the preferred experimenter, this can be strengthened by the test type (e.g. calling might elicit a stringer response compared to the preference test, which would mean that the Calling effect would be larger). If mimicking has an effect, then, in dogs that were mimicked by their preferred experimenter, we expected to see a positive estimate of the before/after variable (it is set to zero before the mimicking test). In dogs that were mimicked by their *non-preferred* experimenter, we expected to see a *negative* estimate of the before/after variable.

Gazing was modelled in a similar way: a baseline probability of gazing at either experimenter was assumed and was then modified by the same structure as above: for the preferred experimenter the same formulation was used (so a positive effect meant that the dog was more likely to gaze or wag at a preferred experimenter); for the non-preferred experimenter the sign of the preference effect was reversed (so if a dog was more likely to gaze at its preferred experimenter, it was less likely to gaze at its non-preferred experimenter). The structure for this part of the model was thus the following:

$\text{Gazing at Preferred} \sim \text{Gaze} + \text{Preference}$
$\times(1 + \text{Group} \times (\text{Before After} \times \text{Test}))$.

$\text{Gazing at Non} - \text{Preferred} \sim \text{Gaze} - \text{Preference}$
$\times(1 + \text{Group} \times (\text{Before After} \times \text{Test}))$.

Taking the ball was modelled as a Bernoulli trial, with the model $\text{Ball}{\sim}\text{Preference} \times (1+\text{Group})$ as the test was only performed after the mimicry. If the dog did not take the ball to either experimenter, the result was coded as missing data and so does not affect the analysis.

Preference is a common across all three responses and tests and is a dog-level latent variable. The other parameters are specific to the responses. We are interested in the difference in the test effects before and after the mimicry phase.

We estimated the consistency of the experiments by calculating the repeatability. This was defined as the variance of the preference effect divided by the sum of the preference and residual variance effects. For gazing this residual variance was set to 1, as this would be the variance of the normal distribution under the threshold interpretation of a probit link (e.g. Agresti 1990, Sect. 4.5.1).

All analyses were fitted using a Bayesian approach with vague prior distributions (all fixed effects had Gaussian prior distributions with mean 0, variance 1, and standard deviations had uniform prior distributions between 0 and 100). The fitting was run in JAGS v4.3.0 (Plummer 2003) through the runjags package (Denwood 2016) in R3.4.4 (R Core Team 2018). Four chains were run and after a burn-in of 10^4 iterations, a further 5×10^4 iterations per chain were run. Results are reported as the posterior mode (the point estimate) and 95% Highest Posterior Density Intervals (HPDIs), which are Bayesian confidence intervals so that we can say that there is a 95% probability that the interval contains the "true" value (there are many ways of defining a confidence interval: the HPDI is the shortest possible interval).

The data and full code to replicate the analyses are provided in the Supplementary Material.

Results

Descriptives of the data obtained in Study 1 and Study 2 are shown in Tables 2 and 3, respectively. As referred, we predicted that dogs who were mimicked by their preferred experimenter would *intensify* their initial levels of affiliation (here estimated by proximity to, gazing at, and taking the ball to the experimenters), while dogs who were mimicked by their non-preferred experimenter would *weaken* their initial preferences—or even switch their preferences. Results from both studies, however, showed no detectable differences in dogs' behaviours when either E1 or E2 mimicked them. For all measures, 0 was within the 50% HPDI (the shortest possible confidence interval; Fig. 2), indicating a large uncertainty about the direction of any effect. This suggests that there were no significant changes in dogs' preferences when they were mimicked by either their preferred or non-preferred experimenter. It is of note that the confidence intervals are wide: even for gazing (which has the shortest confidence intervals), the 50% HPDI suggests that the preference could

Table 2 Descriptives of data obtained in Study 1

	Time in proximity to the "mimicker"	Time in proximity to the "non-mimicker"	Time gazing at the "mimicker"	Time gazing at the "non-mimicker"
Group A				
Before the mimicry phase				
Preference Test 1	13.8 ± 10.8	14.3 ± 10.5	1.8 ± 1.9	3.5 ± 6.9
Calling Test 1	7.1 ± 9	9.9 ± 8.9	3.3 ± 3.4	1.2 ± 1.1
Preference Test 2	12.7 ± 12.8	12.3 ± 15.4	3.3 ± 3.5	1.5 ± 2.3
After the mimicry phase				
Mimicry Test	46.2 ± 31.6	28.3 ± 29.6	4.3 ± 6.1	5.9 ± 5.6
Preference Test 3	11.7 ± 15.1	17.9 ± 14.9	1.7 ± 2.7	2.9 ± 8.9
Calling Test 2	4.5 ± 6.5	11.8 ± 10.5	2.1 ± 2.2	3.5 ± 4.4
Preference Test 4	20.6 ± 14.9	6.2 ± 10.7	1 ± 1.8	1.5 ± 2.1
Ball Test	15.5 ± 14.3	8.1 ± 9.8	1.5 ± 2.7	1.5 ± 2
Group B				
Before the mimicry phase				
Preference Test 1	16.7 ± 15.6	12.7 ± 13.7	3.1 ± 4.8	2.9 ± 5.3
Calling Test 1	11.4 ± 11.9	6.8 ± 7.5	1.4 ± 1.9	2.1 ± 2.6
Preference Test 2	6.2 ± 9.2	16.4 ± 14.8	1.6 ± 2	2.2 ± 5.5
After the mimicry phase				
Mimicry Test	19.5 ± 28.6	39.4 ± 37.7	3.2 ± 4.3	7.5 ± 10
Preference Test 3	15.3 ± 16.3	7.7 ± 12.7	2.1 ± 3.6	1.6 ± 3.3
Calling Test 2	8.7 ± 15.5	4.5 ± 6.5	4.4 ± 6.7	0.9 ± 1.4
Preference Test 4	7.2 ± 12.2	16.9 ± 16.5	2.5 ± 4.1	0.9 ± 1.4
Ball Test	11.3 ± 13.9	15.2 ± 15.7	2.1 ± 3.9	2.5 ± 6.9

Data are shown in seconds

change from 0.5 to between 0.31 and 0.70. Thus, any effect would have to be large to have been estimated.

The poor power of our tests was the result of a low repeatability of the tests, i.e. different tests on the same dogs give different results. Overall, the repeatability for preference was 0.002% with a 95% HPDI of 0.0–0.1%. For gazing, the repeatability was 0.0.17% with a 95% HPDI of 0.0–1.5%.

Of notie, we noticed an increased attrition rate in Study 2 (33%) compared to Study 1 (15%). This is likely explained by the fact that in Study 1, one of the experimenters always moved, which was not the case in Study 2. In this second study, the dogs also stopped moving and laid down.

Discussion

The studies here described did not show any effect of stepping in unison with dogs' walk on the animals' levels of attention and proximity towards the human experimenters. One possible interpretation is that mimicry may not serve an affiliative function in family dogs within the context of interactions with humans—or, at least, with unfamiliar humans. However, one has to consider the possibility that at the basis of these negative results might be some methodological issues.

First, one has to note that, despite the resembling motor patterns between walking and stepping, stepping in unison with the dogs' walk might not have been recognized as mimicry by the dogs. Future studies might have the experimenters show mimicry while staging a four-legged position (i.e. a more dog like shape). Alternatively, future studies might consider experimental designs allowing for actual walking synchrony to be assessed. Actual walking, however, does not rule out potential effects of moving either towards or away from the dogs. Such designs, therefore, might be difficult to plan.

Previous research suggests that the intensity mimicry (here limited to one 90 s session per dog) can impact social outcomes. Sclafani et al. (2015), for example, showed that the increase in social interest observed in their mimicry condition was more robust when monkeys were exposed to five experimental sessions, when compared to three or two sessions. Similarly, studies have also demonstrated the benefits of intensive treatments in children with social impairments. Thus, it seems important for future studies in dogs to account for the intensity of mimicry.

Results here obtained also raise the question of whether family dogs, perhaps due to the bond they establish with their owners, may not have a requirement to create affiliation with an unfamiliar human. Previous studies assessing

Table 3 Descriptives of data obtained in Study 2

	Time in proximity to the "mimicker"	Time in proximity to the "non-mimicker"	Time gazing at the "mimicker"	Time gazing at the "non-mimicker"
Group A				
Before the mimicry phase				
Preference Test 1	11 ± 6	18.1 ± 9.9	0.2 ± 0.4	0.2 ± 0.4
Calling Test 1	6 ± 4.4	14.1 ± 10.1	0.2 ± 0.4	0.3 ± 0.5
Preference Test 2	26.4 ± 16.2	12.9 ± 18	0.3 ± 0.5	0.2 ± 0.4
After the mimicry phase				
Mimicry Test	44.1 ± 25.1	11.7 ± 11.3	0.4 ± 0.5	0.4 ± 0.5
Preference Test 3	7.3 ± 7.9	19.4 ± 14.4	0.4 ± 0.5	0.2 ± 0.4
Calling Test 2	5.2 ± 8.1	13.1 ± 10.5	0.4 ± 0.5	0.3 ± 0.5
Preference Test 4	22.1 ± 15	8.8 ± 9.7	0.1 ± 0.2	0 ± 0
Ball Test	21.1 ± 12.3	8.3 ± 7.4	0.2 ± 0.4	0.1 ± 0.3
Group B				
Before the mimicry phase				
Preference Test 1	21.6 ± 11.5	11.2 ± 11.7	0.4 ± 0.5	0.1 ± 0.3
Calling Test 1	NA ± NA	NA ± NA	NA ± NA	NA ± NA
Preference Test 2	13.9 ± 21.8	29.8 ± 26	0.2 ± 0.4	0.3 ± 0.5
After the mimicry phase				
Mimicry Test	12.1 ± 14.9	52.1 ± 26.2	0.2 ± 0.4	0.2 ± 0.4
Preference Test 3	23.6 ± 13.2	8.4 ± 12.3	NA ± NA	0.3 ± 0.5
Calling Test 2	15.6 ± 11	3.1 ± 3.6	0.2 ± 0.4	0.2 ± 0.4
Preference Test 4	8.9 ± 13.1	24.7 ± 14.3	0.3 ± 0.5	0.3 ± 0.5
Ball Test	10.2 ± 9.5	16.5 ± 12.5	0.2 ± 0.4	0.2 ± 0.4

Data are shown in seconds

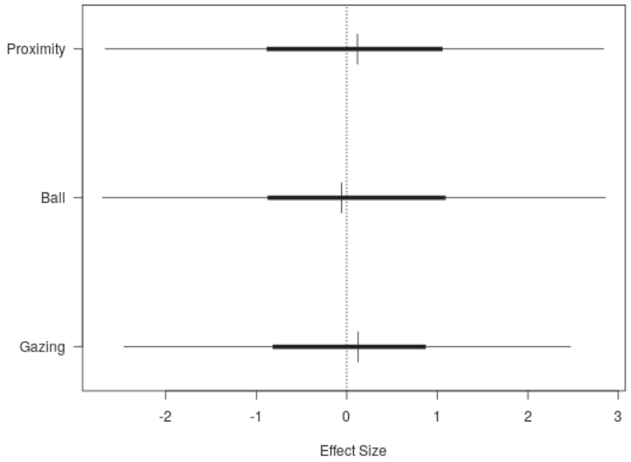

Fig. 2 Estimates of differences in the effect of experimenter 1 or 2 mimicking walking of the dogs on the time spent gazing or in proximity to the first experimenter, or whether the dog took the ball to the preferred experimenter ("Ball"), during different trials. Thick line: 50% profile confidence interval; thin line: 95% profile confidence interval

contagious yawning in dogs have shown that family dogs catch more yawns from familiar than unfamiliar humans yawning (Silva et al. 2012, 2013), while shelter dogs catch more yawns from unfamiliar humans (O'Hara and Reeve 2011). According to O'Hara and Reeve (2011), when human attention is directed towards dogs, contact-deprived ones, may recognize the potential for new social affiliation and respond more conspicuously. Thus, one should consider the possibility that family dogs, as those tested in our study, might be less likely to increase affiliation towards non-familiar humans performing behaviours that match their own. Future studies considering familiarity issues might also test whether a larger effect could be observed in studies involving service dogs and their owners. In addition to the emotional bond they establish with their owners, these dogs are specifically trained to pay close attention to their owner's behaviour so to better assist them.

It is also possible that the dogs in our study did not show the effect because of unknown particularities in our setup. It might, therefore, be fruitful to apply a wholly different approach. For example, future tests could employ a similar method as that used in children by Tunçgenç et al. (2015). In this study infants aged between 12 and 9months were rocked in chairs as they viewed toys (teddy bears in a social condition and colorful boxes in a non-social condition) that rocked synchronously or non-synchronously with them. Later, infants were given the opportunity to select one of the toys. The authors hypothesized that infants would show a pronounced preference for the synchronously moving toy in the social condition than in the non-social condition. This hypothesis was only confirmed for 12 month-olds; 9 month-olds showed no significant preference for synchronous toys either in social or non-social contexts. Similarly, in future studies, small or medium sized dogs could be held and rocked, while presented with different conditions involving humans (perhaps, both familiar and non-familiar to the dogs) rocking in a synchronized or non-synchronized fashion.

We do consider, however, that further investigation of walking behaviour may be warranted. Despite the obvious differences in the anatomical configuration of dog and human walking, it is an activity that humans and dogs frequently engage in together and one that can involve remarkable high levels of synchrony between the two species (e.g., Naderi et al. 2001).

Valuable information might also be provided by future studies introducing additional measures of affiliation and particularly physiological ones, such as oxytocin (e.g., Nagasawa et al. 2015). This particular route of investigation might be of special interest considering current attentions in human research to the hypothesis that being mimicked by others can increase oxytocin secretion (Aoki and Yamasue 2015), notably in individuals having lower than average levels of this hormone.

According to Durandon and Gaunet (2015), the lack of studies investigating a social glue function of mimicry within the particular context of interspecific interactions is mainly due to methodological issues—the larger the phylogenetic distance between the studied species, the greater the challenge for researchers to find common behaviour to both species. Given the tangible and increasing importance that dogs have in human society, finding a ‘social glue’ function of mimicry in dogs would not only be of high theoretical relevance but also of major practical importance. Dog owners and trainers, for example, could try using behavioural matching to facilitate connection and promote social engagement in dogs. Importantly, though, one cannot dismiss the possibility that mimicry may *not* serve an affiliation effect within the particular context of the dog–human interaction as suggested by the results here obtained—robust over the two studies.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

Ethical approval The Doglab of the Max Planck Institute for the Science of Human History has a general approval for conducting non-invasive studies of dog human interactions. There is no particular certificate number.

Informed consent All dog owners signed a consent form that their dogs participated in the research here presented.

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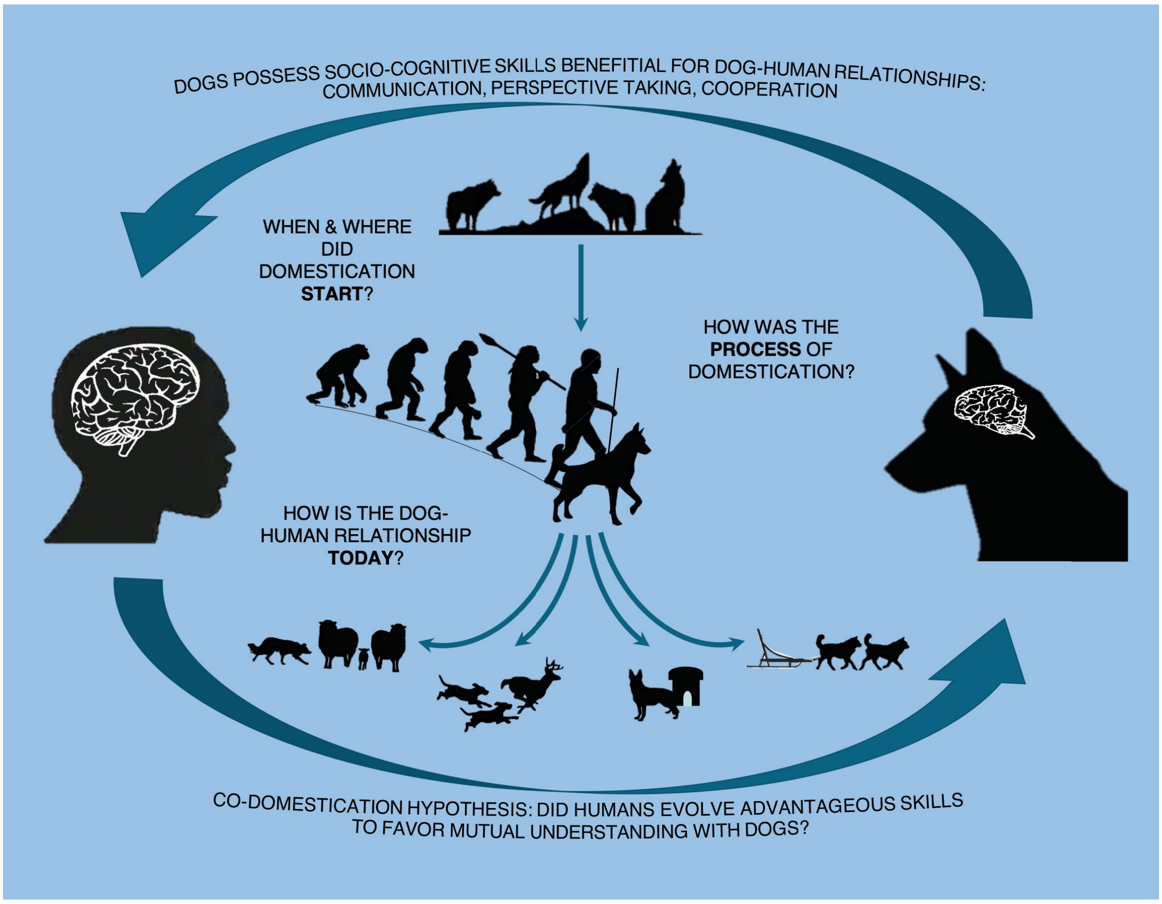
3. Outlook & future direction

This thesis summarizes some of the work about dog-human interaction and adds to the growing literature in this field. In the past 20 years we have learned a lot about dogs' exceptional social communicative skills, but also that they do not perform well in other domains, in particular in physical cognition tasks (see above). However, there are many fields in which our picture of dog cognition and the dog-human relationship is lacking or incomplete.

Figure 1 shows that we can group the questions into three lines of inquiry that should be considered: (1) the *starting point* of dog domestication, (2) the *process* itself, and (3) *outcomes* of domestication.

Figure 1: illustrates the three lines of research that should be considered to further investigate dog-human interactions.



- To further investigate when and where domestication *started,* we need the interdisciplinary approach (see chapter 3.5.). It is, for example, possible that wolves' excellent sense of smell and its potential for use made them valuable for early humans and was one of the reasons they were domesticated (chapter 3.1.).
- In the last 20 years, we have learned a lot about the *process* of domestication, i.e. what has changed during domestication. In order to understand what skills dogs have evolved, the comparison with wolves is crucial and must be further investigated (chapters 1.1. and 1.3.).

- Regarding the *outcomes* of domestication, namely the dog-human relationship, there are many open questions that have not been considered enough yet, for example, whether dogs are capable of skills like empathy (3.2.). The human perspective on dogs (3.3.) and cultural differences in dog-human interactions (3.4.) are also important topics to investigate in order to fully understand the dog – human relationship.

In the following, I will point out areas for future studies in order to be able to complete our knowledge and to answer open questions about the dog-human relationship.

3.1. Smell & cognition

As mentioned above, dogs perceive the world through their noses, but we do not know how exactly their odor perception and cognitive skills are linked together. For example, it is unclear what factors determine whether dogs use their nose or other search strategies. Thus, the question is how exactly dogs decide whether to rely on the olfactory modality or use another modality given the choice. It is likely that the breed, the target of their search, their education and previous experience, and their relationship to the handler might play a role here (Bräuer & Belger, 2018; Hall et al., 2015; Jezierski et al., 2016; Polgár, Kinnunen, Újváry, Miklósi, & Gácsi, 2016). It can be hypothesized that during domestication dogs have undergone a switch in their reliance on different modalities when it comes to constructing cognitive representations (Bräuer and Blasi, submitted).

Even physical issues of odor perception are still open to discussion. It is known that air temperature humidity influence the performance of search dogs, but it is unclear whether this is due to the dogs' physiological conditions or because of environmental conditions that impact the source of the scent (Jones, Dashfield, Downend, & Otto, 2004; Judah, 2007; Pearsall & Verbruggen, 1982; Snovak, 2004; Syrotuck, 2000; Wright & Thomson, 2005). Moreover, it has been recently conjectured that dogs might be able to trace molecules of DNA through olfaction (Woidtke et al., 2017). Chemists, however, doubt that idea, since DNA pieces large enough for individual identification are too large to be sufficiently volatile to find their way into the nose of a sniffing dog (Courts, Euteneuer, & Gosch, 2019; Goss, 2019). Finally, it is also unclear whether dogs have to sniff in order to retrieve useful olfactory information (Laing, 1983; Bräuer and Blasi, submitted).

From a comparative view, it is important to find out how odor perception and cognition are linked together in other macrosmatic animals. Do they also represent what they smell or do they perceive odors just as positive or aversive stimuli? The latter could be hypothesized for rodents, for example, as captive rodents that have no experience with predators will react to odors of their predators (Ylönen, 2001). It is also possible, however, that olfaction is linked with cognition in a similar way in macrosmatic animals as distinct as carnivores (Green, Van Valkenburgh, Pang, Bird, & Curtis, 2012), rodents, and elephants (i.e. Bräuer & Belger, 2018).

Furthermore, it seems important to directly compare odor perception in dogs and humans. Although in general dogs' sense of smell is much more sensitive than humans' (see chapter 1.4), the ability to detect odors is strongly influenced by the kind of odor. Thus, in the detection of some odors, humans outperform dogs and other macrosmatic animals. Human behaviors and affective states are also strongly influenced by the olfactory environment (see McGann, 2017 for a review). Emotional and olfactory processing are closely linked both anatomically and functionally (Flohr, Erwin, Croy, & Hummel, 2017). For example, mothers can recognize their own children by body odor alone (Schäfer, Sorokowska, Weidner, & Croy, 2020), but maternal perception of the child's body odor is related to mother-child bonding (Croy, Mohr, Weidner, Hummel, & Junge-Hoffmeister, 2019). On the other hand, humans with an impaired sense of smell are able to live a quite normal life, although they might show enhanced social insecurity, increased risk for depressive symptoms and increased risk for household accidents (Croy et al., 2012). In contrast to dogs, humans are quite bad at detecting changes in their olfactory environment (Menzel, Hummel, Schäfer, Hummel, & Croy, 2019). But, similar to other animals, odor-mediated communication between humans also carries information about genetic relationships, stress and anxiety levels, and reproductive status. However, this information is not always consciously accessible (McGann, 2017).

In conclusion, it is clear that the sense of smell is more important for dogs than for humans. It can be hypothesized that the main difference in odor perception between dogs and humans is which olfactory information is processed and how. For example, the ratio of portions of the cortex associated with olfactory processing to the rest of the cerebral cortex is higher in dogs than in humans (see Bolon, 2000). Future studies will show whether dogs have a more conscious access to the olfactory information from their environment (i.e. Bräuer & Belger, 2018) and how the odor perception of humans and dogs might complement each other.

3.2. Empathy

Humans invest high cost for their dogs (see chapter 1.2.) and there is also evidence that they empathize with dogs. For example, human participants show similar neural responses when viewing pictures of dogs suffering and of humans suffering (Franklin et al., 2013). Dogs, on the other side, are also highly motivated to support humans (see chapter 1.3.3 and 1.4). However, it is unclear whether they are capable of feeling empathy. Empathy can be defined as any process where the attended perception of another individual's state generates a state in the subject that is more applicable to the other's state or situation than to the subject's own prior state or situation (Hoffman, 2000). Preston and de Waal (2002) distinguish between different classification terms such as *emotional contagion, sympathy* and *empathy*. In these categories, subjects differ in their ability to (i) distinguish between self and other, (ii) be in a matching state and (iii) actually help the other individual (Preston & Waal, 2002).

It is very likely that dogs are able to display emotional contagion in which the subject's state results from the other individual's states. Emotional contagion can, for example, be linked to facial mimicry, an automatic and fast response (less than one second) in which individuals involuntarily mimic others' expressions. Palagi et al. (2015) showed that rapid mimicry within dog–dog dyads leads to longer and more successful play sessions (Palagi, Nicotra, & Cordoni, 2015). Dogs also seem to have the capacity to synchronize behaviorally with humans (reviewed by Duranton & Gaunet, 2015). For example, they show contagious yawning when familiar or unfamiliar humans yawn (O'Hara & Reeve, 2011; Silva, Bessa, & de Sousa, 2012, 2013).

Moreover, there is evidence that dogs are sensitive to the emotions of other individuals. In a number of studies, dogs have shown submissiveness, alertness, increased Cortisol levels, more stressful behaviors and higher heart rates when confronted with a negative emotion of a human or another dog. For example, subjects presented with sounds of real emotional situations behaved differently depending on the presented emotion (Huber et al., 2017; Yong & Ruffman, 2014). D'Aniello et al. (2017) used the olfactory modality and tested transmission of emotional information via chemosignals. They found that dogs react when they are presented only with the odor of human emotions (D'Aniello, Semin, Alterisio, Aria, & Scandurra, 2017). Finally, Morisaki et al. (2009) presented evidence that dogs also react to the emotions of their owners in the moment. Dogs were observed while their owners watched a cheerful or sad movie. The tested dogs gazed longer at their owners during the cheerful movie than the sad one (Morisaki, Takaoka, & Fujita, 2009). Whether this sensitivity towards emotions is simply learned by experience, i.e. that dogs learned to associate a smile with something positive and an angry face or a crying noise with something negative, remains an open question.

While there is evidence for emotional contagion, it is unlikely that dogs are able to feel *sympathy* as Preston and De Waal (2002) define it, i.e. "feeling sorry" for the other individual, while their states are *not* matching. The above-mentioned behaviors suggest that dogs' states were indeed matching with the suffering human or other dog.

Furthermore, from the current study, it is difficult to know whether dogs felt *empathy*. That would be more sophisticated as the subjects` state then depends on the *attended* perception of the other individual's state, and states would match on representation level (Preston & Waal, 2002). The subject then would be able to distinguish between self and other and would *react* to the situation by, for example, helping the emotional individual, especially when they are familiar to the dog. Future studies should address whether dogs are really capable of empathy by creating situations in which real emotions are induced in familiar and unfamiliar persons. In these setups, dogs also should have the chance to react and alter the situation when the persons are suffering with negative emotions.

3.3. Human perspective on dogs

As pointed out in this thesis, there has been a lot of research about how dogs perceive and understand humans. But when we study the dog-human relationship, it is also important to know how humans perceive and understand dogs. For example, the human ability to recognize dog emotions has received only limited attention, although there were some surprising findings. Studies using auditory input demonstrate that humans can recognize some dog emotions, like aggressive barks to strangers (Pongracz et al., 2005). However, when using the visual modality, several studies suggest that children and adults do not reliably understand the body signals of dogs (Bloom & Friedman, 2013; Kerswell, Bennett, Butler, & Hemsworth, 2009; Mariti et al., 2012; Reisner & Shofer, 2008). For example, children often mistake angry dog facial displays for happy ones (Meints, Racca, & Hickey, 2010). This depends on the kind of emotion, but also on how the emotion is presented – i.e. on a picture or on short video clips (Amici, Waterman, Kellermann, Karimullah, & Bräuer, 2019).

Furthermore, it is not clear how co-evolution and/or previous experience with dogs influences humans' ability to recognize dog emotions. According to the co-domestication hypothesis, the human ability to recognize dog emotions may be supported by specially adapted mechanisms. In particular, co-evolution would have led humans and dogs to evolve emotional displays and cognitive skills that favor reciprocal understanding and inter-specific communication, with humans selecting dogs based on their working abilities and communication skills and humans evolving an ability to read dog emotions (Amici et al., 2019; Kaminski & Marshall-Pescini, 2014). Therefore, even though direct experience with dogs (e.g. dog ownership) may still increase the ability to recognize dog emotions, this ability should be partially present also in the absence of experience. However, in this respect, experimental evidence provides contrasting results. Surprisingly, in some studies, inexperienced humans (i.e. non-owners) were better than humans with dog experience (e.g. dog owners) at reading dog emotions (Bloom et al., 2013, Schirmer et al., 2013, Bahlig-Pieren, Z. & Turner 1999). In other studies, the ability to recognize dog emotions did not differ between dog-owners and non-owners (Pongracz et al., 2005) or increased slightly with age and experience (Pongrácz, Molnár, Dóka, & Miklósi, 2011; Schirmer et al., 2013, Wan et al., 2012).

In a recent study, Amici et al. (2020) investigated in particular the human ability to recognize facial expressions associated with dog emotions. Participants were presented with pictures of dogs, humans and chimpanzees showing angry, fearful, happy, neutral and sad emotions, and had to assess which emotion was shown and the context in which the picture had been taken. Participants were recruited among children and adults with different levels of general experience with dogs, resulting from different personal (i.e. dog ownership) and cultural experiences (i.e. growing up or being exposed to a cultural milieu in which dogs are highly valued and integrated in human lives). They found no evidence for co-domestication. According to their results, the ability to recognize dog emotions is mainly acquired through experience. In adults, the probability of recognizing dog emotions was higher for participants who grew up in a cultural milieu with a positive attitude toward dogs, which may result in different passive exposure, interest or inclination toward this species (Amici et al., 2019).

Overall, all the studies mentioned in this chapter provide important information on the human ability to read dog emotions, but do not allow for the drawing of reliable conclusions on our ability to predict dog behavior per se. During everyday interactions, humans can rely on multiple cues to predict others' behavior. Studies of emotion recognition, however, often present still pictures as visual cues, meaning that performance during emotion recognition tasks may underestimate actual human predictive abilities (Donnier, Kovács, Oña, Bräuer, & Amici, 2020). Indeed, predicting the outcome of a social interaction is more important than rating a social action (i.e. classifying it as aggressive, fearful or neutral). This ability may decrease the risk of being injured, for instance, which would be highly adaptive.

Thus, future studies should further investigate how humans perceive dogs by using more ecologically valid setups that allow humans to perceive the whole situation and not only certain aspects of it. In the investigation of communicative and cooperative dog-human interactions, we should also focus more on the role of the human partner (i.e. Henschel et al., 2020). For example, it is important determine which elements of communicative behavior from a human towards a dog are ultimately successful. Individual differences should be taken into account as well. For example, it is possible that a resemblance in personality could lead to better cooperation within a dog human dyad (Chopik & Weaver, 2019; Gosling, Kwan, & John, 2003; Turcsán, Range, Virányi, Miklósi, & Kubinyi, 2012). An open question is how these cross-species communicative skills develop in humans, which factors contribute to individual differences in this regard, how they are related to other socio-emotional competencies, and what consequences they have on both the owner and the dog (e.g., attachment, stress reactivity, leaning velocity, etc.).

3.4. Cultural differences in dog human interactions

There is another important gap in our knowledge about the dog-human relationship. Although it has been very well investigated in Western countries in the last 20 years, we do not know much about this topic in non-Western cultures. Nearly all studies about dog cognition tested dogs owned by people from 'WEIRD' societies, i.e. Western, Educated, Industrialized, Rich, and Democratic societies (Henrich, Heine, & Norenzayan, 2010). However, the majority of dogs in the world, about 75%, is not kept the same way they are in Western countries (Gray & Young, 2011; Kaminski & Marshall-Pescini, 2014). Thus, the field of dog cognition suffers a similar problem to Human Psychology: typically only WEIRD subjects – usually students from the behavioral sciences – are tested. The absence of carefully planned cross-cultural tests means that we do not know whether dogs kept in non-Western cultures perform similarly to "Western" dogs in cognitive tests. It is also unclear whether dogs in non-Western cultures prefer humans to other dogs as social partners (Gácsi, Topál, Miklósi, Doka, & Csanyi, 2001; Miklósi et al., 2003; Topál et al., 2005) and whether non-Western dog-human bonds are comparable to the attachment between human infants and their mothers, as has been suggested for dogs in WEIRD societies (Prato Previde & Valsecchi, 2014).

Previous work provides support both for and against an expectation of differences in dog cognition and dog-human relationships across cultures. Around the world, dogs were and are kept for various functions (Miklósi, 2007; Serpell, 2016; see 1.1 and 1.3.3). These functions differ in the extent to which cooperation with humans is required, and thus, we might expect to see differences among dogs in cultures in which a particular function dominates. Even within a 'WEIRD' context, some differences have been documented among dog breeds that work cooperatively with humans, such as shepherds or boxers, and breeds that work independently from humans, such as ground scent hunting dogs or Siberian Huskies. In particular, it was found that breeds selected to work in close cooperation and continuous visual contact with human partners were better at following the human pointing gesture (Gácsi, McGreevy, Kara, & Miklósi, 2009). Moreover, Heberlein et al. (2017) showed that cooperatively-working dogs were less attentive to the owner's perception when stealing forbidden food (Heberlein, Turner, & Manser, 2017), while McGetrick et al. (2020) found no differences in inequity aversion between cooperative and independent working breeds (McGetrick, Brucks, Marshall-Pescini, & Range, 2020). However, it is not completely clear whether this illustrates breed differences or differences due to the function of these dogs. It is also clear that there are huge individual differences even within a breed, depending on their function (Miklósi, Turcsán, & Kubinyi, 2014; see Wilsson & Sundgren, 1997).

Furthermore, an increasing number of studies are including stray and free-ranging dogs in their samples (Bhattacharjee et al., 2020; Bhattacharjee et al., 2017; Bonanni & Cafazzo, 2014; Hare et al., 2010). Despite their limited contact with humans, these dogs show similar abilities to communicate with humans as family dogs. For example, Bhattacharjee et al. (2017)

found that free-ranging dogs show an age-related plasticity in their ability to follow human pointing and that adult dogs might even be able to adjust their behavior based on the reliability of the human experimenter. Together with research carried out with shelter dogs and pups (see chapter 1.3.1), these findings suggest that domestic dogs may share a subset of "universal" behaviors, at least in the way they react to human communicative cues, regardless of the context in which the dog is found. In other words, dogs vary in their behavior and temperament, but probably not so much in their general cognitive abilities (Miklósi et al., 2014, see also McGetrick et al., 2020).

In terms of the human perspective on dogs all over the world, there has mainly been ethnographic research conducted on how dogs are kept, treated and perceived in non-western cultures (i.e. Haraway, 2016; Kirksey & Helmreich, 2010; Shanklin, 1985). Gray & Young (2011) explored typical dog-human dynamics in 60 different societies. They found that, across the world, some dogs served valuable functions, such as aiding in hunting and pest removal, while some were simply kept for pleasure or companionship. However, positive and negative interactions as well as feeding and sleeping patterns varied substantially across societies (Gray & Young, 2011). Koster (2009), who investigated dog-human relationships in the lowland neotropics, also found considerable cross-cultural variation in the training and care of dogs (Koster, 2009). As Amici et al. (2020) has shown, positive or negative attitudes toward dogs might impact how dogs are understood. In the above mentioned study, in which different groups of humans rated dog emotions from pictures, it was found that persons from cultures in which dogs are often viewed as impure, and are rarely integrated as part of the family, perform worse at interpreting a dog's emotions, compared to persons from cultures that have a generally positive attitude towards dogs (Amici et al., 2019). Based on these findings, we can expect differences in attitudes toward dogs among cultures to be reflected in people's abilities to recognize dog emotions, and perhaps in dog-human bonding in these societies.

It is also important to note that humans were far from a monolithic cultural entity at the time when dog domestication began (Ben-Dor, Gopher, Hershkovitz, & Barkai, 2011; Bräuer & Vidal Orga, in press). The above-mentioned special skills are hypothesized to have been selected for early in the domestication process because their overall effect would have been to increase the efficiency of dog-human cooperation. Comparative psychologists, however, have yet to establish that these skills are universally found among dogs. Given that human cultures are incredibly diverse, the question is how different human cultures might exert *different* selective pressures on dog cognition. As mentioned above, preliminary comparative work on dog keeping across cultures suggests that culture correlates with significant differences in human-dog interactions (i.e. Gray & Young, 2011).

We know, therefore, that there are differences among human cultures in the way dogs are kept, valued and communicated with. What we do not know is whether these differences act as different selective pressures on dog cognition and behavior, and whether any resulting differences are likely to be heritable. Thus, future studies should investigate cross-cultural variation in human attitudes toward dogs and whether these can be predicted by a dog's function in a society and how dogs' cognitive skills and dog-human interactions vary cross-culturally.

3.5. The interdisciplinary perspective

One main conclusion of this work is that in order to fully understand the dog-human relationship we need a truly interdisciplinary perspective (Bräuer & Vidal Orga, in press).

First, interdisciplinary approaches are crucial for understanding the process of dog domestication. Although findings of comparative psychology have shed light on the question of what skills dogs might have been selected for during domestication (see chapter 1.3), there are many compelling questions such as: When and where did the process start? Why were wolves – and not another species – domesticated in the first place? What was the initial advantage for the human to domesticate the wolf?

Second, to better understand the contemporary dog-human relationship, it is important to find ways to quantify the benefit of dog keeping today. One approach could be to attempt to quantify the benefit of dog ownership in various societies all over the world.

Third, the interdisciplinary approach is needed to investigate how dog domestication and human culture have interacted and shaped each other to produce the diversity of dogs and cultures we see today. In particular, it should be investigated (i) how human cultural diversity introduces heterogeneity in the dog-human relationship and in dogs' cognitive and communicative abilities, and (ii) how dog domestication may have influenced human cultural trajectories.

To answer these big questions, we need an interdisciplinary approach in which scientists from many fields work together. To answer the questions about domestication we have to combine approaches not only from comparative psychology and genetics, but also from archaeology, anatomy, anthropology and even paleoclimatology (to determine the climatic circumstances that influenced living conditions, i.e. Reichholf, 2020). To better understand the contemporary dog-human relationship we also need data from sociology in the field of Human Animal Studies. Finally, for investigating the cultural differences in dog-human interactions, we need approaches from anthropological and linguistic data, as it is possible that linguistic patterns provide clues regarding the history of dog-human relationships in particular societies. It might be interesting, for example, to examine patterns of colexification between lexemes for "dog" and those for "wolf" or other wild canids across as many of the world's ~7000 languages as possible. It could then be tested whether observed patterns of colexification reflect what is known from the historical and archaeological record about dog domestication and dog keeping across regions and language families. Similarly, it might be expected that the standard term for "dog" in a language would reflect dogs' dominant function in societies that speak that particular language (Bräuer & Vidal Orga, in press).

In conclusion, to answer all these big questions, we need an interdisciplinary approach in which scientists from the fields of archaeology, linguistics, paleoclimatology, genetics, anatomy, ethology, psychology, sociology, and anthropology work together.

4. Appendix

4.1 Curriculum Vitae

Personal Information

Name: Bräuer, Juliane
Date and place of birth: 30/09/1976, Jena
Nationality: German
Personal Status: married, 2 children

Education

2002–2007	PhD in Biology Supervisor: Prof. Michael Tomasello *Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology (MPI EVAN), Leipzig*
1997–2002	Diploma *Faculty of Biological Science, University of Leipzig, Germany* Studies in Biology *Universities of Würzburg and Leipzig*
1991–1995	Abitur *Albert Schweitzer Gymnasium, Jena*
1986–1991	*POS Karl Liebknecht, Schlöben*
1983–1986	*Grundschule Asmara, Eritrea*

Current Position(s)

Since 2016	Senior Scientist, Head of the DogLab *Department of Linguistics and Cultural Evolution, Max Planck Institute for the Science of Human History (MPI SHH), Jena* Lecturer *Institute of Psychology, Friedrich-Schiller-University (FSU), Jena*

Previous Positions

2013–2015	Postdoctoral Researcher, Coordinator, Lecturer *Institute of Psychology, Friedrich-Schiller-University Jena (FSU), Germany*
2002–2015	Postdoctoral Researcher *Department of Developmental and Comparative Psychology, MPI EVAN, Germany*
2012–2013	Project Coordinator (non-profit sector) *Orang-Utans in Not e.V. (Orangutans in peril), Germany*

Fellowships, Awards and Funding

2021–2024	Research grant: Deutsche Forschungsgemeinschaft
2019–2022	MPG International Max Planck Research School (IMPRS) of the MPI SHH and FSU: Funding for a PhD student position
2016	Research grant: Albert Heim Foundation
2010–2012	Max Planck Society Research Stipend
2007–2010	Deutsche Forschungsgemeinschaft Research Stipend
2007	Max Planck Society Research Stipend

Organisation of scientific conferences, commissions of trust and ad hoc reviewer

2004–present	Ad Hoc Reviewer for: American Journal of Primatology, Animal Behaviour, Animal Cognition, Animal Welfare, Behavioural Processes, Cognition, Current Anthropology, Ethology, Interaction Studies, Journal of Comparative Psychology, PloS ONE, Scientific Reports, Zoobiology
2020	Member of the organizing committee of the Online-Workshop: “The spectrum of teaching in humans and other animals” at MPI SHH
2018	Reviewer for the Mind Science Foundation
2018	Advisory Board of the 6th Canine Science Forum in Budapest
2018	Board for student prize for best presentation/poster at Primate Society of Great Britain Spring Meeting in Portsmouth, UK
2017	External examiner for a PhD commission at the University of Zürich
2013	Scientific Advisory Board at Collaborative Research Project (CRP) Workshop of the ESF Research Networking Programme CompCog
2003	Member of the organization committee of the 8th Conference of the German Society of Primatology, 150 participants, Germany

Career Breaks

1/2005–8/2005	Maternity Leave First Child
10/2008–9/2009	Maternity Leave Second Child

Media Outlets (selection)

Monthly Blog at Psychology Today: https://www.psychologytoday.com/us/experts/juliane-br-uer-phd; HR2 (2020); Welt (2020); Spiegel (2020) MDR (2020); Der Standard (2019); WDR (2019); Spiegel Online (2019); Psychologie heute (2019); Japan Broadcasting Corporation (2018); Deutschlandfunk (2018); Welt-online (2018); BR (2018); MDR (2018); 3sat (2018); Gizmodo (2018); WELT (2017); Daily Mail (2017); MDR (2016); MDR Figaro (2015); Spektrum der Wissenschaft (2015); ARTE (2014); Stern (2012); SWR (2011); WELT (2010); MaxPlanck-Forschung (2009); Canadian Broadcasting Corporation (2008)

Invited Talkes (selection)

2019	Human-environment-interactions, *workshop at the University of Leipzig, Germany*
2018	Dogs: Past and Present – an interdisciplinary perspective, *Rome, Italy*
2017	Anthropology Colloquium, *University of Zürich, Switzerland*
2016	Studienstiftung des deutschen Volkes: Evolutionary Anthropology, *Jena, Germany*
2015	Divisions of Evolutionary Ecology and Behavioural Ecology, *University of Bern, Switzerland*
2014	*Instituto Tecnológico EDUCAN, Madrid, Spain*
2014	Interdisciplinary workshop “Coordination, Collaboration and Cooperation”, *Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*
2013	Plenary Talk 3rd ToK Conference of CompCog, *Vienna, Austria*
2013	*Marine Science Center, University of Rostock, Germany*
2012	*Naturwissenschaftlicher Verein Hamburg, Germany*
2011	Conference “Communicating Disasters” *ZIF, Bielefeld, Germany*
2011	*German Primate Center, Göttingen, Germany*
2010	ESF-Workshop “Recognizing, attracting, directing and sharing attention in human and nonhuman animals”, *Milano, Italy*
2008	Darwin’s Day, *Oslo, Norway*
2004	HOPE International workshop “Evolutionary neighbors: from genes to mind”, *Kyoto, Japan*

In Brief

I am a dog cognition expert and experienced researcher in the field of Comparative Psychology, and was trained by one of the most influential scientists in that field: Michael Tomasello. I worked with several animals, including apes, which – as our closest living relatives – have always been an important model to study the evolution of cognition, but also with dogs, which, during domestication, have adapted to a highly specialized niche – the human environment. I started my career with studies on visual perspective taking and communication in dogs and apes. Whereas visual perspective taking might be widespread in the animal kingdom, dogs have obviously developed special skills during their domestication to perceive human communicative cues. After my PhD, I received a DFG Research-Stipend for studying mental time travel and future planning in great apes, whereI found that apes produce tools for future use. In addition, I was involved in studies about social learning, metacognition and causal reasoning. Another approach that I have been starting to work on was how perception and cognition are linked together. Since 2016 – working at the MPI SHH, I became especially interested in the process of dog domestication and dog human cooperation. Overall, I published 28 research papers / 5 review papers / 4 book chapters / 4 books. My publications have attracted over 2880 citations (2 papers with more than 400 citations), yielding an H-index of 21.

Jena, Juliane Bräuer

Publications

Research papers:	28
Review papers:	5
Book chapters:	4
Scientific books for non-scientific audience:	4
H-index:	21 (Google Scholar)

a) publications in peer reviewed journals

Donnier, S., Kovács, G., Oña, L. S., **Bräuer,** J., & Amici, F. (2020). Experience has a limited effect on humans' ability to predict the outcome of social interactions in children, dogs and macaques. *Scientific Reports, 10*(1), 21240.

Henschel, M., Winters, J., Müller, T. F., & **Bräuer,** J. (2020). Effect of shared information and owner behavior on showing in dogs *(Canis familiaris)*. *Animal Cognition, 23*(5), 1019–1034.

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Silva, K., **Bräuer,** J., de Sousa, L., Lima, M., O'Hara, R., Belger, J., … Tennie, C. (2020). An attempt to test whether dogs *(Canis familiaris)* show increased preference towards humans who match their behaviour. *Journal of Ethology, 38*(2), 223–232.

Bräuer, J., Stenglein, K., & Amici, F. (2020). Dogs *(Canis familiaris)* and wolves *(Canis lupus)* coordinate with conspecifics in a social dilemma. *Journal of Comparative Psychology, 134*(2), 211–221.

Amici, F., Waterman, J., Kellermann, C. M., Karimullah, K., & **Bräuer,** J. (2019). The ability to recognize dog emotions depends on the cultural milieu in which we grow up. *Scientific Reports, 9*(1), 16414.

Belger, J. & **Bräuer** (2018) Metacognition in dogs: Do dogs know they could be wrong? *Journal of Learning & Behaviour 46*(4), 398–413.

Bräuer, J., & Amici, F. (2018). Fake or not: Two prerequisites for jealousy. Commentary on Cook et al. on dog jealousy. Animal Sentience, 22(18).

Bräuer, J., & Belger, J. (2018). A ball is not a Kong: Odor representation and search behavior in domestic dogs *(Canis familiaris)* of different education. *Journal of Comparative Psychology, 132*(2), 189–199.

Lampe, M., **Bräuer,** J., Kaminski, J., & Virányi, Z. (2017). The effects of domestication and ontogeny on cognition in dogs and wolves. *Scientific Reports,* 11690.

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4.2 Ehrenwörtliche Erklärung

Ich erkläre hiermit, dass mir die Habilitationsordnung der Friedrich-Schiller-Universität Jena bekannt ist.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbst, ohne unzulässiger Hilfe Dritter, angefertigt habe.

Alle von mir benutzten Hilfsmittel, persönlichen Mitteilungen und Quellen sind in der Arbeit angegeben.

Bei der Auswahl und Auswertung des Materials haben mir die nachstehend aufgeführten Personen in der jeweils in den Fachartikeln unter "Author contributions" beschriebenen Weise unentgeltlich geholfen:

Federica Amici, Julia Belger, Milena Bös, Josep Call, Theresa Epperlein, Daniel Hanus, Melanie Henschel, Russell Gray, Juliane Kaminski, Mariely Lima, Bonaventura Majolo, Thomas Müller, Robert O'Hara, Simone Pika, Andrea Pitsch, Magdalena Schaub, Katja Schönefeld, Karine Silva, Liliana de Sousa, Katharina Stenglein, Claudio Tennie, Michael Tomasello, Natalie Uomini, James Winters.

Weitere Personen waren an der inhaltlich-materiellen Erstellung der Arbeit nicht beteiligt. Insbesondere habe ich hierfür nicht die Hilfe von Vermittlungs- bzw. Beratungsdiensten in Anspruch genommen und Dritte haben weder unmittelbar noch mittelbar geldwerte Leistungen von mir für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Arbeit stehen.

Die Arbeit wurde weder im Inland noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde vorgelegt. Weder früher noch gegenwärtig, habe ich an einer anderen Hochschule eine Habilitation eingereicht.

Ich versichere, dass ich nach bestem Wissen die reine Wahrheit gesagt und nichts verschwiegen habe.

Jena, Juliane Bräuer

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