The Role of Attention in Perceiving Social Information: 
Behavioral and Electrophysiological Studies

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Preface

The human brain has the ability to process large amounts of sensory information in daily life. This information includes both visual and auditory stimuli among information in other modalities. This visual information includes many of the visual stimuli such as faces and human bodies. However, both faces and human bodies provide important social cues that contribute to the identification of other people, their age and gender as well as their intentions and affective states. Prior studies have shown that both faces and human bodies may engage attention to a greater extent than other objects such as clothes and food (Langton et al., 2008; Ro et al., 2007). Neuroimaging studies have shown that human brain, includes specific regions that preferentially respond to either faces (Kanwisher et al., 1996) or human bodies (Downing et al., 2001). Sides both faces and human bodies share a number of abstract configural properties that may make the perceptual system treat them similarly, for instance, all human bodies share the same set of parts (i.e. heads, arms, torso, legs), analogous to faces (i.e. eyes, nose, mouth) and the perceptual distinctions depend on the exact shape and position of component parts (Reed et al., 2003; 2006; Slaughter et al., 2004; Stekelenburg & de Gelder, 2004).

When both faces and human bodies are presented upside down, reaction times (RTs) and error rates (ERs) are disproportionally increased for inverted than upright faces (e.g. Yin, 1969) and human bodies (e.g. Reed et al., 2003). This inversion effect has often been considered as critical evidence for configural processing of both faces (for a review, cf. Maurer et al., 2002) and human bodies (for a review, cf. Minnebusch & Daum, 2009). However, it is still controversial whether all aspects of configural processing of human bodies occur in an identical manner as for faces (Minnebusch & Daum, 2009). Another recent debate in the literature focused on the relation between selective attention and face processing. Some studies showed that face sensitive N170 ERP component is affected by selective attention (Eimer, 2000a; Holmes et al., 2003; Lueschow et al., 2004) while the other found the N170 is more or less unaffected by attentional selectivity (Carmel & Bentin, 2002; Cauquil et al., 2000). Besides, no study was investigated the effect of selective attention in perceiving human bodies.
Consequently, in the current thesis, I investigate the role of attention in perceiving social stimuli such as faces, human bodies and body parts. In three studies, attention was manipulated sensu Lavie’s perceptual load theory (PLT) to task-irrelevant distractor unfamiliar faces, human bodies, body parts and objects, by superimposing letter strings over distractor and increasing attentional demands of a letter identification task. Specifically, study I was compared the effect of load on distractor unfamiliar faces and houses. Study II additionally investigated effects of stimulus orientation and compared unfamiliar faces and unfamiliar human bodies, either presented intact or perceptually manipulated. Study III indirectly tested encoding of distractor faces, body parts (hands) and objects (houses) by implementing an immediate repetition priming paradigm. In all three studies, event-related potentials were recorded in addition to behavioral performance measures.
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Tarik N. Mohamed

1 Introduction

1.1 Cognitive models of person recognition

Cognitive psychologists are interested in the processes underpinning person recognition. In particular, faces and human bodies have attracted a large number of investigations and raised many discussions during the past decades. Perceiving faces represents one of the most fundamental skills in human cognition. Bruce and Young (1986) have suggested a cognitive model of face perception and recognition in which they divided the cognitive system into different functional and modular units (e.g., different memory stores). Specifically, they distinguish between seven distinct types of information that can be derived from faces such as pictorial, structural, visually derived semantic, identity specific semantic, name, expression and facial speech codes. However, these codes are not themselves the functional components of the face processing system, but rather products of the operation of the functional components represented in a hierarchical manner (Bruce & Young, 1986). The components on the “identity route” of face processing are including following stages as described in the model of Bruce and Young, (1986) and in slight modifications of the original model based on recent research:

1) *Structural encoding stage*: creates a set of descriptions of seen faces that can be used for the variety of independent purposes in subsequent stages. The structural encoding stage includes view-centred and expression independent descriptions as well as more abstract descriptions both global configuration and of facial features (Bruce & Young, 1986; Young et al., 1986). View-centred descriptions provide information for expression and facial speech analyses (Bredart & Bruyer, 1994), while expression-independent descriptions are interconnected with the visual processing and provide information to the face-recognition nits (FRUs).

2) *Face recognition units (FRUs)*: are a long term store of representations of faces already known by the perceiver and one FRU is corresponding to each known face (Young et al., 1985). FRUs are considered to be the key component for familiarity decisions (Bredart & Bruyer, 1994), and contain stored structural codes, which describe one of the faces known to a person (Bruce & Young, 1986). When a face is seen, the strength of a face-recognition it’s signal to the cognitive system will depend on the degree of resemblance between its stored description and the input provided by the structural encoding stage (Bruce & Young, 1986). This unit will not respond to all other visual cues such as voice or body shape, but will respond to the person’s face.
3) **Person identity nodes (PINs):** refer to a second step of person identification, receiving activation from modality-specific FRUs. PINs can be accessed not only via the face, but also via other visual or auditory cues thus, allowing the identification of a particular person and the retrieval of corresponding knowledge about this person such as her/his voice, typical clothes and body actions. Burton et al. (1990) have argued that PINs themselves do not contain semantic information, but simply act as a gateway to semantic information units (SIUs). Information from the analysis of view centred descriptions, FRUs and PINs are provided to the cognitive system, which in turn able to influence all these functional components. Nevertheless, the relation between the above-described functional components and pictorial encoding is not so clear cut (Bruce & Young, 1986).

![Face recognition model](image)

Fig 1. Face recognition model, as suggested by Schweinberger and Burton (2003) and enhanced by Schweinberger (2011).

Schweinberger and Burton (2003) have linked the functional components, as suggested by Bruce and Young (1986) to an event related potential (ERP-) markers, which are found more prominent in response to faces than to other objects. ERPs may reflect activity in different areas in the human brain, which are specifically sensitive to faces and have been
suggested to be involved in the processing of faces (e.g. Haxby et al., 2000). An occipitotemporal negativity around 170 ms, and has been termed N170, which has been associated with structural encoding stage (Bentin et al., 1996). Moreover, FRU activation has been linked to an occipito-temporal negativity at 250 ms and has been termed N250r (Schweinberger & Burton, 2003). Previous studies have also revealed that an occipital positive ERP-component (P100) is larger for faces than objects (Desjardins & Segalowitz, 2009; Herrmann et al., 2005). This could reflect top-down attentional processes related to face perception (Desjardins & Segalowitz, 2009) or alternatively, that P100 is related to specialized pictorial encoding (Schweinberger, 2011) for faces in contrast to other objects (see Fig. 1).

When facial details are not available, other visual cues such as voice, body shape or gait help to identify the person, by establishing identity. Recently, many researchers have shown that human bodies are a special category when compared with other objects such as houses, cars and so on. However, still there is little known about body perception. Neuroimaging studies have suggested neural models of body perception based on differential activations found for faces and human bodies. Neuroimaging studies have shown that there are two cortical regions in the human brain, sensitive to human bodies, the fusiform body area (FBA) and the extrastriate body area (EBA). Equivalent to face sensitive areas have been identified, the occipital face area (OFA) and the fusiform face area (FFA).

Taylor et al. (2007; 2010), have suggested a model for body perception (see Fig. 2). Accordingly, EBA is activated, when the whole bodies are perceived, and body parts, these findings showed that EBA has single unitary populations of neurons with complex tuning

Fig 2. Neural model of body perception as suggested by Taylor et al.(2007). This figure was taken from Minnebusch & Daum (2009). This model is based on similarities between face and body perception and focuses on the EBA and FBA.
function which is responding selectivity to the whole bodies, and drop gradually to body parts. FBA has showed a sharp increase in activation when the headless bodies or large proportion of bodies, such as torso, or legs are presented. Thus, it seems that EBA is responsible for the perception of body parts while FBA may be related to “configural” body processing (for more details cf. section 1.4.1). Up to date, no cognitive model has been suggested to explain human body perception and recognition similar to what has been suggested for face perception and recognition (e.g. Bruce & Young 1986).

1.2 Neural correlates of perceiving social stimuli

Event-related potentials (ERPs) are a highly sensitive measure for addressing questions related to human cognition (Luck, 2005). ERPs are a non-invasive method for measuring brain activity during cognitive processing and provide an important tool for revealing questions about how the human brain, normally processes information (Picton et al., 2000). ERP studies in human face and human body perception have shown components that are generated in specific areas of the human brain, and occur for both categories. However, each component reflects brain activation associated with one or more mental operation(s). In this section I will introduce ERP components sensitive to social stimuli such as faces and human bodies and additionally introduce different areas in the human brain, which selectively respond to those stimuli.

1.2.1 ERP components sensitive to faces, human bodies and body parts

ERP studies have shown that different components are sensitive to faces and human bodies. However, most studies that investigated a face and body perception focused on the few specific components described below.

**P100**

The earliest ERP component of interest in the context of face and body processing is the P100 component - a positive-going deflection over the occipital medial brain region. This component is elicited between 60 and 120 ms after stimulus onset and peaks at 100 ms. The P100 has been shown to be sensitive to changes in basic visual stimulus properties such as contrast, luminance and spatial frequency (Schendan et al., 1998) and has thus been assumed to reflect early visual processing (Clark & Hillyard, 1996; Eimer, 1993; Mangun, 1995). The P100 is found to be affected by top-down processing such as spatial attention (Hillyard et al., 1998) and arousal (Vogel & Luck, 2000), and generated in the lateral extrastriate cortex
(LEC) (Clark & Hillyard, 1995). Forgoing studies have shown an increased P100 amplitude to inverted faces (Itier & Taylor, 2002; 2004a), and human bodies (Minnebusch et al., 2010), compared to upright versions of these stimuli. As described above, studies have also shown larger P100 amplitudes for faces than objects (Desjardins & Segalowitz, 2009; Herrmann et al., 2005). Schweinberger (2011) has suggested that P100 may reflect earlier stages in face processing related to pictorial encoding. However, further evidence is required to resolve whether or not the P100 for human bodies reflected the same pictorial encoding processes as P100 for faces.

N170

The most often examined ERP component sensitive to face processing is N170, a negative component occurring in the time window between 100 and 200 ms after stimulus onset, and typically peaks around 170 ms (Bentin et al., 1996). Face pictures elicit larger N170 amplitudes compared to objects (Rossion & Jacques, 2008) over occipito-temporal areas, eliciting a maximum peak over the right hemisphere (Bentin et al., 1996). The N170 is accompanied by a positive deflection over the central medial regions (see Fig. 3), occurring at the same time interval and termed vertex positive potential (VPP) (Jeffreys, 1996; Rossion & Jacques, 2008).

Fig. 3. The N170 is a negative component recorded from posterior lateral electrode sites following the presentation of faces and car categories (from Rossion & Jacques., 2008). The N170 component is larger for faces than cars and associated with a temporally coincident positivity on the vertex (CZ), the vertex positive potential (VPP), which is larger for faces than objects.
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The N170 is considered as a marker for the structural encoding stage (Schweinberger & Burton, 2003) and it has been reported to be unaffected by priming (Schweinberger et al., 1995), and familiarity (Bentin & Deouell, 2000; Eimer, 2000c; Schweinberger et al., 2002b). However, it is still controversial whether or not N170 is modulated by stimulus repetition. Some studies have reported repetition effects in terms of reduced N170 for repeated vs. non-repeated faces (Jacques & Rossion, 2006; Jemel et al., 2005), while other studies find no such effect (Cooper et al., 2007; Schweinberger et al., 2002a). Most importantly for the current thesis that N170 is delayed and enhanced to the presentation of inverted faces as compared to upright faces (Campanella et al., 2000; Eimer, 2000c; Latinus & Taylor, 2006; Rossion et al., 1999; 2000b). On a behavioural level, the face inversion effect is expressed in poor recognition of faces when presented upside down. It has been argued that inversion of faces disrupts the processing of configural information in faces (see section 1.4.1 for details). Taken together, the N170 has been shown sensitive to configural processing of faces (Latinus & Taylor, 2006).

Studies on body perception have indicated a negative component in a similar time interval between 100 to 200 ms after stimulus onsets (see Fig.4). This component is larger for either faces or human bodies than other objects. Interestingly, inversion of human bodies elicited a similar pattern of inversion as faces, both behaviorally (Reed et al., 2003; 2006) and electrophysiologically (Minnebusch et al., 2009; Stekelenburg & de Gelder, 2004), in that N170 mean amplitude was increased for inverted than upright human bodies.

Fig 4. A body-selective event-related potential (ERP) negative component (N1) peak is centered approximately at electrode P8, the site from which the data in the remaining panels were acquired (from Peelen & Downing, 2007). The body selective N1 component appears in the time intervals between 100 to 200 ms, and it is larger for faces and bodies than objects.
**N250r**

A negative component has been described as a relatively more negative waveform for immediately repeated as compared to non-repeated faces (see Fig.5). This component was observed between 180 and 290 ms at minimum (Schweinberger et al., 1995; Schweinberger, 2011) and 200 till 350 ms at maximum (Neumann & Schweinberger, 2008), most prominent over right inferior temporal regions (Schweinberger et al., 1995). This component has been termed N250r (“r“ for repetition) and was found to be enhanced to familiar as compared to unfamiliar faces (Herzmann et al., 2004; Schweinberger et al., 1995; 2002b). The N250r was larger for repetitions using the same image (Schweinberger et al., 2002b) than across different images of a person (Bindemann et al., 2008; Schweinberger et al., 1995). A positive counterpart of this component, with more positive going ERPs to repeated vs. non-repeated faces, has been identified over frontal central sites in the same latency range (Schweinberger et al., 2004). In general, the N250r has been related to the transient activation of face representations or face recognition units (Schweinberger et al., 2002a; Schweinberger & Burton, 2003) or to activation of pre-semantic representations of faces (Martin-Loeches et al., 2005). The N250r is assumed to be generated in lateral fusiform gyrus (Schweinberger et al., 2004).

![Fig 5. Left: ERP difference between repeated and non-repeated stimuli for faces, ape faces and cars. The N250r largest amplitudes were found for human faces, followed by ape faces and small or absent responses for inverted faces and cars. Right: The N250r voltage maps for all categories. Upper row showed the top view of the N250r, which appears in both human faces and Ape faces, in occipito-temporal regions, while the lower row, showed the effect on the right hemisphere (RH) (figure adopted from Schweinberger et al., 2004).](image-url)
**N400**

The N400 is a negative ERP component between 400 and 600 ms after stimulus onset over central medial sites (Neumann & Schweinberger, 2008; Schweinberger et al., 1995). This component is affected by familiarity (Barrett et al., 1988; Eimer, 2000c; Schweinberger et al., 1995) and has been interpreted as activation of semantic information involved in the identification of familiar faces (Bentin & Deouell, 2000; Cooper et al., 2007; Pickering & Schweinberger, 2003). Face repetitions have also shown to modulate the N400 (Bentin & McCarthy, 1994; Cooper et al., 2007; Henson et al., 2003; Schweinberger et al., 2002a). The N400 may reflect the access to semantic memory codes, as shown by sensitivity of N400 to associative priming (Pfutze et al., 2002; Schweinberger et al., 1995). N400 to “related” persons (e.g. Angelina Jolie and Brad Pitt) has been found less negative / more positive than to non-related persons (e.g. Schweinberger, 1995). Thus, the N400 was suggested to represent activation at the level of person identity nodes (PINs) (Bentin & Deouell, 2000).

**1.2.2 Brain regions involved in processing faces, human bodies and body parts**

The human brain is a complex organ, which processes a large number of different visual stimuli. However, this organ responds in a specific way to social stimuli, in particular to faces and to human bodies. Faces and human bodies are incredibly informative and a single glance provides much information about age, gender, ethnicity, emotion and trustfulness of a person. Neuroimaging studies have shown that there are sensitive areas in the human brain, responding to either faces or human bodies. The face sensitive areas involve the fusiform face area (FFA), a region within the fusiform gyrus (FG), which is more active to faces compared to objects (Haxby et al., 2000; Kanwisher & Yovel, 2006), locations (Haxby et al., 1994) or scrambled faces (Puce et al., 1995). The occipital face area [OFA] (Gauthier et al., 2000) is also sensitive to faces and more specifically, to facial features (Kanwisher et al., 1997; Puce et al., 1996). Finally, the superior temporal sulcus (STS), is involved in more dynamic aspects of facial information processing such as processing expression and gaze (Campbell et al., 1990) and plays an important role in determining where other’s emotions are being directed (Grossman & Blake, 2001). Regions sensitive to processing of human bodies include the extrastriate body area (EBA), located in the right lateral occipito-temporal cortex (see Fig.6), which responds to whole human bodies and body parts (Urgesi et al., 2004). It can also be activated by line drawings, stick figures or silhouettes of human bodies (Downing et al., 2004) and is active for both familiar and unfamiliar bodies and during the recognition of one’s own body (Hodzic et al., 2009).
fusiform body area (FBA), located in the middle of the fusiform gyrus (Downing et al., 2001; 2006; Peelen & Downing, 2005; 2007; Taylor et al., 2007), responds only to either whole bodies or large portion of human body parts (Hodzic et al., 2009). Finally, the inferior partial lobe (IPL) may be active during body and body part identification (Minnebusch & Daum, 2009).

Prior studies have reported that FBA resembles FFA in terms of activation for facial features (Tong et al., 2000). More specifically, that study reported activation of the FBA to presentations of eye regions. Moreover, FFA also responded to presentations of whole bodies (presented without head part) (Downing et al., 2006). Taylor et al. (2007; 2010) have reported differences in EBA activation for different body parts in that stronger responses were elicited for human torsos than for hands. These findings suggest that faces and human bodies are special categories in the human visual system.

1.3 The role of perceptual load in perceiving social stimuli

Attention is proposed to resolve ambiguities in neural coding which arise when multiple objects are processed simultaneously (Luck & Ford, 1998), demonstrating a specific role of attention in visual perception (for more details see, Deco & Rolls, 2005). It has long been debated whether or not attentional capacity is limited. One view was that humans have a limited capacity such that it is difficult to carry out multiple discriminations in parallel. Accordingly, perception is thought to be a limited process that requires selective attention to
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proceed (Broadbent, 1958; Treisman, 1969). In contrast, another view suggested that perceptual analysis operates without capacity limitations or voluntary control. Accordingly, perception is unlimited and can be automatically performed on several objects in parallel (Deutsch et al., 1967; Deutsch & Deutsch, 1963). These rival views of selective attention have led to theoretical impasse, which has seemed to be resolved when Lavie (1995) suggested a hybrid model of selective attention. In this “perceptual load” account, she compromised between different views on selective attention by proposing that selective attention includes a limited capacity or resources. If relevant material imposes high perceptual load, the task will exhaust all available attentional capacity thus, preventing the processing of irrelevant information (Lavie, 1995; 2005). In this case, selective attention to the relevant information is required (Muggleton et al., 2008). In contrast, if relevant material impose low perceptual load, substantial capacity will remain available and automatically “spill over” to the processing of irrelevant information (Lavie, 1995; 2005; 2010).

The literature distinguishes between perceptual load assumed to be related to attentional capacity, from more general aspects of tasks difficulty. The task difficulty is assumed to affect processing speed, without any influences of attentional processes. For instance, task difficulty could be altered by changing the quality of sensory information provided by stimulus (i.e. signal-to-noise ratio) and by manipulating spatial frequencies, superimposing noise or reducing presentation time (Jacques & Rossion, 2007b; Lavie & Robertson, 2001). Degrading stimuli increases the task difficulty without increasing the attentional demands.

The human brain is expected to respond to irrelevant information even if people intended to ignore them, but according to perceptual load theory this is supposed to occur only under conditions of low perceptual load. By contrast, high perceptual load should reduce or eliminate the brain response to irrelevant information (Lavie & Tsal, 1994). Neuroimaging studies have shown that neural activity for irrelevant information in areas of the visual cortex depend on the level of perceptual load (Pinsk et al., 2004; Rees et al., 1997; 1999; Schwartz et al., 2005). In these studies, activity to irrelevant information in the visual cortex was eliminated by high perceptual load (Pinsk et al., 2004; Rees et al., 1997). Yi et al. (2004) showed that when subjects attempted to ignore pictures of places presented in the background while monitoring for face repetitions at fixation, activity in the parahippocampal place area (PPA) to the background scenes was substantially reduced by a load increased for the face identification task.
Perceptual load has been shown to influence ERPs to irrelevant stimuli during earliest stages of visual processing. The P1 component was reduced under high perceptual load, compared to low load (Handy et al., 2001; Handy & Mangun, 2000) while N1 component was increased under high load than low load (Fu et al., 2008; 2009; 2010). The effect of load on N1 with increased N1 under high perceptual load has been localized to temporal parietal occipital region by using dipole modeling (Fu et al., 2008). Handy and co-workers showed that P1 and N1 were affected by attention modulations, suggesting that perceptual load was able to modulate spatial selection at relatively early stages of information processing in human cortex, potentially in extrastriate visual cortex (Fu et al., 2010; Handy et al., 2001; Handy & Mangun, 2000). It has been suggested that faces and human bodies can engage attention to a greater extent than other objects (Langton et al., 2008; Ro et al., 2007). However, when attention was manipulated according to the perceptual load theory (PLT), explicit recognition of faces is reduced under high perceptual load compared to low perceptual load (Jenkins et al., 2002). In contrast, the magnitude of repetition priming was unaffected by perceptual load. Perceptual load was manipulated to superimposing letters strings on distractors of famous faces, by varying the task. Under high perceptual load, participants were instructed to detect an “X” or an “N” among different letters. Under low perceptual load, they had to perform a color discrimination task.

A previous study investigated if the N250r to irrelevant faces is moderated by the level of perceptual load (Neumann & Schweinberger, 2008). Subjects attended to letter strings superimposed on briefly (200 ms) presented famous prime faces. Here, they identified “X” or “N” either among identical (low load) or different letters (high load). Subsequently, prime distractor faces were either immediately repeated as a probe or a different face was presented. Subjects were instructed to detect occasional butterflies to ensure that participants attended to the probe presentation. The results have shown that N250r was elicited for familiar face repetitions irrespective of load (Neumann & Schweinberger, 2008). Up-to-date, no study has measured brain activity using ERPs for dissociating effects of load on irrelevant social stimuli apart from faces (i.e. body parts or whole human bodies). This thesis focuses on the influence of attention to irrelevant distractors faces, bodies or body parts on the N170 ERP component. An additionally aim is the influence of attention to unfamiliar faces and body parts on repetition-sensitive ERPs, specifically on the N250r.
1.4 Cognitive and neuronal mechanisms sub-serving face and body perception

Researchers have long been interested in understanding separate and shared cognitive processes underlying human face and body perception. However, perception of social stimuli such as faces and human bodies may fundamentally differ from the perception of inanimate objects such as buildings, tools and furniture. Both faces and human bodies can carry a lot of information that facilitates social communication between humans. Apart from facial expressions, gestures convey the intentions of a communicator. Ro et al. (2007) have shown that both faces and human bodies engaged attention to a greater extent when compared to other objects. Faces and bodies may thus, be equally salient and common in daily life and both can convey similar information such as identity, expression or emotional states (de Gelder, 2006; 2009; 2010; Stekelenburg & de Gelder, 2004).

A critical common phenomenon observed for both faces and human bodies is the observation, that RTs and error rates are dramatically increased when pictures of these stimulus classes were presented in an upside-down orientation (Reed et al., 2003; Rhodes et al., 1993; Yin, 1969; Yovel et al., 2010). As described earlier, EEG components supposedly reflecting early stages of face and body processing are also affected by stimulus inversion. For instance, increasing negativities in the N170 amplitude are often observed for inverted compared to upright stimuli (cf. section 1.2.1). In the following sections I will discuss the influence of configural processing and the role of prominent feature neurons as alternative explanations for the inversion effect.

1.4.1 Configural processing of faces and human bodies

Adults demonstrate remarkable skills for individuating hundreds of familiar people via their faces, even at distance or in poor lighting conditions (Bahrick et al., 1975; Levin & Beale, 2000; O'Toole et al., 1998). When either familiar or unfamiliar faces are presented upside down, ERs and RTs increased for inverted compared to upright faces (Bentin et al., 1996; Freire et al., 2000; Haxby et al., 1999; Rhodes et al., 1993; Yin, 1969). Although a decline in recognition memory has also been reported for inverted presentations of other categories of mono-oriented objects such as houses, this inversion effect was much larger for faces than for objects (Yin, 1969). It has been argued that the disproportionate inversion effect observed for face can be considered as evidence for configural processing of faces (Maurer et al., 2002).
According to Maurer et al. (2002), configural processing involves three different stages. The first stage includes sensitivity to first order relational information, which specifies the spatial relation between facial parts. Overall, the arrangement of facial features is relatively constrained, such that aligned horizontal eyes within a face occur above the central nose, itself occurring above the mouth (Rhodes et al., 1993). A second stage is termed holistic processing. In this stage, an integration between the arrangement of the facial features and the external contour results in an individual representations of a face as whole (Mondloch et al., 2002). Finally, the third stage, second order relational information refers to the specific individual’s metric and spatial distance between internal features such as the distance between right and left eye (Maurer et al., 2002; Mondloch et al., 2002).

Several studies have examined face processing by trying to disrupt configural information in faces. Prominent methods to achieve this include the use of thatcherized faces (i.e. selectively inverting eyes and mouth region of a face) (Boutsen & Humphreys, 2003), rearranging facial features (Tanaka & Farah, 1993) or presenting faces upside down (Eimer, 2000b; Freire et al., 2000; Leder & Bruce, 2000; Valentine & Bruce, 1986). Nonetheless, the most commonly used method to disrupt configural processing is face inversion.

In contrast to configural processing of faces, feature or part-based processing (also referred to as analytical processing, cf. Latinus & Taylor, 2006) is assumed to prevail for other inanimate objects and object recognition may operate through recognition of single object parts (Biederman, 1987). There is some evidence in the literature indicating that...
upright faces may be processed in a holistic manner while inverted faces - similar to objects - are being processed in part-based manner (Latinus & Taylor, 2006). However, the idea of configural face processing is a matter of controversy in the literature. Some researchers assume that faces are processed exclusively holistically (Goffaux & Rossion, 2006; Hole et al., 1999; Le Grand et al., 2002; Pellicano & Rhodes, 2003) while others have suggested that faces are processed both holistically and part-based (Collishaw & Hole, 2000; Tanaka & Farah, 1993). Conversely, it is also controversial whether other objects can utilize configural processing mechanisms similar to faces. Candidates may be human bodies or other homogeneous objects such as landscapes (Rhodes et al., 1993) for which the perceiver has developed expertise in distinguishing individual members at a subordinate level.

Studies using human bodies have shown that inverting bodies results in increased RTs and ERs compared to upright bodies (Reed et al., 2003; 2006) and this inversion effect is larger for bodies than for other objects (Minnebusch et al., 2009; Stekelenburg & de Gelder, 2004). Similar to the observations for faces, electrophysiological studies have shown that N1 component in response to inverted compared to upright human bodies was increased in amplitude and delayed in latency (Minnebusch et al., 2009; Stekelenburg & de Gelder, 2004). Accordingly, both behavioral and electrophysiological studies have suggested that human bodies might rather be processed configurally (i.e. similar to faces) than in a part-based manner through an assemblage of features (de Gelder, 2009; Minnebusch & Daum, 2009).

However, it is still unresolved if all of the three stages of configural processing (according to Maurer et al., 2002) subserve body processing (Minnebusch & Daum, 2009, see Fig.7). Specifically, the involvement of the holistic processing stage is a matter of current investigation (Bauser et al., 2011). In that study, Bauser and co-workers (2011) investigated the holistic processing of human bodies and faces using a composite illusion task. Results show that matching performances of the upper body halves were not different depending on aligned or misaligned presentations, suggesting that human bodies were not processed holistically in that particular study while faces were better matched when misaligned. However, when comparing inverted presentations of aligned and misaligned bodies, an inversion effect emerged, with better recognition performances for upright compared to inverted bodies, but not for faces. Minnebusch et al. (2009), have suggested that a specialized mechanism is involved in processing of human bodies. Critically, this mechanism is dissociable from those mechanisms involved in face or object processing.
1 Introduction

1.4.2 The role of feature neurons in face and human body processing

A recent approach has provided an alternative explanation for the inversion effect, which was observed for faces by showing the contributions of separate and specific feature neuron populations. Neuron populations in the anterior inferior temporal cortex (Gross et al., 1972; Rolls et al., 1977), partial cortex (Leinonen & Nyman, 1979), frontal cortex (Pigarev et al., 1979) and the amygdala (Sanghera et al., 1979), were activated by faces. These neurons transmit activation to brain systems, which are concerned with identification of social responses to faces.

Some single-cell studies have shown that specific neuron populations in macaques are being activated by perception of isolated eyes - i.e. occurring without the face context - in the right superior temporal sulcus (rSTS) (Perrett et al., 1982; Rolls et al., 1980). Critically, these eye selective cells do usually not respond to eyes presented in the context of a face (Perrett et al., 1982). In contrast, face-selective neuron populations respond both to isolated face parts such as eyes, as well as to whole faces (Perrett et al., 1982). Neuroimaging studies have revealed that fusiform gyrus (FG) is involved in face recognition (Haxby et al., 2000; Kanwisher et al., 1997; McCarthy et al., 1997) while eyes are likely being processed within inferior and medial occipital gyri (Haxby et al., 2000). Rossion et al. (2000a) have shown that face parts (e.g., eyes) in comparison to whole faces or other facial features result in greater activation in the left, but not the right, FG, when participants performed a part discrimination task. Relevantly, prior studies have shown that FG and STS are the main sources of activation indicated by the N170 ERP component (Itier & Batty, 2009).

Eimer (1998) has shown N170 mean amplitudes are unaffected by the presence vs. absence of eyes in upright faces, when participants discriminated faces from objects. This may indicate that in the context of upright faces, eye cells do not contribute to the neuronal activation indicated by the N170. Itier and co-workers (2007; 2011), had participants perform an orientation discrimination task on eyeless vs. intact faces. They demonstrated that while intact faces produced the usual pattern seen for face inversion on the N170, eyeless faces were entirely unaffected by inversion (see Fig. 8). This study provides evidence that eyes neurons play the critical role for the larger N170 negativity for inverted faces. While eye selective neurons are inhibited in the context of upright faces, inversion eliminates the face context, causing the release of eye-selective neurons from inhibition. Accordingly, N170 mean amplitude is increased due to the additional contribution of activation from the eye neurons.
Comparable to faces, human bodies activate specific neuron population in inferior temporal cortex (ITC) (Desimone et al., 1984; Kiani et al., 2007) and anterior superior temporal sulcus (STS) (Jellema & Perrett, 2003; Oram & Perrett, 1994). Extending the neuronal model suggested by Itier et al. (2007), I propose the existence of specific feature neurons to be responsible for the inversion effect observed for human bodies. Specifically, I assume that head-selective neurons are inhibited in the context of upright human bodies and are released from inhibition when human bodies are inverted, resulting in the increased negativity of the N1 component (see Fig. 9). Accordingly, my prediction is that when heads are removed from bodies, no inversion effect should occur.

Fig. 9. Suggested neural model for the early stages of body processing as indexed by the N1. The ‘+’ signs signify the neurons are active. The ‘-’ sign followed by a question mark indicates a possible inhibition mechanism.
1.5 Rationale and objectives of the present thesis

As detailed above, there is evidence for special processing of both faces and human bodies. Differences to the processing of other objects may result from configural processing of these faces and human bodies while objects are thought to be processed in a part-based manner. Configural processing has been reported to be severely disrupted by inversion. Differences with respect to the processing of faces and human bodies is not only evident on the behavioral level, but can also be measured by ERPs. Electrophysiological studies have shown conflicting evidence about the influences of selective attention on the N170 to faces. While some studies have reported attentional modulation (e.g., Holmes et al., 2003; Lueschow et al., 2004), others found a respective attention modulation in the N170 amplitude (e.g., Carmel & Bentin, 2002; Cauquil et al., 2000). However, no study so far investigated the role of selective attention in the processing of human bodies.

Here, several aspects of the role of attention in face and body processing shall be addressed.

1) The first paper is examined the influence of perceptual load (Lavie, 1995) on several ERP components to unfamiliar faces and objects (P100, N170, and late negative component).

2) The second paper addressed two questions. First, the combined effects of inversion and attention on ERP components to unfamiliar faces and human bodies were tested. Second, the contribution of a prominent feature neurons were tested by removing eyes and heads from face and body stimuli, respectively.

3) Finally, the third paper investigated the encoding of faces, body parts and objects under high and low perceptual load. Additionally, it was tested whether a previously described effect of intact encoding of familiar faces (Neumann & Schweinberger, 2008) can be extended to unfamiliar faces.
2. Overview of the present studies

In this section I will discuss three publications that investigated effects of perceptual load on processing of faces, human bodies and body parts. It is currently debated whether or not selective attention influences early processing of faces and no study so far has investigated this topic in either human body or object processing. Accordingly, this was the aim in studies I and II. Attention was manipulated in all three studies sensu Lavie’s perceptual load theory. Study I examined the influence of perceptual load on the processing of irrelevant distractors unfamiliar faces and houses. Study II tested the combined effects of selective attention and inversion in processing of irrelevant distractors unfamiliar faces and human bodies. Additionally, a contribution of feature neurons to inversion effects were examined by presenting faces and human bodies either intact (Exp.1) or manipulated by removing eye regions from faces and cropping heads from human body images (Exp.2). In study III, the neural repetitions effects were tested for faces, body parts and objects. Attention was manipulated for first presentations of these stimuli and effects of distractor repetition were investigated.

In the current studies I aim to investigate, first, the effect of perceptual load on the processing of faces and objects, and I expected that perceptual load may be influences on the early processing of faces, but not objects. Second, given that human bodies and faces cause similar inversion effects, I further hypothesized that these effects should occur under low, perceptual load but not high perceptual load. Third, assuming that features neurons play an important role for the prominent inversion effects observed for faces and human bodies, I expect that such an effect will be absent when prominent features (eyes from faces and heads from human bodies) are removed. If it is correct that N250r repetition effect found previously irrespective of load (Neumann & Schweinberger, 2008) can be attributed to the use of familiar faces, my fourth prediction is that an N250r should be absent for unfamiliar faces. Fifth, if N250r is specific to faces, no comparable effect should be found for houses or body parts.
2.1 Perceptual Load Manipulation Reveals Sensitivity of the Face-Selective N170 to attention (Mohamed et al., 2009)

While a substantial body of evidence exists concerning the specialty of human faces in the human visual system, little is known about the influence of selective attention on the early processing of faces and objects. While some researchers reported an influence of selective attention on the N170 (e.g. Holmes et al., 2003; Jacques & Rossion, 2007b), others found no such evidence (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000). For example, Holmes et al. (2003), presenting face pairs concurrently with house pairs and investigated the influence of attention allocation to cued faces vs. houses on the N170 response. N170 was enhanced when attention was allocated to faces compared to when attention was allocated to houses. The authors concluded that spatial attention modulated the face-sensitive N170 (see also, Lueschow et al., 2004). Jacques et al. (2007b), reported face sensitive N170 component was reduced under high load compared to low load. High load in that study was induced by increasing the noise ratio for face images.

Conversely, Cauquil et al. (2000) claimed that N170 is unaffected by selective attention. In that study, N170 to different stimulus categories was recorded (i.e. upright and inverted faces with opened or closed eyes, phase scrambled faces, eyes, lips and flowers). Participants had to respond to either isolated eyes or to faces with closed eyes. N170 was unaffected by selective attention (see also, Carmel & Bentin, 2002).

In the current study we compared attentional effects on the N170 for unfamiliar faces and houses. Attention was manipulated sensu Lavie’s perceptual load theory (Lavie, 1995; 2005) to brief (200 ms) presentation of distractor images from both categories (faces vs. houses). Target letter strings were superimposed on irrelevant distractor unfamiliar faces or houses. Participants were instructed to detect an “X” or an “N” among different letters (high load) or identical letters (low load). Over the course of the experiment, EEG was recorded continuously and analyzed for effects of perceptual load separately for both distractor types.

Behavioral results revealed that perceptual load was successfully manipulated, in that RTs and error rates (ERs) were increased under high load compared to low load. The P100 mean amplitudes were larger for face than house distractors. The N170 was larger to faces than houses. The N170 was affected by perceptual load. Critically, the N170 to faces was reduced under high load while the N170 to houses was increased in the same condition. A late negative component (LNC) was generally larger under low load than under high load for both distractor types. However, the load effect was slightly larger for faces than houses.
We speculated that face selectivity of the N170 may have been reduced or abolished under high load. This resulted in the decreased N170 for faces when attentional capacity was not available. The increase in N170 amplitudes to houses could be caused by a degraded representation of the house under high load, evoking a certain degree of face selectivity for the houses. Under low load, capacity mandatorily spills over to distractor faces, which as a consequence evoked large N170. Conversely, houses were classified as objects under low load and accordingly evoked smaller N170. Overall, we concluded that early stages of face processing as indexed by the N170 strongly depend on selective attention.

An open question referred to the influences of perceptual load on encoding of other object categories. This appears to be particularly relevant for the highly homogenous object categories of human bodies, which share certain properties with faces such as a disproportionate inversion effect and the preferential engagement of attention. Thus, study II investigated the combined effect of attention and inversion for both faces and human bodies.
2 Studies

2.2 Combined Effects of Attention and Inversion on Event Related Potentials to Human Bodies and Faces (Mohamed et al., 2011)

Human bodies are classified faster than other objects and may engage attention in a similar way as faces (Downing et al., 2004; Langton et al., 2008; Ro et al., 2007). Neuroimaging studies have shown different areas in the human brain, which responding selectively to faces (Kanwisher et al., 1996; 1997) or human bodies (Downing et al., 2001; 2006), compared to objects, suggesting that faces and human bodies may undergo specialised processing.

When faces or human bodies are presented upside-down, RTs and ERs are typically increased for inverted compared to upright orientations. The existence of a comparable inversion effect found for human bodies and faces may indicate similar underlying mechanisms for the processing of these stimuli (Reed et al., 2003; 2006; Yovel et al., 2010). Moreover, ERP studies have reported an inversion effect on both the faces sensitive N170 and the N1 to human bodies, in that consistently N1 amplitudes are increase and delayed for inverted compared to upright presentations (Minnebusch et al., 2009; Stekelenburg & de Gelder, 2004). These results suggest that both faces and human bodies might be processed in configural or holistic manner.

Recently, single-cell studies on macaques have suggested an alternative approach for interpreting the inversion effect for faces. Itier and co-workers (Itier et al., 2007; Itier & Batty, 2009) have suggested a neuronal model and explained face inversion effects with additional recruitment of eyes selective neurons, when faces are inverted. Analogously, we proposed that the body inversion effect could be interpreted due to additional recruitment of separate neuron populations activated for human bodies and heads (Wachsmuth et al., 1994).

Study II investigated the combined effect of perceptual load and inversion on ERP correlates to distractor faces and human bodies. Attention manipulation and task were identical to study I. However, in the present study distractor faces and bodies were either presented upright or inverted. In Experiment 1, all stimuli were intact. In Experiment 2, stimuli were manipulated by removing eyes from faces and cropping head parts from human body images.

Behavioural results indicated successful perceptual load manipulation, with increased RTs and ERs under high load compared to low load conditions. In ERPs for both experiments, an inversion effect was seen in P100, with larger P100 for inverted than upright stimuli. Load had little overall effect on N170 amplitudes. The only significant effect was an
N170 reduction under high perceptual load compared to low load for upright faces, in line with study I. Finally, the LNC exhibited a strong effect of load with larger negativity under low load compared to high load for all distractors types and both intact stimuli and manipulated stimuli.

Inversion effects were elicited for both faces and human bodies irrespective of perceptual load, with increased N170 amplitudes for inverted than upright intact stimuli. By contrast, eyeless faces evoked a small “inverted inversion effect” over more posterior electrodes (PO10, P10), in that upright eyeless faces elicited larger negativity than inverted eyeless faces. Inversion effect for headless bodies were found in the usual direction, though reduced, with increased N170 over more anterior sites (P8) for inverted than upright headless bodies. We interpreted the inversion effect for intact stimuli as reflecting the disruption of configural processing of both stimulus types, resulting in an increased difficulty of encoding. Alternatively, it may reflect a release of features (e.g., eye or head) neurons from inhibition in the context of holistic stimulus (e.g., upright intact face and upright intact body) presentation. For manipulated stimuli an inverted inversion effect occurred for eyeless faces may be explained by reduced activity of face selective neurons for inverted vs. upright eyeless faces.

LNC was larger under low load than high load, comparable to study I. It was suggested that LNC belongs to the family of posterior visual processing negativities reported both from recordings from the scalp (Czigler & Csibra, 1990; Schweinberger et al., 1994) and intracranially from the ventral temporal cortical surface (Engell & McCarthy, 2010). The present modulation may indicate residual capacity available for and involuntarily (Lavie, 2005) allocated to, task irrelevant distractors processing.
2.3 Face and object encoding under perceptual load: ERP evidence (Neumann et al., 2011)

In the well-known cognitive model of face recognition by Bruce and Young (1986), functional components are thought to reflect different stages involved in face recognition. Critically, representations of individual faces are thought to take place at the level of face recognitions units (FRUs). Earlier studies have indicated an ERP marker, the N250r, reflecting the transient activation of these face recognition units (Schweinberger & Burton, 2003). The N250r is an occipito-temporal ERP modulation between 200 and 350 ms, elicited by immediate repetitions of a face identity. The N250r is larger for faces than objects (Schweinberger et al., 2004). However, foregoing studies have shown that N250r-like modulations can be elicited by famous names (Pfutze et al., 2002), familiar buildings (Engst et al., 2006), everyday objects (Henson et al., 2004) and names of famous people (Martin-Loeches et al., 2005).

Study III involved an immediate repetition priming paradigm adopted from an earlier study (Neumann and Schweinberger, 2008). Perceptual load was manipulated to prime presentations as described for study I. In the present study, distractor faces, body parts and houses were then followed by a) a repetition of the distractor stimulus, b) a new exemplar from the same category as the distractor, or c) a butterfly, to which participants responded.

The hypotheses for this study were as follows: i) if familiarity of the initial face presentation (prime) has driven the N250r modulation under high perceptual load in the previous study (Neumann & Schweinberger, 2008), no such effect should be seen for unfamiliar faces in the present study; and ii) if the N250r is specific to faces, then no such modulation should occur for other objects such as body parts (i.e. hands) and houses under conditions of high perceptual load during prime presentations.

Behavioral results showed that perceptual load was successfully manipulated, in that the RTs and error rates (ERs) were increased under high load than under low load. However, ERs were slightly larger for hand distractors under low perceptual load, compared to house and face distractors. ERPs to second (probe) presentations were analyzed. P100 was larger for faces than for the other categories (hands or houses) while no P100 differences were observed between hands and houses.

Larger N170 were observed for faces and hands compared to houses. N250r were identical under high and low load for faces while no comparable effect was observed for either hands or houses. N400 component was more negative for houses than faces or hands.
Most critically, these findings indicated that N250r is specific to faces and occurs independent of load and task-relevance, suggesting that initial encoding and reactivation of a structural facial representation (Herzmann & Sommer, 2007) does not require selective attention. Conversely, no such comparable effect for houses or hands suggests that no comparable representation was formed for either category, both under high and low perceptual load.

In conclusion, combining the results of the current study and the study of Neumann and Schweinberger (2008) provides strong evidence for the idea that N250r is face-specific, occurs for task irrelevant distractors faces and is unrelated to the familiarity of the face and perceptual load during initial presentation.
3 General Discussion

3. General Discussion

The role of selective attention on the processing of social stimuli such as faces, human bodies and body parts is controversially discussed. In the current thesis, processing of these stimuli under perceptual load is addressed. Study I has compared encoding of distractor unfamiliar faces and distractor houses in conditions of restricted availability of attentional capacity (i.e. high perceptual load) vs. spare resources (i.e. low perceptual load). Study II further investigated the link between faces and body perception on the one side and perceptual load on the other side. Specifically, study II was tested the combined effects of perceptual load and orientation on processing of human bodies and faces. In study III, activation beyond the level of structural encoding of faces, body parts and objects under perceptual load was tested. In a modified version of the paradigm used in studies I and II, repetition modulations in ERPs specifically the N250r were measured while attention to the first presentations was manipulated sensu Lavie’s perceptual load theory. Results of both study I and study II (Exp.1) have suggested that early structural encoding of face processing, which is thought to be indexed by the N170 (Bentin et al., 1996) is affected by manipulations of selective attention. These results are in line with previous studies (e.g., Holmes et al., 2003), showing that N170 amplitude is influenced by selective attention. An additional result of study II was shown the face-inversion effect (i.e. larger N170 for inverted vs. upright faces) that was larger under high load than under low load while no such observation was made in the case of human bodies. When manipulating face and human body images by removing eyes from face images and cropping heads from body images the pattern for the inversion effects were slightly changed, suggesting that certain feature neurons (head neurons in the case of human bodies and eye neurons in the case of faces) may make important contributions to the inversion effects reported in the literature. Detailed discussions of the ERP results of Exp. 1 are given in section 3.2 & 3.3. ERP results from Exp. 2 are further discussed in section 3.3. Study III, revealed that N250r occurred for repetitions of faces, but not for repetitions of body parts (hands) or objects (houses). Importantly, increasing perceptual load to the first presentations of these categories had no effect on the repetition effect in the N250r for faces. Small N400 modulations were elicited by all categories, irrespective of perceptual load. ERP Results will be further discussed in section 3.4.
3 General Discussion

3.1 Effect of perceptual load on behavioural performance

Prior studies laid out evidence to suggest that the relationship between face and body on the one hand and attention on the other hand may be special in the sense that the processing of these stimuli was prioritized over the processing of other types of visual stimuli (Langton et al., 2008; Ro et al., 2007). In the current experiments, behavioral performances were measured for responses given in the letter search task. Letter strings were superimposed on task-irrelevant distractors (face, body, body parts and houses) and were presented briefly (200 ms). Subjects were instructed to identify an “X” or “N” among six identical (low load) or different letters (high load).

Across all experiments, RTs and error rates (ERs) were increased under high load compared to low load. These results are in line with previous studies that used a very similar task (Jenkins et al., 2002; 2005). It is worth noting that Jenkins and colleagues (2002; 2005), presented only faces (familiar or unfamiliar) as task-irrelevant distractors. Here, we used different highly heterogeneous categories such as houses, hands, human bodies and faces. However, perceptual load theory would predict that behavioral performance to the targets letters should be constant and independent of the distractor category under both conditions of load (high vs. low). Considering that both faces and human bodies have been argued to capture attention (Langton et al., 2008; Ro et al., 2007), one could presume that increased reaction times and error rates may occur if one of these categories appears as a distractor. In contrast, the current results largely support this prediction of the PLT: In all three studies, RTs to letter strings were unaffected by the respective distractors category both under high and low load. In both study I & II the same was true for error rates. As an exception, error rates (ERs) in study III were slightly increased when letter strings were superimposed on hands compared to faces and houses. This increase of ERs when hands were presented as distractors could be due to systematic differences in contrast and luminance of hands compared to both faces and houses, possibly making it more difficult to recognize letters superimposed on hands.

In sum, the present results have confirmed some of the prediction of the PLT, in that task-irrelevant distractors - no matter which category they belong to - did not affect behavioral responses to target letter strings. In conclusion, increasing perceptual load had almost identical effects on participant’s behavioral performances for all categories.
3.2 Visual properties of social stimuli as indexed by P100

Prior studies have shown that P100 is sensitive to basic visual stimulus properties such as contrast and luminance (Schendan et al., 1998) and thus has been assumed to reflect early visual processing (Clark & Hillyard, 1996; Eimer, 1993; Mangun, 1995). In the present studies I and II, larger P100 amplitudes were found for both faces and human bodies in comparison to houses. These results are consistent with previous studies which also have reported larger P100 for faces than other stimuli such as buildings (Herrmann et al., 2005). The P100 for human bodies was larger in amplitude in study II - Exp. 1, than P100 to houses in study I, which would in principle be in contrast to the results of a previous study of Thierry et al. (2006) showing smaller P100 amplitudes for human bodies than faces. One discrepancy between the P100 results in the current thesis and Thierry et al. (2006) is that Thierry and co-workers used cropped body stimuli, in which upper or lower parts were entirely removed. Here, we used either intact or headless bodies in study II. However, P100 results here were from two different studies with different participants and designs, which could alternatively explain the recent P100 effects. Larger P100 to faces than other objects have been discussed to reflect cognitive processing specific to faces presumably on a pictorial encoding stage (Herrmann et al., 2005; for an overview, cf. Schweinberger, 2011)

Additionally, P100 inversion effect was found in study II for both faces and human bodies, with larger positivity for inverted than upright presentations. These findings are replicated earlier reports (Itier & Taylor, 2002; 2004a; 2004b; Linkenkaer-Hansen et al., 1998; Minnebusch et al., 2010). Such an early inversion effect has been interpreted in terms of reflecting low-level differences between upright and inverted presentations such as the location of certain high/low-contrast regions of the stimuli. For faces, eye and eye brows regions could be most prominent in terms of high local contrast (Jacques & Rossion, 2007a) while the same may apply for heads in human bodies (Minnebusch et al., 2010).

When the images of faces and human bodies were manipulated (Study II, Exp.2) a small effect of perceptual load was shown on P100, in terms of larger P100 under low load than high load for eyeless faces and headless bodies. These findings are in line with studies that used simple visual stimuli (Fu et al., 2008; 2009; Handy et al., 2001; Handy & Mangun, 2000), suggesting that perceptual load affects processing during an initial sensory-level. However, for both intact human bodies and faces, this effect of perceptual load on the P100 amplitudes was absent, suggesting that no influences of perceptual load on the early component (P100) for both intact stimuli
3.3 Structural encoding of social stimuli as indexed by N170

The N170 event-related potential component is considered as a marker for the structural encoding stage during face perception (e.g. Eimer, 2000c; Eimer & McCarthy, 1999; Schweinberger & Burton, 2003). Here it was tested whether N170 to distractor (i.e. unfamiliar faces, human bodies and houses) was influenced by perceptual load. In study I, the N170 mean amplitude to both faces and houses was affected by perceptual load, in terms of a reduction of the face-sensitive N170 under high load while an opposite pattern was found for houses with increasing the N170 mean amplitudes under high load than under low load. Similarly, study II revealed a similar pattern on the N170 mean amplitude for upright faces while no such effect of perceptual load was seen for the N170 of upright human bodies; inverted faces and inverted bodies or manipulated stimuli (eyeless faces or headless bodies) in either orientation (upright vs. inverted).

Other studies (e.g. Carmel & Bentin, 2002; Cauquil et al., 2000) have not found any influence of selective attention on the N170 and are at variance with the present results. These present results could be related to the configural processing of faces and human bodies (Minnebusch & Daum, 2009) on one side, and part-based processing for object on the other side (Biederman, 1987). It has noted that configural processing of human bodies is a matter of the current debate (Minnebusch & Daum, 2009), whereas there is considerably evidence for configural processing of faces, comes from inversion effect (Yin, 1969).

I suggest that perceptual load has an influence on configural face processing, in particular during holistic stage in configuration continuum. This is the reason why no effect of perceptual load was found for inverted faces or eyeless faces, because both eyeless faces and inverted faces are not processed in a holistic manner (see Fig. 9, Latinus & Taylor, 2006). I suggest that if human bodies were processed in a holistic fashion, similar to faces, then the effect of perceptual load should have emerged in body N170 component similar to human faces. In contrast, the present results have shown that no such effect of perceptual load was found either for human bodies (both intact and headless) irrespective of orientation. This suggests that human bodies are not processed holistically (cf. also Bauser et al., 2011). Alternatively, human bodies may be processed by a specialized mechanism that is separate from processing of faces and objects (Minnebusch et al., 2009).

For houses (and maybe other objects), a part-based processing mechanism is involved (Diamond & Carey, 1986), which may be inaccessible under high load. However, these
results from (study I) have indicated that N170 to houses was increased under high load compared to low load conditions.

Fig10. The model of face processing for either upright different face stimuli vs. inverted (from Latinus & Taylor, 2006).

One could speculate that a certain degree of holistic processing may initially be evoked by houses under high load only, when these stimuli are presented briefly (200 ms), while under low load processing relies solely on the part-based mechanism, which may cause N170 increase under high load. The differential perceptual load effect under high load for faces and object suggest that for faces, holistic processing is decreased under high load, causing N170 reduction while for houses, holistic processing is actually initiated under high load and part-based processing is reduced. The increase of holistic processing leads to the increase of the N170 amplitude. Future research may further test holistic processing of faces and human bodies using the composite illusion under varying load conditions. Under high load, an increased N170 should occur for aligned, but not for misaligned houses or faces. This effect should be absent under low load, with no differences in N170 between aligned and misaligned stimuli.
Apart from the influence of attention, orientation effects on the N170 mean amplitudes were examined for faces and human bodies. Inversion effects were separately investigated for intact human bodies and faces (Exp. 1) and eyeless faces and headless bodies (Exp. 2) in study II. The N170 inversion effect should occur under low load, but were not expected for either category under high load. In contrast to this idea both intact faces and human bodies evoked larger N170 mean amplitude for inverted than upright stimuli (Exp. 1) irrespective of perceptual load. The N170 inversion effect is often thought to reflect disruption of configuration processing of either faces (Itier et al., 2006; Itier & Taylor, 2002; Rhodes et al., 1993; Rossion et al., 1999; 2000b; Yin, 1969) or human bodies (Minnebusch et al., 2009; Reed et al., 2003; 2006; Stekelenburg & de Gelder, 2004). For faces, this effect has been suggested to reflect encoding difficulties (Rossion et al., 1999; 2000b) or a release of feature (e.g. eye) neurons from inhibition by context holistic representation of faces (Itier et al., 2007; Itier & Batty, 2009). Analogously, one could speculate that inversion effects for human bodies could reflect release of head neurons by inhibition in the context of body neurons (Perrett et al., 1991; Wachsmuth et al., 1994).

It is worth noting that N170 inversion effect for intact faces and human bodies were found rather wide-spread over the occipito-temporal sites, whereas headless bodies caused a qualitatively similar, but slightly reduced, inversion effect only over more anterior sites (P8). Surprisingly, eyeless faces elicited slightly an “inverted” inversion effect over more posterior sites (P10/PO10), with more negative N170 amplitudes to upright than inverted eyeless faces.

This inverted inversion effect on eyeless faces could be interpreted due to the reduction of neuronal activity of face-selective neurons in case of eyeless faces were presented upside down. As mentioned above, inversion of intact faces additionally activates eye-selective neurons, causing the N170 increase and probably “masking” the reduction of activity of face-selective neurons. In contrast, removing eyes prevents the activation of eye-selective neurons for the inverted presentations and only the reduction of the face-selective neurons causes the N70 reduction in this condition, resulting in the inverted inversion effect. It has to be noted that the present N170 reduction for inverted eyeless faces is in contrast to the results of Itier et al. (2007). However, in that study, the authors used cropped faces (i.e. removed upper forehead and lower chin regions), perhaps in order to equate shapes of faces and houses. This cropping may have reduced activation of face neurons in the upright versions already thus, affecting the size of the face inversion effect.
3 General Discussion

For human bodies, inversion effects were found for intact and headless versions under both load conditions over anterior sites (P8). This seems to suggest that removing heads is not a sufficiently strong manipulation for eliminating the N170 inversion effect. However, the results for the headless bodies are in contrast to results from an earlier study (Minnebusch et al., 2009), which reported an inverted inversion effect on the N170 for headless bodies. This discrepancy could be due to the different paradigm of study in which stimuli were presented twice and participants had to perform a same/different judgment on the second presentations. Additionally, brain activity was also measured to second presentations. Therefore, this effect as reported by Minnebusch et al. (2009) may be caused by the, repetition of inverted headless bodies, which may have increased sensitivity to these images and decreased the N170 for inverted in comparison to upright stimuli.

ERP inversion effects on the N170 mean amplitudes, as described above for human bodies and faces, have similarly been reported for biological motion of point-light walker stimuli, suggesting to reflect impaired configural processing of biological motion when presented in the upside-down orientation (Jokisch et al., 2005). Alternatively, the inversion effect for inverted biological motion is mainly carried by the local motion of the feet and may thus, rather reflect impaired processing of the local orientation of this particular part of the body (Troje & Westhoff, 2006). In principle, some motion cue within a body could thus explain the inversion effects that were found in the present experiments for intact and headless bodies. However, all body images used here had been taken in a standard posture, without obvious motion cues. Still, reliable inversion effects were found, arguing for a contribution of the configural processing for inverted orientations in body processing.

3.4 Activation of FRUs and PINs under load as indexed by N250r and N400

In study III, neural repetition effects for irrelevant distractors (unfamiliar faces, hands and houses) were measured in an immediate repetition priming paradigm, as has been used in a previous study (Neumann & Schweinberger, 2008). Attention to distractors was manipulated according to perceptual load theory on the initial presentations of those stimuli by superimposing letter strings on distractors just as in studies I and II. These initial presentations were followed by probes, which were either repetitions of the same stimuli, presentations of different stimuli from the same category or are presentations of butterflies. Subjects made an additional response on butterfly presentations in order to assure attention to probe presentations. Results have shown that repeating faces were elicited an N250r
irrespective of load during initial presentations while no such modulation occurred for repetitions of hands or houses even under low load. Accordingly, these results are extended previous findings that showed a similar pattern, but used famous faces only (Neumann & Schweinberger, 2008).

The above mentioned study has suggested that familiar distractor faces transiently activated stored facial representations (FRUs) and accordingly, one could assume that this effect is specific to repetitions of familiar faces. However, repetitions of unfamiliar faces revealed very similar repetition effects under high load, suggesting that initial encoding of a new FRU for unfamiliar faces or activation of newly acquired structural representations (Herzmann & Sommer, 2007), may have taken place under both high and low perceptual load.

Although human body parts and faces have both been described to engage attention and to be classified faster than other objects (Ro et al., 2007) and both of them cause greater activations in specialized brain regions when compared to objects (Morris et al., 2008; Myers & Sowden, 2008; Orlov et al., 2010), no such modulation (N250r) has been elicited by irrelevant hands or houses. A recent behavioral study (Lavie et al., 2009) showed that view-independent object representations are being formed under low perceptual load, by demonstrating repetition priming from irrelevant objects under low load. This finding appears to contradict the absence of repetition related neural modulations such as the N250r in the present experiment. However, it is difficult to relate those results with the present ones, since no behavioral measure of priming was collected in the study III. However, the entire absence of an N250r in this study is in line with previous studies (c.f. Schweinberger et al., 2004). Here, the N250r is found highly specific to faces and is not elicited by other categories such as body parts or houses.

The N400 modulations, i.e. slightly less negative going ERPs to repeated than non-repeated presentations was found for all distractors and under both load conditions over the central medial region. This finding suggests that distractors were able to activate representation in both PINs for faces and comparable semantic representations (SRs) for objects to a small extent. It is therefore, possible that the present N400 modulation reflects enhanced access to PINs for faces and SRs for other objects and body parts which are stored at a post perceptual stage. Prior studies interpreted this N400 modulation in face processing as reflecting facilitation of the access to semantic information, which even occurred when
the task did not require semantic categorization (Kiefer, 2005). In sum, the N400 result suggests minimal semantic processing of all distractors in the results of study III.

### 3.5 LNC for the social stimuli vs. objects

In both study I and II, a late negative component (LNC) was prominent over occipito-temporal regions under low load while it was considerably decreased under high load conditions for all stimuli (faces, bodies and houses). In study I, a larger LNC was found for faces than for houses under low load condition while no differences in LNC amplitudes were seen under high load conditions. LNCs for both distractor types were larger over the right as compared to the left hemisphere. In study II, LNC was larger for both intact faces and eyeless faces than human bodies or headless bodies under low load condition while again no differences were found under high load. The LNC results are in line with several recent studies reporting similar modulations over analogous electrode sites (Allison et al., 1994; 1999; Engell & McCarthy, 2010). The precise underlying mechanism of this effect is still unclear and requires further direct investigation. However, larger late negative deflections seems to be elicited in situations of increased recruitment of attentional resources such as it should occur for distractor objects under low perceptual load in the present design. Accordingly, the effect of perceptual load on the LNC may indicate the “spill-over” of residual capacity to the irrelevant distractor, as suggested by the perceptual load theory (Lavie, 1995; 2005).
4. Outlook

The present (study I) has shown that perceptual load has an influence on both faces and objects processing, while no effect of perceptual load was found for human bodies in study II. Further, perceptual load had no influence on ERPs to face repetitions in study III while no repetition effect was observed for both human body parts (i.e. hands) and objects (i.e. houses). In the current studies, few categories were employed, in order to compare social stimuli such as faces, human bodies and body parts with artificial objects such as houses. Still some unresolved questions related to the role of attention in human body and object perception and more general research questions regarding body processing will be briefly addressed in the following sections.

4.1 A functional cognitive model of human body processing

In the most widely spread model of face recognition (Bruce & Young, 1986), different functional components have been suggested to be involved in the processing of faces. Schweinberger and Burton (2003) have linked ERP components to these functional processes. In contrast to the extensive number of related studies of faces, little is known about functional cognitive components involved in recognition of human bodies so far. One common effect found in the field of body processing in analogy to a similar effect reported for faces comes from the phenomenon expressed in the inversion effect (IE). However, IEs have been reported in both behavioral and electrophysiological research for human bodies (Reed et al., 2003; Stekelenburg & de Gelder, 2004), indicating that human bodies processing may involve a structural encoding stage, similar to what has been suggested for faces (Bentin et al., 1996; Bruce & Young, 1986). IEs have been found in the present study II.

Evidence for an even earlier cognitive component comes from the present P100 results. In the study I, larger P100 was found for faces than for objects while in study II both faces and human bodies elicited comparable P100 mean amplitudes. Schweinberger (2011) suggested that larger P100 to faces may reflect a cognitive processing stage prior to structural encoding, termed pictorial encoding. Thus, I assume that comparable P100 amplitudes for human bodies and faces may indicate a pictorial encoding stage, which may also be involved in the processing of human bodies. In figure 11, I describe a functional cognitive model of human body processing in analogy to the traditional cognitive model of face processing (Bruce & Young, 1986). As described above, pictorial and structural
I suggest that following structural encoding, human body recognition units (BRUs) may be activated independently of view-point for presentations of human bodies, probably stronger for familiar than for unfamiliar bodies. Activation from the BRU may be conveyed to a subsequent stage that is involved in person identification and termed person identity node (PIN). In study III, the N400-modulations, typically associated with activation on PIN level (Schweinberger & Burton, 2003) were observed for both human body parts and faces. This may be considered as evidence for activations of person identity nodes by human bodies or body parts, to the same extent as activation by faces.
4.2 Effects of familiarity on the N170 to human bodies

The vast amount of visual information in daily life can contain both familiar and novel aspects. Despite the variety in terms of color, texture and form, we are usually able to differentiate between these stimuli and recognize many of them.

However, the recognition of human bodies of familiar and well-known people will be easier if combined with corresponding face information. Evidence for this comes from a study of Bindemann and colleagues (2010), showing that the combined presence of a body and a face will facilitate detection of a person, when compared to presenting a body or a face in isolation. Body information helps to create a visual representation of familiar people that may help for recognizing them without necessarily having to being able to discriminate their faces or facial features. To my knowledge, no study so far investigated the effect of body familiarity on the early neural processing as indexed by the N170. In the literature of human face perception, many studies have investigated the influence of face familiarity on the face-sensitive N170. Results have shown that N170 to human faces is unaffected by familiarity (Schweinberger et al., 1995). Therefore, it would be relevant in future research to investigate the effect of familiarity on the early processing of human bodies as indexed by the N170.

4.3 Should we strictly analogize face and body perception?

In daily life we usually do not experience the face without a body and vice versa. Certain information from both faces and human bodies such as facial expression and body gestures or body actions facilitate the social communication between people (Downing et al., 2004; Peelen & Downing, 2007). Body parts such as hands convey important information about social states of the person. A shaky hand, for instance, could reveal that this person experiences stress or trouble. Interestingly, in the study of Bindemann and colleagues, (2010), RTs for detecting a human body combined with a face was shorter than detection speed of both isolated faces or bodies. This result suggests the importance of the combined presence of faces and human bodies. I think that both faces and bodies play an important role when presented in combination in social perception.
4.4 The influence of perceptual load on the processing body parts and objects

In the current thesis I reported influences of perceptual load on processing of unfamiliar faces and houses while no effect of perceptual load was found on processing of human bodies (study II). These findings raise the questions of the influence of perceptual load on body parts such as hands or torso. I would predict perceptual load has no influence on human body parts such as hands, in analogy to the findings reported for whole human bodies and headless bodies. Another question may be related to the influence of perceptual load on objects apart from houses. In particular, we showed in the current thesis that perceptual load influences processing of houses (study I). However, it remains open if similar effects can be observed for other living and non-living object categories such as animals, fruit, furniture, household items or others.
5 Summary

Attention has become a particularly active and vigorous area of research in cognitive psychology and cognitive neuroscience. Research has shown that human bodies and faces may be prioritized for attentional selection, when compared to other objects. More generally, the visual system may assign attentional priority to those stimuli that are represented in strongly selective cortical regions, as suggested for faces and human bodies. In the current thesis I investigated the role of attention in perceiving social stimuli in comparison to objects. In three studies, attention was manipulated sensu Lavie’s perceptual load theory (PLT) to task-irrelevant distractor unfamiliar faces, human bodies, body parts and objects, by superimposing letter strings over distractors and increasing attentional demands of a letter identification task. Specifically, study I was compared effect of load on distractor unfamiliar faces and houses. Study II additionally investigated effects of stimulus orientation and compared unfamiliar faces and unfamiliar human bodies, either presented intact or perceptually manipulated. To test potential contributions of specific neuronal populations to inversion effects, as suggested by others, eye regions were removed from face’s images and head regions from body’s images. Study III indirectly tested encoding of distractor faces, body parts (hands) and objects (houses) by implementing an immediate repetition priming paradigm. In all three studies, event-related potentials were recorded in addition to behavioral performance measures.

In both studies I and II, effects of perceptual load were found for upright faces, with decreased the N170 amplitudes under high load. In contrast, study I revealed an N170 increase in this condition for houses. However, no effect of load was observed for human bodies in study II. Similarly, no effect on the N170 was found for manipulated stimuli. However, inversion effects with increased negativities for inverted than upright orientations occurred for all categories except eyeless faces irrespective of load. Eyeless faces showed the opposite pattern, with decreased the N170 for inverted than upright orientations. Finally, study III demonstrated that N250r, a repetition-sensitive component, is highly specific to faces, but occurs irrespective of perceptual load to initial face presentation. No comparable effect was found for either hands or houses.

In sum, these findings suggest that perceptual load may affect both holistic and part-based aspects of structural encoding of faces and objects, respectively. In contrast, no effect of load can be seen for human bodies, suggesting that human bodies may neither be processed in a holistical, nor in a purely part-based manner. Instead, I think that body
processing occurs within a specialized mechanism that is dissociable both from mechanisms responsible for processing of faces and objects.

The results of the study III indicate that irrelevant and unfamiliar distractor faces may activate facial representations to a similar extent under low and high perceptual load. Further, this study corroborates earlier findings that indicated that N250r is an ERP component that occurs selectively for immediate repetitions of faces.

In conclusion, selective attention plays an important role during encoding of faces and objects while it seems to have less an effect on the processing of human bodies.
6 Zusammenfassung

6. Zusammenfassung

Ein wichtiges und besonders aktives Feld innerhalb der kognitiven Psychologie und der kognitiven Neurowissenschaften beschäftigt sich mit Aufmerksamkeit. Studien konnten zeigen, dass menschliche Körper und Gesichter bevorzugt beachtet werden, wenn sie in Konkurrenz zu Objekten auftreten. Es ist denkbar, dass das visuelle System die Priorität bei selektiver Aufmerksamkeit auf solche Stimuli legt, die in spezialisierten kortikalen Regionen repräsentiert werden, wie es für Gesichter und menschliche Körper diskutiert wird. In dieser These wird untersucht, welche Rolle Aufmerksamkeit bei der Wahrnehmung sozialer Reize im Vergleich zu Objekten spielt.


Studie III verdeutlichte, dass die wiederholungssensitive EKP-Komponente N250r spezifisch für Gesichter, allerdings unbeeinflusst von Aufmerksamkeits-manipulationen, auftritt. Kein vergleichbarer Wiederholungseffekt wurde für Hände oder Häuser nachgewiesen.

Insgesamt deuten die hier dargestellten Befunde darauf hin, dass Perceptual Load holistische bzw. merkmalsbasierte Anteile der strukturellen Enkodierung von Gesichtern und Objekten beeinflusst. Im Unterschied hierzu wurde kein Einfluss von Perceptual Load auf die Verarbeitung menschlicher Körper gefunden, was nahelegt, dass diese weder holistisch, noch merkmalsbasiert verarbeitet werden. Stattdessen könnte die Verarbeitung von menschlichen Körpern durch einen spezialisierten Mechanismus erfolgen, der abgrenzbar von den korrespondierenden Verarbeitungsmechanismen für Gesichter und Objekte ist.

Ergebnisse aus Studie III legen nahe, dass irrelevante unbekannte Distraktorgesichter mentale Gesichterrepräsentationen in gleichem Ausmaß unter hoher und niedriger Aufmerksamkeitsauslastung aktivieren. Zusätzlich untermauern die Befunde, dass die N250r eine spezifisch für unmittelbare Wiederholungen von Gesichtern auftretende EKP-Komponente darstellt.

Schlussfolgernd lässt sich sagen, dass selektive Aufmerksamkeit eine wichtige Rolle beim Enkodieren von Gesichtern und Objekten spielt, aber möglicherweise geringeren Einfluss auf die Verarbeitung menschlicher Körper hat.
7 References


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7 References


7 References


Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S. et al. (2000b). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not


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<tr>
<td>EEG</td>
<td>Electroencephalogram</td>
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<td>PLT</td>
<td>Perceptual Load Theory</td>
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<td>FRUs</td>
<td>Face Recognition Units</td>
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<td>PINs</td>
<td>Person Identity Nodes</td>
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<td>FFA</td>
<td>Fusiform Face Area</td>
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<td>OFA</td>
<td>Occipital Face Area</td>
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<td>EBA</td>
<td>Extrastraite Body Area</td>
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<tr>
<td>FBA</td>
<td>Fusiform Body Area</td>
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<td>RTs</td>
<td>Reaction Times</td>
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<td>Error Rates</td>
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<td>ms</td>
<td>milliseconds</td>
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<td>N</td>
<td>Negative Component</td>
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<td>Positive Component</td>
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<td>LNC</td>
<td>Late Negative Component</td>
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<td>OTL</td>
<td>Occipital Temporal Left</td>
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<td>OTR</td>
<td>Occipital Temporal Right</td>
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<tr>
<td>OM</td>
<td>Occipital Medial Region</td>
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<td>CM</td>
<td>Central Medial Region</td>
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<td>FG</td>
<td>Fusiform Gyrus</td>
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<td>STS</td>
<td>Superior Temporal Sulcus</td>
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<tr>
<td>rSTS</td>
<td>Right Superior Temporal Sulcus</td>
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<tr>
<td>LEC</td>
<td>Lateral Extrastriate Cortex</td>
</tr>
<tr>
<td>VOC</td>
<td>Ventral Occipital Cortex</td>
</tr>
<tr>
<td>ERPs</td>
<td>Event Related Potenials</td>
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<tr>
<td>OTC</td>
<td>Occipito-Temporal Cortex</td>
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<tr>
<td>MOG</td>
<td>Middle Occipital Gyrus</td>
</tr>
<tr>
<td>Abbreviation</td>
<td>Description</td>
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<tr>
<td>HDR</td>
<td>Hemodynamic Responses</td>
</tr>
<tr>
<td>SRs</td>
<td>Semantic Representations</td>
</tr>
<tr>
<td>SSD</td>
<td>Stored Structural Descriptions</td>
</tr>
<tr>
<td>LOTC</td>
<td>Lateral Occipito-Temporal Cortex</td>
</tr>
<tr>
<td>VOTC</td>
<td>Ventral Occipito-Temporal Cortex</td>
</tr>
<tr>
<td>SIU</td>
<td>Semantic Information Unit</td>
</tr>
<tr>
<td>P100</td>
<td>Positive component occurred in time intervals 060-120 ms and peaked around 100 ms at occipital medial areas</td>
</tr>
<tr>
<td>N170</td>
<td>Negative component appears in time intervals between 100 to 200 ms and peak around 170 ms after stimulus onset.</td>
</tr>
<tr>
<td>N250r</td>
<td>Early repetition effect, which occurred in the time intervals between 200 and 350 ms</td>
</tr>
<tr>
<td>N400</td>
<td>Late repetition effect which occurred in the time intervals between 350 and 550 ms, due to face and object repetition</td>
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Ich erkläre, dass mir die geltende Promotionsordnung der Fakultät für Sozial- und Verhaltenswissenschaften der Friedrich-Schiller-Universität Jena bekannt ist.


Ich erkläre weiterhin, dass ich diese Dissertation noch nicht als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung, oder eine gleiche, eine in wesentlichen Teilen ähnliche oder eine andere Abhandlung bei einer anderen Hochschule bzw. anderen Fakultät als Dissertation eingereicht habe. Ich versichere, nach bestem Wissen die reine Wahrheit gesagt und nichts verschwiegen zu haben.

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