The Temporal Context of Face Perception:

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Correlates

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Preface

The human face is a stimulus of outstanding importance in our environment and carries a wealth of socially relevant information, among them a person's gender, age, emotional expression, gaze direction, or identity. Although faces as a stimulus class are very uniform, sharing a common configuration of given features, our ability to recognize familiar people by their face is impressively good, even across changes in perspective or illumination. This is even more fascinating when we consider that this ability is far worse for unfamiliar faces, and that the physical differences between certain encounters with the face of a given identity can be even higher than those between faces of different persons. Some factors determining differences between faces, such as gender, or identity, are relatively constant over time, or, in the case of age, only change on a relatively longer time scale, but others, such as emotional expressions or gaze direction, can vary from moment to moment.

Especially on a shorter time scale, the perception of a given face was also found to be influenced by preceding perceptual experiences, i.e., the temporal context of that face. Adaptation-related aftereffects (AEs) and repetition priming (PR) are two of such phenomena which seem to be contradictory from a behavioural perspective. AEs were typically observed as contrastive biases in the perception of ambiguous faces following unambiguous "adaptors". After prolonged exposure, or, adaptation, to a female face for example, an androgynous face would more likely be perceived as male, whereas following adaptation to a male face, the same androgynous face would more likely be perceived as female. Quite contrary to this, PR was defined by behavioural facilitation, when a response-relevant face was preceded by a face of the same person as compared to that of a different person. For example, participants would be faster to classify the face of Brad Pitt as "familiar" when it is preceded by another image of Brad Pitt, as compared to an image of a different celebrity, e.g., Harrison Ford. However, AEs and PR were associated with similar neural effects observed with brain-imaging or electrophysiological techniques in recent studies.

Therefore, a question that was sometimes addressed but not yet resolved concerns the relationship between AE and PR, especially regarding the neural processes associated with both of these phenomena. To address this point, a novel paradigm was set up to induce both AEs and PR within the same experiment, using the same stimuli, timing parameters, and task. A first study with this paradigm and simultaneous EEG recordings allowed us to look at the behavioural, as well as the neural correlates of these effects, and enabled us to draw conclusions about their relatedness. In a second study, we continued on the results of the first study with a further investigation of the role of adaptor stimuli for AEs. A third study used

imaging techniques with a variant of our novel paradigm to learn more about the brain regions possibly associated with behavioural AE and PR.

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1. Effects of Face Repetition - Behavioural and Neural Correlates

1.1 Adaptation and adaptation-related aftereffects

The perception of a given stimulus can be influenced by adaptation-related aftereffects (AEs), which are typically observed as contrastive biases after prolonged exposure to a preceding stimulus. This phenomenon, that was already noted by Aristotle (Parva Naturalia), was often described for lower-level stimulus qualities such as colour, texture (Durgin & Proffitt, 1996), line orientation (Clifford, Wenderoth, & Spehar, 2000), or motion (Anstis, Verstraten, & Mather, 1998; Clifford, 2002). For example, viewing an upward moving object for some time causes a subsequent stationary object to appear moving downwards. The existence of AEs is particularly interesting with respect to the neural systems underlying perception, as adaptation, also termed the "psychologist's microelectrode" (Frisby, 1979, p. 89), allows us to draw conclusions about brain processes as well.

More recently, AEs have been found for higher-level stimuli, such as faces. In a pioneering study, Webster and MacLin (1999) described the face distortion AE, where following adaptation to geometrically distorted faces, undistorted faces were perceived as distorted in the direction opposite to the adaptor. This result was attributed to a re-calibration of our perceptive system, especially because adaptation to undistorted faces did not induce any perceptual biases. Over the years, research on such figural AEs continued to play an important role (e.g., Carbon et al., 2007; Jeffery, Rhodes, & Busey, 2007; Zimmer & Kovács, 2011a). Moreover, other studies showed AEs in the perception of various socially relevant information in faces, such as gender (Kloth, Schweinberger, & Kovács, 2010; Kovács et al., 2006; Kovács, Zimmer, Harza, & Vidnyanszky, 2007; Webster, Kaping, Mizokami, & Duhamel, 2004), ethnicity, expressions (Webster et al., 2004), age (Schweinberger et al., 2010), gaze (Jenkins, Beaver, & Calder, 2006; Kloth & Schweinberger, 2008), and identity (Hills, Elward, & Lewis, 2010; Hole, 2011; Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes, Jeffery, Clifford, & Leopold, 2007).

Progress in this field was highly related to the availability of sophisticated image manipulation techniques, first and foremost image caricaturing and morphing (Benson & Perrett, 1991; Tiddeman, Burt, & Perrett, 2001). After defining certain anchor points in two faces, which capture the characteristic features of each face, the shape and texture of two faces can be averaged using a tessellation method. This technique can be used to create photo-realistic averages (morphs) of different weights between two or more faces. Therefore, a morphing continuum with certain levels between two images, e.g., between two individual

faces, or between averages of female and male faces, can be generated. Similarly, caricatures of individual faces can be prepared by changing the shape (and/or texture) of that individual face away from that of an average face.

This thesis primarily focuses on face identity and face gender AEs. Face identity AEs were first shown by Leopold et al. (2001), using unfamiliar, but experimentally familiarized faces. Leopold et al. created so-called "anti-faces" and showed that adaptation to anti-faces shifted the perception of faces lying on a trajectory between the anti-face, the average face, and the original face towards that original face. Such face identity AEs were replicated ever since in several studies (Leopold, Rhodes, Muller, & Jeffery, 2005; Rhodes, Evangelista, & Jeffery, 2009; Rhodes & Jeffery, 2006). While all of these findings involved faces the participants were unfamiliar with before the actual experiment, some recent studies investigated identity AEs in familiar face perception (Hills et al., 2010; Hole, 2011). Hills et al. (2010) showed that following adaptation to the face of a famous identity 1, a face morphed between the famous identities 1 and 2 was more often perceived as identity 2, and vice versa following adaptation to identity 2. They also found that AEs were smaller when different images of identity 1 or 2, which were not used to create the morphs, were chosen as adaptors, and that AEs were also induced by adaptation to written names, voices, faces of associated identities, imagined faces, and artist-drawn caricatures. Note that, although some authors suggest striking differences in the processing of unfamiliar and familiar faces (Megreya & Burton, 2006), a recent study by Laurence and Hole (2011) did not find a difference in identity AEs between both levels of familiarity, while own face adaptation led to reduced AEs. The effects of face gender adaptation (Kloth et al., 2010; Kovács et al., 2006; Webster et al., 2004) are very similar in principle. For example, Webster et al. (2004) observed a shift of the gender boundary towards the adapted gender, i.e., androgynous test faces were more often perceived as female following adaptation to male faces, and vice versa.

Various factors determine the presence and size of AEs in face perception. Webster and MacLin (1999) were the first to show that AEs depend on the stimulation used. Although there was a transfer of face distortion AEs over different identities, some manipulations, such as different orientations of adaptor and test stimulus, reduced the effects in their study. Other studies showed that the use of different adaptor and test images also reduced AEs (Hills et al., 2010). The influence of timing parameters on AEs was also studied intensively. Recent studies (Leopold et al., 2005; Rhodes et al., 2007) showed that the longer the adaptor and the shorter the test stimulus durations were, the stronger AEs were. Another line of research showed that AEs can be relatively insensitive to certain variations of the adaptors, such as in

contrast, colour, or size (Yamashita, Hardy, De Valois, & Webster, 2005), or in viewpoint, inversion, or vertical stretching (Hole, 2011).

Although the overall picture of behavioural AEs is very clear, the neural correlates of these effects are more complicated. First of all, studies on neural correlates of adaptation can be differentiated into studies on general adaptation effects and effects specific to the adapted dimension (the term "specific" will be used synonymously in the following), and secondly, such effects have been investigated with different methods in different paradigms. One strand of research used electroencephalography (EEG) in combination with the event-related potential (ERP) technique to measure the brain-electrical correlates of adaptation effects. The categorical adaptation effects reported by such studies are a prominent example for more general adaptation effects, typically observed as an reduced N170 component for test faces following face as compared to non-face adaptors (Amihai, Deouell, & Bentin, 2011; Kloth et al., 2010; Kovács et al., 2006). In the study of Kovács et al. (2006) for example, N170 reductions were observed for face and hand test stimuli following within-category adaptors as compared to cross-category or Fourier phase randomized (noise) adaptors. For both hands and faces, the authors also reported behavioural AEs on the gender classification of androgynous test stimuli following within-category female adaptors as compared to cross-category or noise adaptors. Although the ERP effect seems in line with the behavioural results, it is better considered as a general categorical adaptation effect in the comparison of a target category with noise stimuli, for which there is no meaningful perceptual category present. Furthermore, categorical adaptation effects were reported to be non-specific to facial identity, at least if faces are compared with another meaningful category, such as Easter eggs (Amihai et al., 2011). As categorical adaptation effects are most prominent for N170, this component was also proposed to be the earliest component reflecting the processing of stimulus category (Ganis, Smith, & Schendan, 2012). This is also broadly in line with a long tradition of research showing a sensitivity of N170 for face stimuli versus stimuli from other categories (for reviews, see Eimer, 2011; Rossion & Jacques, 2008). Note that, however, categorical adaptation effects also seem to depend on the paradigm used, since a recent study failed to replicate comparable N170 effects in a rapid-adaptation study (Nemrodov & Itier, 2012).

Very recent studies also reported ERP adaptation effects specific to the adapted dimension, which can be related to specific behavioural AEs more intuitively. A study by Kloth et al. (2010) reported gender-specific adaptation effects in behaviour and ERPs. Weak gender-specific adaptation was found for N170, which was slightly reduced for androgynous test faces following male as compared to androgynous face adaptors, but a later centro-

parietal P3-like component showed prominent gender-specific modulations in terms of a more positive P3 following male adaptor faces. As this P3 effect was observed only for the most female of the androgynous test faces, Kloth et al. suggested that it might reflect perceptual novelty defined by the difference between adaptation and test. Using a face distortion AE paradigm, Zimmer and Kovács (2011a) observed stronger distortion-specific adaptation effects for the N170, in that N170 amplitudes for ambiguous test faces were equally reduced following both expanded and contracted adaptor faces when compared to veridical face adaptors. Interestingly, categorical adaptation effects were also found for the N170 (but also P1 and P2, see their Fig. 3), showing reduced amplitudes following all face adaptors as compared to Fourier phase randomised adaptor faces. Authors argued that the observed distortion-specific adaptation effect might be related to the detection of facial configurations and to re-calibration processes of the perceptual system after adaptation. In another study on face distortion AEs, Burkhardt et al. (2010) found a similar modulation of a later component, termed as P250 (which might be another name for a later P2, see their Figs. 3 and 8). In a first classification experiment, Burkhardt et al. observed a reduced P250 for distorted faces irrespective of the direction of the distortion. A subsequent adaptation study showed that P250 amplitudes were reduced for only slightly distorted test faces following adaptors that increased the perceived distortion of the respective test faces as compared to adaptors that reduced the perceived distortion. Burkhardt et al. also argued that adaptation to distorted faces might shift the norm towards the respective distortion, which seems to be reflected by the P250 component in this case. Altogether, there are only a few studies that observed adaptation effects specific to the adapted dimensions, and the results were quite variable regarding the ERP effects. Therefore one should be careful in linking ERP results to behavioural AEs, at least as long as no more objective measures of relatedness, such as correlations, were reported.

The ERP literature also contains an impressive amount of studies, which aimed to address adaptation processes without any measures of behavioural AEs. Some of the most prominent examples are rapid-adaptation studies (e.g., Eimer, Kiss, & Nicholas, 2010; Nemrodov & Itier, 2012) or studies using the adaptation approach as a tool to investigate other neural processes, such as the time course of the contribution of shape and texture information for face processing (Caharel, Jiang, Blanz, & Rossion, 2009), or the perceptual encoding of familiar versus unfamiliar faces (Caharel, Jacques, d'Arripe, Ramon, & Rossion, 2011). Although findings with such paradigms made substantial contributions to the understanding of face processing, they are not easily reconciled with studies of behavioural

AEs. Additionally, the adaptation term used in the current thesis focuses on the neural processes associated with the behavioural AE, whereas the described studies use that term in a more general way. Therefore, these and related studies will not be discussed in more detail in the context of this thesis.

Functional magnetic resonance imaging (fMRI) was also often used to investigate adaptation processes, because, although lacking temporal resolution, its high spatial resolution allows concluding about brain areas associated with certain perceptual processes. In relation to the concept of repetition suppression (RS) measured in single-cell recordings in monkeys (Desimone, 1996), a reduction of the blood oxygen level dependent (BOLD) signals in certain brain areas for repeated versus non-repeated stimulus presentations has been found with fMRI, and was termed as fMRI adaptation (fMRIa; Grill-Spector & Malach, 2001). Although fMRIa has proven a powerful tool in recent cognitive neuroscience, it is still not straightforward to link effects in fMRI to behavioural effects (see, e.g., Gotts, Chow, & Martin, 2012; Grill-Spector, Henson, & Martin, 2006). As a large part of studies using fMRIa probed more general characteristics of the processing system, and only some studies addressed effects possibly related to behavioural AEs (Cziraki, Greenlee, & Kovács, 2010; Kovács, Cziraki, Vidnyanszky, Schweinberger, & Greenlee, 2008), it is even more important to be aware that "adaptation" of the fMRI signal does not necessarily correlate with behavioural AEs.

For fMRI, the current thesis again focuses on adaptation effects, which are observed with typical behavioural AE paradigms. Using a gender AE paradigm, Kovács et al. (2008) found categorical adaptation in the fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997) and occipital face area (OFA; Gauthier et al., 2000). Kovács and colleagues observed response reductions for test faces following adaptation to faces as compared to Fourier phase randomized face images (noise). In another study, Cziraki et al. (2010) tested categorical adaptation behaviourally and with fMRI. In their study, participants categorized composite face/hand test stimuli as either faces or hands, and prior adaptation to faces or hands led to significant contrastive AEs. They also observed reduced BOLD signals for category-congruent adaptor-test pairs in the FFA and extrastriate body area (Downing, Jiang, Shuman, & Kanwisher, 2001) for faces and hands, and these effects were stronger in trials in which adaptation successfully biased perception away from the adaptor category as compared to trials where adaptation did not lead to a contrastive bias. Similarly, Furl, van Rijsbergen, Treves, and Dolan (2007) reported correlates of facial expression and identity AEs in the medial temporal lobe, but not in the FFA or OFA. Interestingly, the authors observed

increased activity following adaptation, especially when the test stimulus was perceived in contrast to the adaptor. Again, the neural correlates of AEs appear as not completely uniform when measured with fMRI, but separate analyses with respect to the given response proved a useful tool to investigate the link between neural and behavioural data more directly.

1.2 Priming

Priming (PR) is another phenomenon related to the temporal context of face processing. Here, the perception and processing of a given stimulus typically benefit when this stimulus is preceded by the same or a related as compared to a different, unrelated one. PR was often considered a memory phenomenon related to implicit memory processes and perceptual representations (for a review, see Tulving & Schacter, 1990), and traditionally investigated as the difference between repeated, i.e., primed, words versus non-repeated, unprimed words. Furthermore, PR was also found for non-linguistic visual stimuli such as objects or faces (e.g., Ellis, Young, Flude, & Hay, 1987). Although PR was suggested to be associated with perceptual as well as conceptual, e.g. semantic, processes, the focus of the current thesis is on the perceptual side, especially on face repetition PR (therefore simply referred to as PR in the following), because this seems more closely related to the common perceptual view on AEs for faces (e.g., Webster & MacLin, 1999).

In face perception, PR has been investigated in immediate and long-term repetition contexts. In a classical study of long-term effects of face repetition by Ellis et al. (1987), participants were presented with a set of famous face images or the respective written names in a first phase of their Experiment 1, and in a second phase, images that were already presented, different images of the same persons, or images of different famous persons were presented intermixed with unfamiliar faces. Ellis et al. showed that participants' familiar/unfamiliar decisions for the faces presented in the second phase of the experiment were faster if these faces had been encountered previously, whereas previous encounters with the name of the respective person yielded no such effect. In two additional experiments, Ellis et al. found that similar PR effects could also be obtained for personally familiar faces, and that PR was maximal when the same image was used in both experimental phases, while significant, but reduced, when a different image of the same famous person was used. A considerable amount of other studies also probed face processing with long-term PR (e.g., Ellis, Flude, Young, & Burton, 1996; Ellis, Young, & Flude, 1990; Schweinberger, Pickering, Burton, & Kaufmann, 2002).

Another line of research focused on face PR in immediate repetition contexts, where prime and test stimulus were presented in quick succession (e.g., Bindemann, Burton, Leuthold, & Schweinberger, 2008; Brooks, Rosielle, & Cooper, 2002; Calder & Young, 1996; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). For example, Schweinberger, Pickering, Jentzsch, et al. (2002) found faster reaction times (RTs) when familiar test faces (S2) were preceded by the same image (*primed same*) or a different image of the same person (*primed different*) as compared to the image of a different person (*unprimed*). Furthermore, the fact that the primed same condition yielded faster RTs than the primed different condition suggested a degree of image-specificity of this PR effect (also see, e.g., Bindemann et al., 2008; Ellis et al., 1987). Schweinberger, Pickering, Jentzsch, et al. (2002) also reported ERP correlates of the observed effects, which are addressed in more detail below.

In a recent debate on the importance of the paradigm for PR, the question of whether PR is dependent on the cognitive system involved or not was discussed. On the one hand, Ellis et al. (1990) observed PR only when a familiarity decision was required for test stimuli, whereas no such effects were found when expression or gender of the test stimuli had to be judged, irrespective of the task during first presentation. Therefore, they argued that PR is associated with the system that responds to familiarity of faces. On the other hand, some studies (Ganel & Goshen-Gottstein, 2002; Goshen-Gottstein & Ganel, 2000) reported PR effects using a gender classification task at test, but only when external features of face stimuli were cropped, and argued that the presence of external features can mask PR effects in gender classification tasks by leading participants to base their decisions on simple heuristics. They suggested that the system underlying PR processes both gender and identity. Nevertheless, reports of face PR effects in gender classification tasks are very scarce in the literature. In a long-term PR study, Wiese, Schweinberger, and Neumann (2008) showed that PR effects measured with a gender task depend on the task used in the priming phase, and other studies could only induce such effects using stimulus classes different from faces (e.g., McNeill, Burton, & Ellis, 2003). Therefore, this discussion seems not to be resolved as of yet.

Similar to adaptation, PR was also assessed with electrophysiological measures such as ERPs. One ERP component, the N250r, was found to reflect face PR in several studies (Bindemann et al., 2008; Schweinberger, Huddy, & Burton, 2004; Schweinberger, Pickering, Burton, et al., 2002). In proximity to the negative going wave N250, the N250r ("r" for "repetition") was typically observed as increased negativity for repeated as compared to non-repeated faces over occipito-temporal recording sites at around 230 - 280 ms after stimulus

onset. In a study by Schweinberger et al. (2004) participants had to detect butterflies among S1-S2 pairs of upright human and ape faces, cars and inverted faces. For human faces and ape faces, the N250r was increased when the S1 was identical to the S2, whereas no such modulation was found for inverted faces or cars. Because several studies did not find face repetition or PR effects on earlier ERP components such as the N170 (Amihai et al., 2011; Schweinberger, Pickering, Burton, et al., 2002; Schweinberger, Pickering, Jentzsch, et al., 2002; but see also Campanella et al., 2000; Jemel, Pisani, Rousselle, Crommelinck, & Bruyer, 2005), the N250r is often considered as the earliest ERP correlate of individual recognition (for related recent findings, see Gosling & Eimer, 2011). This is also in line with other studies showing that the N170 is not modulated by face familiarity (Eimer, 2000), and the idea that the N170 reflects face encoding on a structural, but not identity level (Sagiv & Bentin, 2001). Although in some studies (e.g., Schweinberger et al., 2004) no behavioural measures were taken, other studies showed a clear analogy between behavioural and ERP PR effects (Bindemann et al., 2008; Schweinberger, Pickering, Jentzsch, et al., 2002). In these studies, the pattern of RTs was mirrored by the N250r modulation, in that famous test faces following same image primes yielded the shortest RTs coupled with the highest N250r amplitudes, faces following a different image of the same person showed longer RTs and a smaller N250r, whereas faces following an image of a different person showed the slowest RTs and smallest N250r. This at least suggests that the N250r increments observed in PR paradigms are associated with behavioural PR, although more direct measures of relatedness could substantiate this point here as well.

The picture for fMRI research on priming seems less clear, although behavioural and brain imaging data were both typically obtained using stimulus repetition paradigms. Many studies observed reduced BOLD responses for repeated as compared to non-repeated stimuli in extrastriate regions of the visual cortex (for a review on object and word processing, see Henson, 2003), but it also might be worth to consider the paradigm applied to investigate such effects. While blocked designs were often used, other paradigms, such as event-related paradigms, have become more frequent over the last years. Event-related fMRI allows analyses of BOLD signal for single stimuli or stimulus pairs, and can therefore be used to realize experiments equivalent to behavioural studies of PR, especially in the immediate repetition context. Interestingly, while immediate repetitions typically yield the strongest effects (Sayres & Grill-Spector, 2006), RS was also observed after longer delays, such as several days (van Turennout, Ellmore, & Martin, 2000).

In several studies on face perception (Andrews & Ewbank, 2004; Davies-Thompson, Gouws, & Andrews, 2009; Henson, Shallice, Gorno-Tempini, & Dolan, 2002; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008), RS was observed in certain cortical regions sensitive to faces, such as the OFA (Gauthier et al., 2000), and FFA (Kanwisher et al., 1997), but also the object-selective lateral occipital cortex (LO; Malach et al., 1995). For example, Andrews and Ewbank (2004) reported image size independent RS in a face-selective region of the fusiform gyrus when the same face was presented repeatedly within a block of 12 faces as compared to 12 different faces. Andrews and Ewbank also found repetition enhancement in the superior temporal lobe when the presented stimuli differed in viewpoint or expression, while no RS was observed for image repetition in that region. They concluded that the inferior temporal lobe might be important for the processing of invariant aspects of faces, while the superior temporal lobe might be involved in the detection of changeable aspects of faces. This is in line with the idea that FFA processes facial configuration (Kanwisher, Tong, & Nakayama, 1998), as also suggested by Haxby, Hoffman, and Gobbini (2000) in their functional model of the face processing network. In an event-related fMRI study on categorical perception of facial identity (Beale & Keil, 1995), Rotshtein, Henson, Treves, Driver, and Dolan (2005) presented pairs of famous faces, which were identical or physically differed by a fixed amount on a morphing continuum, either within an identity category or between two identities. Rotshtein et al. found RS in the OFA when the same image was repeated, whereas responses in the FFA were reduced for both identical and within-category pairs, suggesting a sensitivity of OFA for physical differences between face images and a role of FFA in individual recognition. Additionally, identity-specific RS in anterior temporal regions was modulated by pre-experimental familiarity with the faces used in this study. Interestingly, Henson, Shallice, and Dolan (2000) also suggested a role of familiarity in determining whether RS was observed in a PR paradigm, as they observed RS only for the repetition of familiar faces and objects, whereas a response enhancement was measured for unfamiliar stimuli. Note that, however, the role of FFA in identity perception is not that clear as of yet. For example, a recent fMRI study (Davies-Thompson et al., 2009) could not find differences in fMRI adaptation between blocked presentations of different images of the same famous identity and images of different famous identities in FFA (or OFA), suggesting that the paradigm used might play a role here.

While many studies on RS did not use behavioural measures, some studies also tried to relate PR to modulations of the BOLD responses more directly. Using a word discrimination task in fMRI, Maccotta and Buckner (2004) found correlations between (long-term) PR and

response reductions in frontal regions of the brain, and suggested that behavioural benefits are linked to the facilitation of frontally mediated processes. Although this study alone does not allow inferences about causality, it was also shown that transcranial magnetic stimulation during the first presentation of objects hindered later behavioural PR effects and frontal RS for repeated objects, whereas RS in occipital cortices was still visible (Wig, Grafton, Demos, & Kelley, 2005). Although this study offered an interesting link between frontal RS and conceptual PR processes, the relation between the perceptual processing in occipital cortex and behavioural PR remained unclear. Other studies also did not succeed in solving this issue. A study by Sayres and Grill-Spector (2006) did not find a clear relationship between RTs and RS, and Ganel et al. (2006) could not disentangle "priming" and RS, as they found RS over all experimental conditions. Still, there is an ongoing debate on if (see, e.g., Buracas, Fine, & Boynton, 2005) and how BOLD responses could be linked to behavioural PR (for reviews, see Gotts et al., 2012; Grill-Spector et al., 2006).

1.3 Adaptation and priming - Similarities and differences

Although the behavioural outcomes of AEs and PR seem quite different, there are some aspects they seem to share, regarding both their behavioural outcomes and their neural correlates. First of all, behavioural as well as neurophysiological experiments investigating AEs and PR often share a common experimental trial procedure, which is primarily characterized by a sequence of two stimuli (S1 and S2), wherein the S2 has to be responded to by the participant. Both effects show some degree of independence from image differences between first (S1) and second presentation, i.e., test (S2). While, to some point, AEs have been found to be independent of size (Zhao & Chubb, 2001), viewpoint (Jiang, Blanz, & O'Toole, 2006), retinal position (for a review, see Zimmer & Kovács, 2011b), and geometrical distortions (Hole, 2011), PR is (at least partly) unaffected by changes in size, position, and mirror reversal (Brooks et al., 2002), as well as geometrical distortions (Bindemann et al., 2008). In addition, in studies comparing S1-S2 pairs where either the same image or different images of one person were used, a certain degree of image-specificity was observed for both AEs (Carbon & Ditye, 2012; Carbon et al., 2007; Hills et al., 2010) and PR (Bindemann et al., 2008; Schweinberger et al., 2004; Schweinberger, Pickering, Jentzsch, et al., 2002), in that the respective effect was smaller when different as compared to identical images were used as S1 and S2. Note that, however, this similarity between AEs and PR has to be considered with some caution, as in the case of AEs, the different image condition typically means that the image used as S1 was not used to create the test morph, and even in the same image

conditions, S1 and S2 are usually not identical images, as it is the case in PR studies. It was also shown that both AEs and PR can be longer lasting: Face distortion AEs in famous faces can survive 24 hours (Carbon et al., 2007), or even 7 days (Carbon & Dityte, 2011) between adaptation and test. Similarly, PR was also reported after long delays between S1 and S2 (see Cave, 1997 for an example in object recognition).

Studies on AEs and PR also differ in various ways. Regarding paradigms that are typically used to induce behavioural effects, the dissimilarity of timing parameters is quite obvious. While PR is often investigated using S1 and S2 durations of about 1000 ms, AEs are strongest for relatively shorter test stimuli (e.g., 300 ms) following longer S1s (seconds to minutes; for a parametric account for face identity AEs, see Leopold et al., 2005). In a recent study on object perception, Daelli, van Rijsbergen, and Treves (2010) observed AEs for short (50 ms) and PR for longer (3100 ms) intervals between S1 and S2, and suggested a role of S1-S2 delay in determining whether AE or PR was present. Interestingly, smaller, but reliable AEs can be induced by adaptation periods similar to or even shorter than the primes used in most PR studies. For example, Kovács and colleagues (Kovács et al., 2008; Kovács et al., 2007) found gender AEs after 500 ms presentation of the S1. Therefore, it is not yet clear if timing parameters alone can explain whether AE or PR is induced in a stimulus repetition paradigm. Additionally, studies on AEs and PR often used very different stimulus materials, most probably due to the need for ambiguous test faces to observe AEs. Typically, such stimuli are created by morphing between two veridical faces (Hills et al., 2010) or a veridical and an average face (Leopold et al., 2001), although other options such as composites of two different stimuli were sometimes used (Cziraki et al., 2010). Comparably sophisticated image manipulations are not necessary in PR experiments, in which the use of veridical faces as S1 and S2 is common (Bindemann et al., 2008; Schweinberger et al., 2004; Schweinberger, Pickering, Jentzsch, et al., 2002). Moreover, AE and PR were often observed with different tasks. In studies on AEs, participants typically have to decide whether the ambiguous test stimulus looks more like one or the other extreme of the dimension of interest, e.g., whether an androgynous face looks male or female (Kloth et al., 2010), or whether a 50/50% morph between identities 1 and 2 looks like identity 1 or identity 2 (Hills et al., 2010). This task is more specific than the familiarity decision task typically used in PR experiments (e.g., Ellis et al., 1987; Schweinberger, Pickering, Jentzsch, et al., 2002). But it should be noted that in some cases, PR was also observed on a gender decision (Goshen-Gottstein & Ganel, 2000), or with a direct naming task that could be regarded as pretty close to the identity decision used in some studies on AEs (Hills et al., 2010; Hole, 2011). In summary, timing and task parameters,

as well as stimulus features are possible factors to determine whether AEs or PR are observed in stimulus repetition paradigms, both behaviourally and neurally.

The neural correlates of AEs and PR are heavily discussed at present. In ERPs, categorical and specific adaptation effects were observed as modulations of relatively early components such as the N170 (e.g., Amihai et al., 2011; Kloth et al., 2010; Kovács et al., 2006; Zimmer & Kovács, 2011a) or the P250 (Burkhardt et al., 2010), whereas the first component revealing reliable PR effects is the N250r (Bindemann et al., 2008; Schweinberger et al., 2004; Schweinberger, Pickering, Jentzsch, et al., 2002). Regarding the limited body of evidence for specific ERP adaptation effects, the relation of these effects and PR is still unclear from such data. However, categorical adaptation effects and PR seem to be associated with different ERP components possibly reflecting different brain processes. In the case of fMRI, suppressions of the BOLD signal have been related to both AEs (Cziraki et al., 2010; Furl et al., 2007) and PR (see Gotts et al., 2012 for a recent discussion of this issue; but also Henson et al., 2002; Summerfield et al., 2008). Although the observation of such effects in similar cortical structures, for example the FFA and OFA, might indicate that similar processes are involved, a study by Furl et al. (2007) suggested that some caution might be appropriate regarding such interpretations. Furl et al. found that while FFA and OFA activity was reduced for repeated face presentations only, effects specific to the response of the participants were observed over the anterior medial temporal lobe. Still, fMRI evidence is also not sufficient to conclude about whether categorical and specific adaptation effects and PR share the same neural locus, and perhaps common mechanisms.

In line with neural data, both AEs and PR have led to various assumptions about underlying brain processes, which were typically allocated to higher-level regions of the perceptual system. Many previous studies reckoned that facial adaptation reflects processes of high-level brain areas (for a recent review, see Webster & MacLeod, 2011), especially after ruling out retinotopic contributions to AEs (e.g., Rhodes et al., 2004). Nevertheless, how certain facial dimensions are coded in the brain is still under investigation. Leopold et al. (2001) reported face identity AEs after adaptation to anti-faces, and therefore suggested that facial identity is coded relative to a prototype or average face, well in line with a norm-based implementation of the "multidimensional face space model" by Valentine (1991). Furthermore, it was shown that these AEs are specific for the identity opposite to the adapted one (Rhodes & Jeffery, 2006), and that face identities might be coded with respect to gender-specific prototypes (Rhodes et al., 2011). Regarding the coding of faces of different gender, the existence of general versus gender-specific neuron populations is still discussed (Jaquet &

Rhodes, 2008; Little, DeBruine, & Jones, 2005). Common to most accounts is the idea that adaptation has a re-calibrating or re-normalizing role for our perceptual system, for example by shifting the centre of face space in the adapted direction. However, there are researchers who share a more "perceptual" view (e.g., Webster & MacLin, 1999), whereas others argue that this re-calibration might also affect memory representations (Carbon & Ditye, 2011, 2012; Carbon et al., 2007).

Similarly to AEs, PR was also associated with higher level face processing. First and foremost, the influential model of familiar face recognition by Bruce and Young (1986) explained earlier findings of PR (e.g., Bruce & Valentine, 1985) with residual activation of so-called "face recognition units" (FRUs), which are thought to be higher-level units activated by any view of the face of a given identity. Additionally, this model also accounted for semantic PR effects as residual activation of so called "person identity nodes" (PINs). In some contrast to this initial and quite abstract model, Burton, Bruce, and Johnston (1990) proposed an adapted version of the Bruce and Young model called "interactive activation and competition model" (IAC). Burton et al. showed that the IAC model could account for a range of findings of that time, and, by using a simulation approach they proved that their model, which also incorporates FRU and PIN concepts, can predict different kinds of PR (e.g., semantic PR and repetition PR). Other studies (e.g., Calder & Young, 1996) tested assumptions of the IAC on repetition PR more rigorously and also reported evidence in favour of the predictions of the model.

Despite functional similarities of AEs and PR (see above) and reports of adaptation- (e.g., Cziraki et al., 2010) and PR-related BOLD reductions (see, e.g., Gotts et al., 2012) in FFA, which is thought of as a candidate region including something like FRUs, a more direct link between AEs and the FRU concept is missing as of yet. Interestingly, Hills et al. (2010) made an attempt to explain several kinds of face identity AEs within the IAC model and suggested mechanisms for their implementation. A different account to understand the brain processes associated with AEs and PR was made recently by Huber and colleagues (Huber, 2008; Huber & O'Reilly, 2003; Rieth & Huber, 2010), whose model incorporates two processes, synaptic activation and depletion, which work on different time scales. The shorter activation response is assumed to be related to PR, whereas depletion is thought to last longer and to determine the strength of AEs. Although their model is first of all a computational one, some empirical evidence was also presented, showing that short prime-target intervals induce PR, whereas longer intervals lead to AEs in identification tasks for words (Huber, 2008) or faces (Rieth & Huber, 2010). These results also point to a role of S1-S2 delay for the presence

of AEs or PR quite different from that suggested by Daelli et al. (2010), who found that short adaptor-target intervals induce AEs and longer intervals reveal PR in the perception of ambiguous objects, which might be due to the use of entirely different paradigms in both studies. In summary, although significant progresses are being made, a conclusive account of face perception explaining both AEs and PR is currently not available.

2.   Research Objective of the Current Thesis

After reviewing the literature on AEs and PR in face perception, it seems clear that both phenomena, although having different behavioural consequences, are nevertheless similar regarding some functional properties and neural correlates. Although there have been some attempts to relate these repetition-related phenomena to each other, a satisfying rationale has not yet been found. One reason for this is that both AEs and PR were typically investigated in separate experiments using different paradigms, tasks, and stimuli, so that a multitude of factors might have determined the respective outcomes. However, to directly compare AEs and PR, both phenomena should be investigated within the same paradigm and subjects. Using such an approach, the present thesis aimed at providing further evidence for the relationship between AEs and PR. Note, however, that the development of a complete account of face perception incorporating both phenomena is beyond the scope of this thesis.

Study I of this thesis (also published as a separate research article in *Cortex*) was designed to test if both AE and PR can be elicited within the same paradigm and subjects. We investigated both phenomena within the same S1-S2 paradigm, only varying the S1 and S2 stimuli, but keeping all other factors, such as timing and task, constant. The simultaneously recorded ERPs allowed us to compare the behavioural and neural correlates of both phenomena directly and to draw first conclusions about the factors determining AEs and PR. Study II (as a separate research article also under revision in *PlosOne*) was set up to take a closer look at the factors driving AEs in a modified version of the initial paradigm. ERPs were also recorded, and a high amount of trials in conditions where AEs were expected rendered response-specific analyses (Cziraki et al., 2010; Furl et al., 2007) of the ERPs possible. This method was introduced as another way to quantify brain correlates of specific adaptation, which were rarely observed (or even considered) in previous studies. Finally, Study III (as a separate research article also submitted to *Journal of Neurophysiology*) focused on the brain-imaging correlates of AEs and PR induced within a gender adaptation paradigm. While in Study I, S1 and S2 stimuli and therefore the identity congruence between S1-S2 pairs were manipulated, only the S1 was varied in Study III. Holding the S2 constant at an androgynous level ensured that all observed BOLD differences between conditions were not due to differences in the S2 per se, but related to the preceding stimulation. The following chapters contain the manuscripts on these three studies.

3. The Present Studies

3.1 Neural correlates of priming and adaptation in familiar face perception

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Abstract

Priming (PR) and adaptation-related aftereffects (AEs) are two phenomena when recent perceptual experiences alter face perception. While AEs are often reflected in contrastive perceptual biases, PR typically leads to behavioural facilitation. Previous research suggests that both phenomena modulate broadly similar components of the event-related potentials (ERPs). To disentangle the underlying neural mechanisms of PR and AE, we induced both effects within the same subjects and paradigm. We presented pairs of stimuli, where the first (S1) was a famous face (identity A, B or C), a morph between two famous faces (50/50% A/B), or a Fourier phase randomized face (as a control stimulus matched for low-level visual information) and the second (S2) was a face drawn from morph continua between identity A and B. Participants' performance in matching S2s to either A or B revealed contrastive aftereffects for *ambiguous* S2 faces, which were more likely perceived as identity B following the presentation of A and vice versa. *Unambiguous* S2 faces, however, showed PR, with significantly shorter response times, as well as higher classification performance, for identity-congruent than for incongruent S1-S2-pairs. Analyses of the simultaneously recorded ERPs revealed clear categorical adaptation at around 155-205 msec post-stimulus onset. We also found amplitude modulations for *unambiguous* S2 faces following identity-congruent S1 faces, related to PR, starting at 90 msec and being most pronounced at around 205-255 msec. For *ambiguous* S2 faces, we also observed an ERP effect at around 205-255 msec that was correlated with behavioural AEs. Our results show that face PR and AEs are present simultaneously within a single paradigm, depending on the ambiguity of S2 faces and/or on the similarity of S1 and S2, and suggest that exclusive mechanisms might underlie both PR and AEs and that object-category and identity processing might run in parallel during face processing.

Introduction

Human faces contain a large variety of socially relevant information - amongst them a person's identity, emotional state, gender, or age. However, rather than being exclusively determined by information in the stimulus, the perception of a certain face also depends on its specific perceptual history, or, its temporal context, as suggested in several previous studies.

A whole tradition of research has focused on repetition priming (PR). PR is typically associated with faster and/or more accurate responses when a face is preceded by the same face, both in immediate and long-term repetition contexts. Ellis et al. (1987) showed that participants classified faces being familiar/unfamiliar faster when these faces have been encountered previously. This effect was also observed in immediate repetition contexts (Schweinberger et al., 2002b). Schweinberger and colleagues reported faster response times (RTs) for familiar test faces (S2) following the same image (primed same) or a different image of the same person (primed different) when compared to S2s following the image of a different person (unprimed). Additionally, the primed same condition exhibited faster RTs than the primed different condition, suggesting some image-specificity of the effect (as also found by Ellis et al., 1987). Finally, event related potential (ERP) recording techniques revealed PR-related modulations of the occipito-temporal N250r ERP component, as well as of later components (Schweinberger et al., 2002b).

In other paradigms, prolonged exposure to faces leads to robust adaptation-related aftereffects (AEs; Leopold et al., 2001; Rhodes et al., 2003; Webster et al., 2004; Webster and MacLin, 1999; Yamashita et al., 2005). The behavioural consequences of these effects are of contrastive nature and typically observed as biases in the perception of faces that were ambiguous with respect to the adapted dimension. For example, Webster and MacLin (1999) showed that after adaptation to distorted faces, undistorted faces were perceived as distorted in the direction opposite to the adaptors, while adaptation to undistorted faces did not induce any bias to the perception of test faces. AEs were also reported in the perception of socially relevant information such as face gender (Kloth et al., 2010; Kovács et al., 2006, 2007; Webster et al., 2004), ethnicity, expressions (Webster et al., 2004), age (Schweinberger et al., 2010), gaze (Jenkins et al., 2006; Kloth and Schweinberger, 2008), and identity (Hills et al., 2010; Leopold et al., 2001; Rhodes et al., 2007). Unlike adaptation effects to basic, low-level visual dimensions— i.e. motion, orientation, spatial frequency, or texture (for review see Anstis et al., 1998; Clifford, 2002; Durgin and Proffitt, 1996; Frisby, 1979), facial adaptation is associated with high-level brain areas, containing face-selective neurons.

In a study on face identity aftereffects, Hills et al. (2010) quantified face identity aftereffects to different types of adaptors for familiar faces. After an adaptation period, participants allocated morphs between two identities (identities 1 and 2), each of which was preceded by a top-up adaptor, to either identity 1 or 2. Hills et al. found strong aftereffects in the form of a shift of identity thresholds towards the adapted identity relative to a baseline. For example following adaptation to identity 2, participants were more likely to classify a morphed test face as identity 1. In a series of experiments, the authors found that this effect was the most pronounced if the adaptor and test stimuli were identical images, but it also could be observed for different adaptor and test image pairs. Additionally, Hills et al. (2010) reported face identity aftereffects following adaptation to written names, voices, faces of associated identities, as well as imagined faces and caricatures, the latter showing the strongest effects over all experiments.

Although the behavioural aspects of both repetition PR and AEs are very different, there are some functional properties they seem to share. High-level aftereffects were reported to be independent of size (Zhao and Chubb, 2001), viewpoint (Jiang et al., 2006), and retinal position (for review see Zimmer and Kovács, 2011a) to a certain extent. It has also been reported that both face distortion and identity AEs are reduced for different as compared to same image adaptors (Carbon and Ditye, 2012; Carbon et al., 2007; Hills et al., 2010), and that face distortion AEs can be even observed after 24 h (Carbon et al., 2007) or even as long as 7 days (Carbon and Ditye, 2011) between adaptation and test. Interestingly, repetition PR was also reported for even very long S1-S2-delays (cf. Cave, 1997 for an example in object recognition), and found to be insensitive to physical differences between S1 and S2, such as size, position and mirror reversal (Brooks et al., 2002), as well as geometrical distortions (Bindemann et al., 2008). In the latter study, the authors also reported reduced PR effects when S1 and S2 were different images belonging to the same identity, as also observed in other studies (Schweinberger et al., 2002b, 2004).

Because there are differences, but also similarities, in the behavioural correlates of repetition PR and AEs, the degree to which the two repetition-related phenomena share the same neural mechanisms is currently under heavy discussion. One line of experiments studies the suppression of the blood oxygen level dependent (BOLD) signal during stimulus repetition, measured by functional magnetic resonance imaging (fMRI) and termed fMRI adaptation (fMRIa; for reviews see Grill-Spector et al., 2006; Krekelberg et al., 2006). fMRIa was previously observed in both adaptation (Cziraki et al., 2010; Kovács et al., 2008) and PR experiments (Davies-Thompson et al., 2009; for examples on word and object recognition, see

Grill-Spector et al., 2006; Henson, 2003) in various cortical structures such as the fusiform face area (FFA; Kanwisher et al., 1997) or the occipital face area (OFA; Gauthier et al., 2000) and other cortical areas.

In electrophysiological studies, correlates of AEs have been reported as early as 140-200 msec post stimulus onset (N170 time window). Kovács et al. (2006) observed attenuations of the N170 component for S2s following adaptation to *category*-congruent S1s (see also Kloth et al., 2010), while N170 AEs to *identity*-congruent S1s seem small or absent (see also Amihai et al., 2011). The electrophysiological correlates of PR are less clear as yet. While some studies found early ERP effects of PR (e.g., Jemel et al., 2005) or of categorical perception of facial identity (Campanella et al., 2000), other studies suggested that the N170 is insensitive to short-term repetition PR of familiar faces (Amihai et al., 2011; Schweinberger et al., 2002a, 2002b). An ERP component more closely associated with face repetition PR, the N250r, usually occurs around 230-280 msec after stimulus onset (Schweinberger et al., 2002b, 2004). Schweinberger et al. (2004) presented upright human and ape faces, cars and inverted faces in a stream of S1-S2 pairs, and found an increased N250r component induced by identical as compared to different S1 and S2 faces. A similar but smaller effect was found for ape faces, but not for cars or inverted faces. The authors considered this effect as a correlate of individual recognition (for related recent findings, see Gosling and Eimer, 2011). This is also in line with studies demonstrating that the N170 is not sensitive to face familiarity (Eimer, 2000), and with the idea that N170 reflects structural encoding of the faces occurring prior to person identification (Sagiv and Bentin, 2001).

What are the factors determining whether repetition PR or AEs are observed in a certain study? One of the major differences between experimental paradigms leading to PR or AEs is the stimulus timing: while studies of AEs typically use a long adaptation period (seconds to minutes) prior to a short test stimulus (Leopold et al., 2005), studies of PR use shorter S1 stimuli (typically, less than 1000 msec), but relatively longer S2 presentations. Considering this, S1-S2 timing might be a crucial factor in determining which effect is observed, as also suggested by a recent study of object perception. Daelli et al. (2010) presented ambiguous S2 stimuli preceded by proto-typical S1s and observed aftereffects when the delay between S1 and S2 was short (50 msec), whereas PR effects were found for long (3100 msec) S1-S2 delays. However, other data suggest that PR and AE might be observed at similar timing parameters as well: Kovács and colleagues (Kovács et al., 2007, 2008) reported gender aftereffects, which were induced by relatively short (500 msec) adaptation periods.

Repetition PR and AEs studies also differ in the stimulus material used, as PR is typically observed for unambiguous test faces, and AEs are observed for faces that are ambiguous with respect to the relevant dimension. Additionally, participant's task is typically more specific in adaptation (e.g., identity 1/identity 2; Hills et al., 2010), than in PR studies, where participants typically have to report whether a face is familiar or unfamiliar (Ellis et al., 1987; Schweinberger et al., 2002b). Altogether, it seems that S1-S2 timing, task parameters, and stimulus features might all account for the different effects of recent perceptual experience on behaviour and neural mechanisms. However, to our knowledge, so far nobody compared the behavioural and neural correlates of repetition PR and AEs for familiar faces directly. Here we present a behavioural and an ERP-experiment using a novel paradigm that permits to investigate both effects within the same paradigm.

Experiment 1

In Experiment 1, we tested whether repetition PR and AEs could be induced within a single experiment using identical task and timing parameters. In an S1-S2 paradigm, images drawn from morphing continua between faces of two famous identities served as S2. They were preceded by an S1 face belonging to either one of the two original identities of each continuum or a unique third identity. In this experiment, we also asked whether the manipulation of S1 and S2 is able to change the absence or presence of PR and AE, and whether both effects could be observed simultaneously.

Materials and Methods

Participants. Twenty right-handed students of the University of Jena took part in the experiment (19 female, mean age = 22.8 years, range 19-31 years). All participants had normal or corrected to normal vision, gave written informed consent and received course credit for their participation. The experiment was carried out in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of the Friedrich Schiller University.

Stimuli. Stimuli comprised 42 famous faces (21 female) collected from the public domain of the worldwide web. We formed 14 same-gender triplets consisting of three unique identities (A, B and C) with no or little semantic overlap. For each triplet, we created a morphing continuum between identities A and B using Sierra Morph™ (version 2.5) software. While all identities of a triplet served as first stimulus ($S1_A$, $S1_B$, or $S1_C$), morphs between A and B were used as second stimulus (S2; 11 images per continuum, from 100/0%

to 0/100% identity A/B in 10% steps). Beforehand, excessive hairstyles were cropped and faces were aligned to the same pupil position. Images were converted to greyscale and subjectively equated for luminance and contrast. In some cases, manual corrections were applied to remove strands of hair, paraphernalia or extensive make-ups. All editing was done by Adobe Photoshop CS2 (Adobe Systems Inc.). Final image size was 531 x 704 pixels. Faces were presented with PsychToolbox 3.0.8 (Brainard, 1997) in MATLAB 7.6 (MathWorks Inc.) at visual angles of 7.2 x 5.2° or 9.0 x 6.5° on an liquid crystal display (LCD) monitor (mean luminance[1]: 85 cd/m²) on a grey background for S2 faces and S1 faces, respectively. The S1 faces were presented 25% larger than S2 faces to avoid any possible effects based on retinal positions or illusory movements in the faces due to the short inter-stimulus-interval (ISI).

Procedure. Participants were tested individually in a dimly lit chamber. Head position was fixed via a chin rest and the distance to the screen was 65 cm. Participants matched morphed S2 faces to one of their original identities (A or B) presented next to each other on a subsequent choice-screen, whereas they were asked to simply fixate the S1 stimuli (see Fig. 1). S2 stimuli were presented according to the method of constant stimuli.

Each trial started with a fixation period of 1000 msec, after which an S1 was shown for 500 msec (see Fig. 1, upper panel). Following a 50 msec blank screen, the morphed S2 was presented for 300 msec. Next, participants matched the S2 face via button press to one of the two endpoints of the respective morph continuum, which were presented on the left and right sides of the centre of the screen for 1500 msec (positioned randomly, with identity A being presented on the left side for half of the trials, stimulus size: 7.2 x 5.2°, inter-stimulus distance: 9.2°). Note that there was no spatial overlap between S2 and the faces of the subsequent choice-screen. Responses were only scored within 1500 msec. If no response was detected, the message "Bitte schneller reagieren!" ("Please respond faster!") was displayed for 1000 msec. The inter-trial interval (ITI) was fixed at 500 msec.

The experiment was composed of three blocks in randomized order. Each block included one unique S1 identity (i.e. either $S1_A$, or $S1_B$, or $S1_C$) for each of the 14 different identities, presented randomly within the block. The experiment consisted of a *practice phase* (28 trials), and an *experimental phase* (462 trials). Trial procedure of the practice phase was similar to

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[1] The luminance of all stimuli (in size of the S2, presented twice and each time until the measurement was done) was measured with a Tektronix J16 Photometer with a J6523-2 narrow angle (1°) probe, the lens of which was fixated centrally in front of the screen, at a distance of approximately 65 cm (Experiment 1) or 90 cm (Experiment 2) and in a height of 117 cm, which approximates the eye position of an average-sized participant. The optic of the photometer was set according to the respective distance to the screen. The 1° probe aimed at the nasion of the presented faces, as the area around nasion is thought to reflect a mean luminance of the whole face.

that of the experimental phase, but different morph levels were used as S2 (i.e., 95/5%, 85/15%, 15/85% and 5/95% identity A/B) and each identity triplet and S1 condition appeared at least once. Participants were allowed a fixed 1 min rest every 77 trials in the experimental phase. In total, the experiment lasted about 40 min.
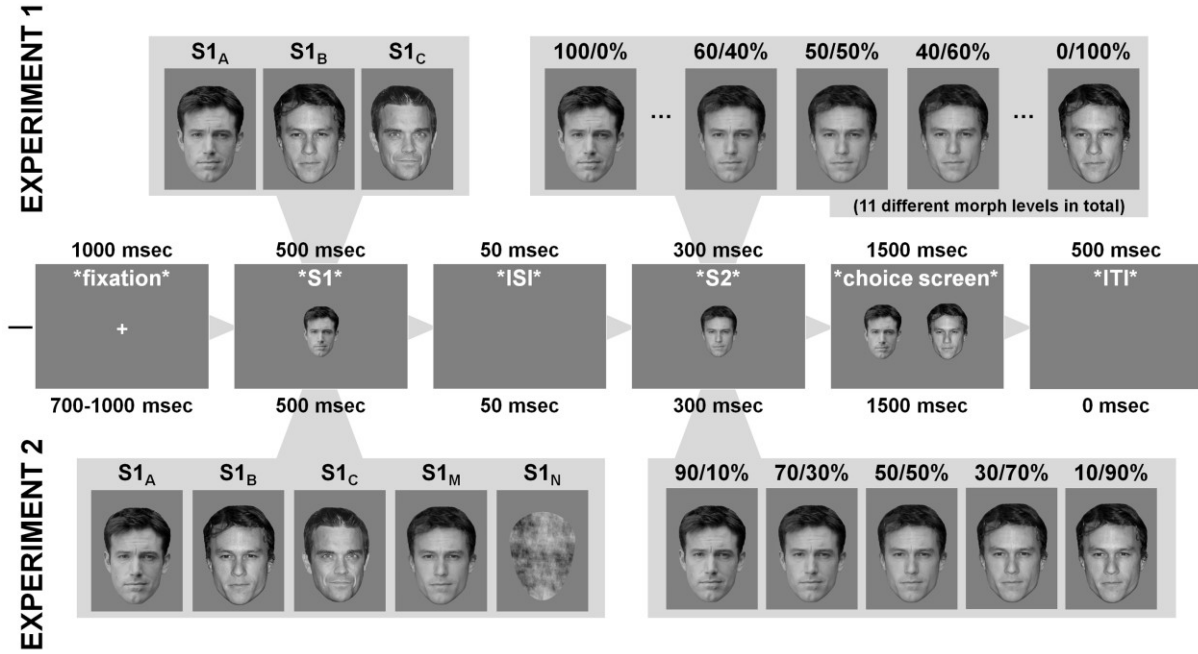
Figure 1. Trial structure of Experiments 1 (upper half) and 2 (lower half). Note that the expressions in asterisks are for illustration only and were not presented on the screen.

Behavioural data analysis. We performed analyses of variance (ANOVA) with repeated measures on S1 condition (3; $S1_A$, $S1_B$, or $S1_C$) and S2 morph level (11) for accuracies (in proportion endorsed as identity B) and for response times (RT). Epsilon corrections for heterogeneity of covariance according to Huynh and Feldt (1976) were used throughout, where appropriate. Errors of omission (missing key press) and trials with response times (RTs) faster than 200 msec were excluded from the analyses (for both categories in total, .006% of all experimental trials). To assess identity-specific effects over the morphing continuum, we compared the $S1_A$ and $S1_B$ conditions post-hoc, using paired samples t-tests at each S2 morph level. Only significant t-tests are reported.

In addition, we calculated the individual magnitudes of RT PR effect as the mean of the absolute differences between $S1_A$ and $S1_B$ at morph levels 100/0% (corresponding to identity A), 90/10%, 10/90% and 0/100% (identity B), and of aftereffect for accuracy data as the mean of the absolute differences between $S1_A$ and $S1_B$ at morph levels 60/40%, 50/50%, and

40/60%. We determined the relationship between PR and aftereffect using the Pearson correlation coefficient.

Results

Analyses of accuracies revealed strong identity-specific aftereffects, in that participants were more likely to classify ambiguous S2 faces as identity A following presentation of $S1_B$ and vice versa, while S2 faces following presentation of $S1_C$ led to classification scores somewhere in between [main effect of S1 condition: $F(2,38) = 6.85$, $p = .007$, $\varepsilon_{HF} = .74$, $\eta^2_p = .27$; see Fig. 2A]. This effect was most pronounced at ambiguous S2 morph levels and was reversed to priming direction at unambiguous S2 morph levels [corresponding to the ends of the morph-continuums; interaction of S1 condition and S2 morph level: $F(20,380) = 10.56$, $p < .001$, $\eta^2_p = .36$]. PR means that participants were more likely to classify S2 as identity A following presentation of $S1_A$ and as identity B following presentation of $S1_B$. These observations are also supported by the post-hoc t-tests that showed higher proportions of identity B responses following $S1_A$ as compared to $S1_B$ at 60/40%, 50/50% and 40/60% identity A/B morphs, all ps $< .01$. The PR effect was based on a significantly higher proportion of trials endorsed as identity B for 100/0% and 0/100% S2s following $S1_B$ as compared to $S1_A$, $t(19) = -2.42$, $p = .026$, $d = -.76$ and $t(19) = -2.46$, $p = .024$, $d = -.83$, respectively.

This suggests that while subjects' perception is biased away from the identity of S1 for ambiguous S2 morph levels (aftereffects) it is biased towards the identity of the S1 (PR) for unambiguous S2s, a conclusion supporting previous results for objects (Daelli et al., 2010).
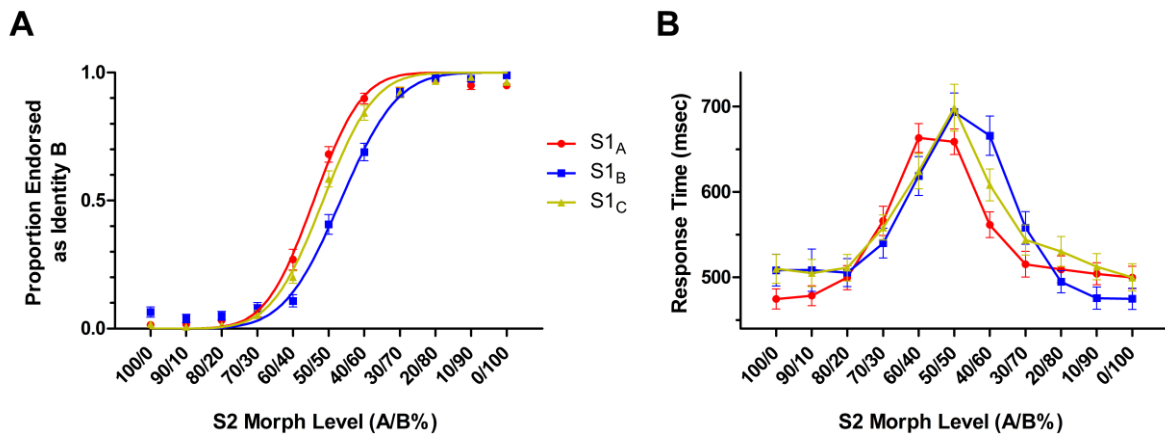
Figure 2. A: Accuracy data (in proportion endorsed as identity B) and B: response times (in msec) at each S2 morph level following $S1_A$, $S1_B$, and $S1_C$. Error bars show ±1 standard error of the mean (SEM).

RTs revealed an interaction of S1 condition and S2 morph level, $F(20,380) = 5.55$, $p <$ .001, $\eta^2_p = .23$ (see Fig. 2B), which seemed to consist of two components. For unambiguous identity A S2 stimuli (corresponding to 100/0% and 90/10% A/B morph-levels), responses were significantly faster following presentation of $S1_A$ as compared to $S1_B$ and $S1_C$, and vice versa for unambiguous identity B S2s, suggesting identity-PR effects. Post-hoc t-tests showed significantly faster RTs for the 100/0% (i.e., identity A) S2s following $S1_A$ as compared to $S1_B$, $t(19) = -2.22$, $p = .039$, $d = -.49$, while $S1_B$ led to faster responses when compared to $S1_A$ for the 10/90% and 0/100% S2s, $t(19) = 2.70$, $p = .014$, $d = .49$, and $t(19) = 2.28$, $p = .034$, d =.44, respectively. Furthermore, while participants responded slower to ambiguous S2 stimuli in general [main effect of S2 morph level: $F(10,190) = 140.66$, $p < .001$, $\varepsilon_{HF} = .59$, $\eta^2_p = .88$], the peak of the response time curve was shifted towards 100/0% morph levels for S2s following $S1_A$ and towards 0/100% morph levels for S2s following $S1_B$. This effect was reflected in significant differences between $S1_A$ and $S1_B$ at morph levels 60/40%, $t(19) = 2.20$, $p = .041$, $d = .50$, as well as 40/60%, $t(19) = -4.28$, $p < .001$, $d = -1.20$. As the ambiguous morph levels were also subject to contrastive aftereffects (see the proportion endorsed as B), the dependency of RT distribution from S1 condition is in line with what was observed in adaptation studies using several morphing steps of auditory stimuli as S2 (e.g., Zäske et al., 2009).

Correlation analyses (as described in the Methods section) revealed no significant relationship between the observed PR effect in response times and the contrastive aftereffect in accuracies, $r(18) = -.019$, $p = .937$.

Finally, since our sample of 20 participants contained one male participant only, we also tested the 19 female participants separately but the results did not differ from the reported analyses qualitatively.

Discussion

In Experiment 1, we observed both face repetition PR and AEs within the same paradigm, only by varying the ambiguity of the test faces. PR was expressed as reduction of RTs, as well as slightly higher classification performance, for identity-congruent S1-S2 pairs, and was only found for unambiguous S2 stimuli with the highest identity strengths. In contrast, AEs were induced for ambiguous S2 faces, in the sense that perception was biased away from the identity of the adaptor.

These findings are in line with the respective literature: The observation of PR for very similar pictures of the same identity has often been described (e.g., Schweinberger et al., 2002b), and there are also reports of face identity adaptation effects for ambiguous S2 faces

following unambiguous S1 faces (Hills et al., 2010). Note that the strong identity-specific AEs observed in our study were induced by short adaptation periods of only 500 msec (similar to Kovács et al., 2007), and despite the fact that contributions of low-level adaptation were ruled out by a large size change from S1 to S2 (e.g., Rhodes et al., 2004).

We also found an interesting result regarding the response time curves over the morphing continuum. While prior presentation of identity C S1s showed a distribution of response times with its peak over the ambiguous 50/50% S2, this peak was shifted towards either identity A or B, if the congruent S1 was presented previously. In other words, the morph level leading to maximal RT is shifted according to the biased perception of S2. Although it appears as the RT reflection of AEs, this shift is not typically reported in prior face adaptation studies, since researchers often focused solely on classification performance measures. Nevertheless, such peak shifts were already described in an auditory adaptation study (Zäske et al., 2009) where authors suggested that this effect might reflect altered response uncertainty following adaptation.

As a sideline, our correlation analyses did not reveal any relationship between the strength of PR and AE in our subjects, which may be additional evidence for the independence of the two phenomena. Since adaptation and PR were typically investigated in isolation in the past, future studies are needed to elucidate this point further.

In Experiment 1, PR and AEs were induced within a single paradigm, but never observed simultaneously (i.e., for the same S2 stimuli). In addition to pointing to the important role of stimulus ambiguity and/or to the similarity of S1 and S2, our results could suggest that different mechanisms – although possibly subserved by the same neuron populations – might underlie both PR and AEs. To obtain further evidence on their neuronal processing, we examined ERP correlates of these effects in Experiment 2.

Experiment 2

The purpose of Experiment 2 was to investigate the electrophysiological correlates of repetition PR and AEs within a single paradigm. Therefore, we adapted the existing paradigm of Experiment 1, introducing two new control conditions, and we recorded ERPs simultaneously.

Materials and Methods

Participants. Twenty-two right-handed students of the University of Jena contributed data (16 female, mean age = 23.9 years, range 19-40 years). All participants had normal or corrected to normal vision and gave written informed consent and received course credit for participation. Data from six additional participants had to be excluded from the analysis due to hardware problems ($N = 1$) or extensive electroencephalogram (EEG) artefacts and drifts ($N = 5$). The experiment was carried out in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of the Friedrich Schiller University.

Stimuli. Stimuli and presentation properties were identical to those of Experiment 1, with the following exceptions. In Experiment 2, we only presented five morph levels from each A-B continuum as S2 faces, corresponding to 90/10%, 70/30%, 50/50%, 30/70% and 10/90% identity A/B. Second, we included two additional S1 conditions: the 50/50% A/B morph level of each morph continuum [$S1_{M(orph)}$] and the Fourier phase randomized version of the identity C face of each triplet [$S1_{N(oise)}$] created by MATLAB 7.6 (MathWorks Inc.), using the algorithm of Näsänen (1999). The $S1_N$ was included as additional control for effects of low-level visual information. In Fourier phase randomized images, the amplitude distribution of frequency components matches that of the original images, but the position of these frequency components in the image is completely random, rendering the detection of any shape in the image impossible. In Experiment 2, a CRT (cathode ray tube) monitor was used for stimulus presentation (mean luminance: 15 cd/m²).

Procedure. Participants were tested individually in a dimly lit chamber. Head position was fixed via a chin rest, and the distance to the screen was approximately 90 cm. As in Experiment 1, participants' task was to fixate the S1 stimuli and to match the subsequently presented morphed S2 faces to one of their original identities (A or B). S2 stimuli were presented according to the method of constant stimuli.

Each trial started with a fixation period (randomised between 700 and 1000 msec) while the rest of the trial structure was identical to that of Experiment 1 (see Fig. 1, lower panel). The inter-stimulus distance between the two faces on the choice-screen was reduced to 6.5° to reduce saccades. There was no additional ITI between trials.

Experiment 2 was comprised of five blocks ($S1_A$, $S1_B$, $S1_C$, $S1_M$, and $S1_N$), presented in a random order. Every experimental block included one unique S1 stimulus for each of the 14 triplets (i.e., 14 different S1s). In the *experimental phase* of Experiment 2, each of the S2 faces was presented three times in every condition. Altogether, there were 25 different conditions (5 S1 conditions x 5 S2 morph levels) with 42 trials per condition (14 identity

triplets x 3 repetitions), adding up to 1050 trials. Participants were allowed to take a fixed 1 min rest every 105 trials in the experimental phase. The total experimental time including the *practice phase* (30 trials; similar to that of Experiment 1) was about 75 min.

ERPs. We measured the EEG using a 64-channel Biosemi Active II system (Biosemi, Amsterdam, Netherlands). Electrode positions were Fp1, FT9, AF3,F1, F3, F5, F7, FT7, TP9, FC3, FC1, C1, C3, C5, T7, TP7, PO9, CP3, CP1, P1, P3, O9, P7 P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, FT10, AF4, Afz, Fz, F2, F4, F6, F8, FT8, TP10, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, PO10, CP4, CP2, P2, P4, O10, P8, P10, PO8, PO4 and O2 (according to the extended international 10/20 system). EEG was recorded using a combined ground/reference (CMS/DRL) circuit (cf. to http://www.biosemi.com/faq/cms&drl.htm). Additionally, we recorded the horizontal electrooculogram (EOG) from the outer canthi of both eyes, and the vertical EOG bipolarly from above and below the left eye. All signals were recorded at a sampling-rate of 512 Hz (bandwidth: DC to 120 Hz). We segmented the EEG offline into 500-msec-long trials with 100 msec pre and 400 msec post S2 stimulus onsets. All signals were corrected for ocular artefacts automatically with BESA 5.1.8.10 (MEGIS Software GmbH, Graefelfing, Germany) and recalculated to average reference. Trials with amplitudes exceeding 100 µV were automatically removed and the remaining trials containing artefacts were rejected on the basis of visual inspection. If no behavioural response was detected in a trial then it was excluded from further analyses. After this procedure, 78% of the trials per condition were retained, corresponding to a mean of 33 trials per average (range across conditions: 30-35). ERPs were calculated by averaging the trials within each condition for every channel and every participant. ERPs were digitally filtered (zero phase shift) with a 0.3 Hz high-pass (6 dB/octave) and a 40 Hz low-pass filter (12 dB/octave).

Behavioural data analysis. We performed ANOVAs with repeated measures on S1 condition (5; $S1_A$, $S1_B$, $S1_C$, $S1_M$, or $S1_N$) and S2 morph level (5) for accuracies (in proportion endorsed as identity B) and response times. Epsilon corrections for heterogeneity of covariance according to Huynh and Feldt (1976) were used throughout, where appropriate. Errors of omission (no key press) and trials with response times (RTs) faster than 200 msec were excluded from the analyses (in total, .002% of all experimental trials). As for Experiment 1, we compared the $S1_A$ and $S1_B$ conditions post-hoc using paired samples *t*-tests at each S2 morph level. Only significant results are reported.

In addition, we calculated the magnitude of PR effect for the RT data as the mean of the absolute differences between $S1_A$ and $S1_B$ at morph levels 90/10% and 10/90%, as well as the

magnitude of aftereffect for accuracy data, expressed as the absolute difference between $S1_A$ and $S1_B$ at morph level 50/50%.

ERP data analysis. We calculated mean amplitudes for P1, N170 and P2 ERP components over a 50 msec time window, centred on the respective peaks of the grand average over all conditions and subjects except $S1_N$.[2] The time windows were 90-140 msec for P1, 155-205 msec for N170 and 205-255 msec for P2. All repeated measures ANOVAs for the mean amplitudes of each ERP component included the factors hemisphere (2), S1 condition (5; $S1_A$, $S1_B$, $S1_C$, $S1_M$, or $S1_N$) and S2 morph level (5). P1 mean amplitudes were measured at O1 and O2 with electrode position described by the hemisphere factor. For N170, electrode position (4; P7/P8, P9/P10, PO7/PO8, and PO9/PO10) was included as additional factor. Since pilot experiments suggested different effects on the P2 ERP components recorded over O1/2, PO7/8, and P7/8, as compared to I1/2, PO9/10, and P9/10 electrodes, the factors electrode position (3; P, PO, or O position) and electrode row (2; superior and inferior) were added to the ANOVA for P2. Epsilon corrections for heterogeneity of covariance according to Huynh and Feldt (1976) were used throughout, where appropriate. Post-hoc tests of significant interactions, comprising experimental factors, included separate ANOVAs with repeated measures on S1 condition (5) and S2 morph level (5) for each electrode of the respective overall analysis. If such an ANOVA yielded a significant interaction of S1 condition with S2 morph level, we compared $S1_A$ and $S1_B$ conditions at each S2 morph level, as well as $S1_M$ and the mean of $S1_A$ and $S1_B$ conditions at the 50/50% morph level, with paired samples t-tests. The latter comparison was also tested if there was only a significant main effect of S1 condition.

Additionally, we calculated the magnitude of the ERP PR effect as the mean of the absolute differences between $S1_A$ and $S1_B$ at morph levels 90/10% and 10/90%, and the magnitude of the ERP adaptation effect as the absolute difference between $S1_M$ and the mean of $S1_A$ and $S1_B$ at morph level 50/50% for each ERP component, electrode cluster[3] and hemisphere separately. The behavioural PR effect and aftereffect were then correlated with these ERP measures using the Pearson correlation coefficient, the significance of which was tested two-tailed.

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[2] The $S1_N$ condition was not included in the grand average calculation, because it exhibited strong signal differences as compared to all other S1 conditions, which could have affected the measurements.
[3] In detail, we first calculated the magnitude of PR effect and aftereffect at each electrode as described. We then calculated the mean of the effects over the left and right hemisphere electrodes that were also included in the ANOVAs for P1 and N170 ERP components. For the P2 component, the means were calculated over superior and inferior electrodes (as used in the ANOVA) for left and right hemisphere.

Results

Behavioural data. The behavioural results during ERP recordings replicated the major findings of the first experiment. Analysis of accuracy data showed strong identity-specific aftereffects, similar to Experiment 1. Prior presentation of $S1_A$ resulted in a higher proportion of identity B responses, and vice versa for S2s following $S1_B$. The other three S1 conditions did not bias the classification [main effect of S1 condition: $F(4,84) = 4.63$, $p = .011$, $\varepsilon_{HF} = .58$, $\eta^2_p = .18$; see Fig. 3A]. The effect was again most pronounced at the ambiguous S2 morph level and was reversed to PR direction at unambiguous S2 morph levels [interaction of S1 condition and S2 morph level: $F(16,336) = 16.10$, $p < .001$, $\varepsilon_{HF} = .48$, $\eta^2_p = .43$]. Post-hoc t-tests indicated a higher proportion of identity B responses following $S1_A$ as compared to $S1_B$ for the ambiguous 50/50% S2, $t(21) = 5.84$, $p < .001$, $d = 1.99$, and a lower proportion of identity B responses following $S1_A$ as opposed to $S1_B$ for the 10/90% S2, $t(21) = -2.32$, $p = .030$, $d = -.70$, suggesting significant identity-specific AEs and PR, respectively.
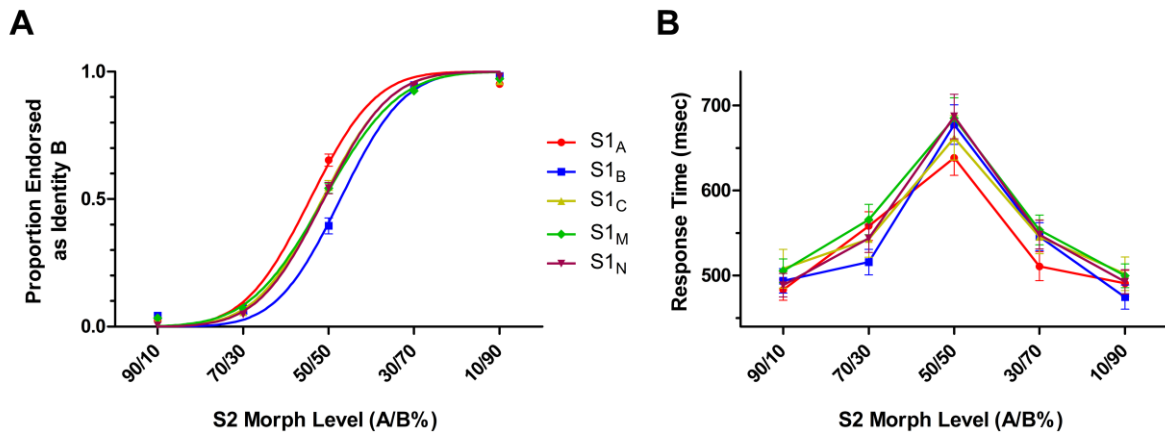
Figure 3. A: Accuracy data (in proportion endorsed as identity B) and B: response times (in msec) at each S2 morph level following $S1_A$, $S1_B$, $S1_C$, $S1_M$, and $S1_N$. Error bars show ±1 standard error of the mean (SEM).

RTs exhibited slower responses to more ambiguous stimuli [main effect of S2 morph level: $F(4,84) = 137.73$, $p < .001$, $\varepsilon_{HF} = .34$, $\eta^2_p = .87$], and a prominent peak shift in RT curves depending on S1 condition [interaction of S1 condition and S2 morph level: $F(16,336) = 7.10$, $p < .001$, $\varepsilon_{HF} = .71$, $\eta^2_p = .25$; see Fig. 3B]. This peak shift was reflected in slower RTs for 70/30% S2 following $S1_A$ as compared to $S1_B$, $t(21) = 3.84$, $p = .001$, $d = .57$, and faster RTs for 50/50% and 30/70% S2s following $S1_A$ as compared to $S1_B$, $t(21) = -2.82$, $p = .010$, $d = -.38$, and $t(21) = -3.55$, $p = .002$, $d = -.45$, respectively. Although we observed an identity-specific PR effect in accuracy data, such an effect did not reach the criteria of statistical significance for response times. Nevertheless, there was a small numerical effect in this

direction, in that RTs for 90/10% (i.e., identity A) S2 were faster following presentation of $S1_A$ ($M = 483$ msec) as compared to $S1_B$ ($M = 494$ msec), and vice versa for 10/90% S2 ($M = 491$ msec following $S1_A$, and $M = 475$ msec following $S1_B$).

ERP data. Figure 4 shows a sample ERP for the 90/10% S2 recorded over PO8. Analyses of the P1 (see Fig. 5, upper panels) revealed an identity-specific amplitude reduction for S2s following identity-congruent S1s, quantified by an interaction of S1 condition and S2 morph level, $F(16,336) = 3.17$, $p < .001$, $\varepsilon_{HF} = .95$, $\eta^2_p = .13$. Post-hoc t-tests showed reduced P1 amplitudes for 90/10% S2s following $S1_A$ as compared to $S1_B$ at O1 and O2, as well as reduced amplitudes following $S1_B$ as compared to $S1_A$ for 30/70% S2s at O2 and for 10/90% S2s at O1 and O2, all ps < .05. There were no differences between $S1_M$ and the mean of $S1_A$ and $S1_B$ conditions at morph level 50/50% for O1 and O2 electrodes, all ps > .20.

Additionally, we found a main effect of S1 condition, $F(4,84) = 12.51$, $p < .001$, $\varepsilon_{HF} = .49$, $\eta^2_p = .43$. S2 faces following Fourier face S1s showed the smallest P1 amplitudes,[4] while those following identity C S1s showed the highest amplitudes. The factor hemisphere did not show any effects, all ps > .20.
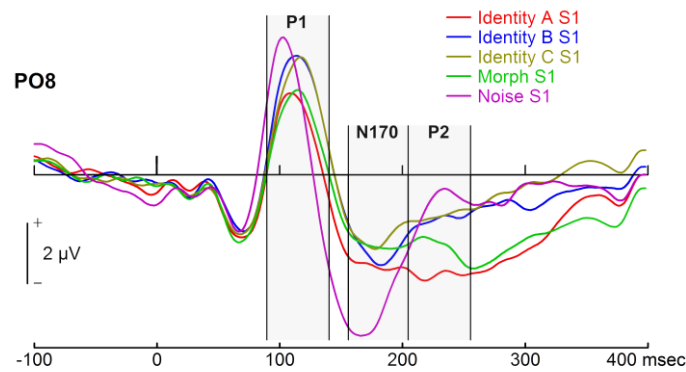
Figure 4. Sample ERPs for a 90/10% S2 following identity A, B, C, and Morph, as well as Noise S1s at PO8. The light grey areas show the analysed time windows.

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[4] The P1 peak was earlier for S2s following $S1_N$ as compared to the other S1 conditions, and therefore not centred to the time window used. As the time window captured only the late part of P1 here, this measurement was biased and therefore not interpreted.
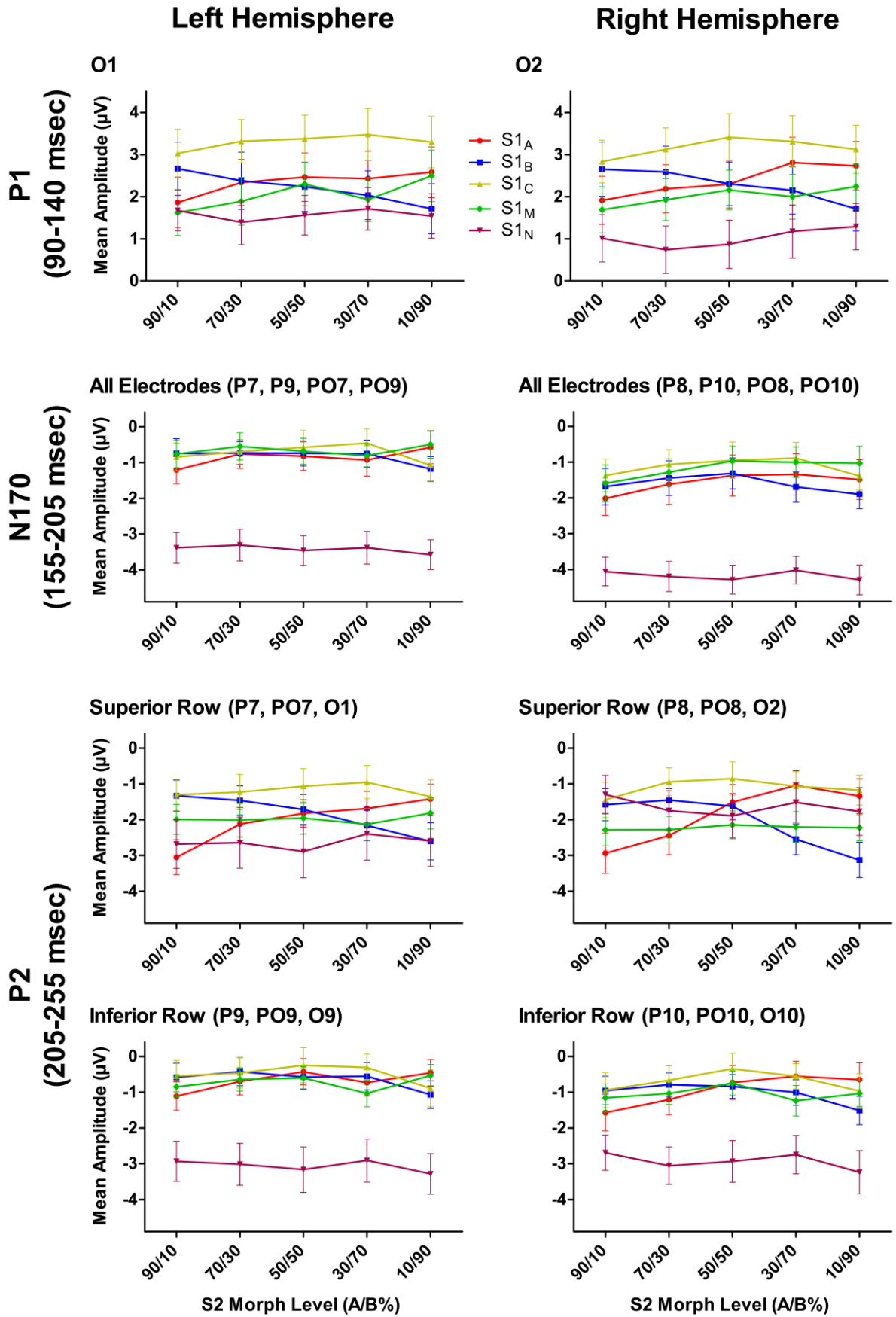
Figure 5. P1, N170, and P2 mean amplitudes at each S2 morph level following identity A, B, C, and morph, as well as noise S1s for representative left and right hemispheric electrode clusters. Error bars show ±1 standard error of the mean (SEM).

For the N170 (see Fig. 5, middle panels), we observed a prominent categorical adaptation effect, with amplitude reductions for S2s following face S1s ($S1_A$, $S1_B$, $S1_C$, and $S1_M$) as compared to $S1_N$ [main effect of S1 condition: $F(4,84) = 36.63$, $p < .001$, $\varepsilon_{HF} = .46$, $\eta^2_p = .64$]. This effect was further qualified by an interaction of electrode, S1 condition, and S2 morph level, $F(48,1008) = 2.96$, $p < .001$, $\eta^2_p = .12$, revealing identity-specific amplitude reductions at electrodes of the superior row. Post-hoc t-tests showed reduced N170 amplitudes for 90/10% S2s following $S1_A$ as compared to $S1_B$ at P7 and PO7, and reduced amplitudes following $S1_B$ as compared to $S1_A$ for 30/70% S2s at P8 and for 10/90% S2s at P7 and PO7, all $ps < .05$. We also found differences between $S1_M$ and the mean of $S1_A$ and $S1_B$ at morph level 50/50% for P7 and P8, $t(21) = 2.39$, $p = .026$, $d = .28$, and $t(21) = 2.25$, $p = .035$, $d = .15$.

P2 data (see Fig. 5, lower two panels) exhibited very prominent identity-specific amplitude reductions [interaction of S1 condition and S2 morph level: $F(16,336) = 5.18$, $p < .001$, $\varepsilon_{HF} = .69$, $\eta^2_p = .20$], further qualified by interactions with the factors row and electrode [interaction of row, S1 condition, and S2 morph level: $F(16,336] = 4.79$, $p < .001$, $\eta^2_p = .19$, and interaction of electrode, S1 condition, and S2 morph level, $F(32,672) = 3.06$, $p < .001$, $\eta^2_p = .13$]. Post-hoc tests revealed identity-specific reductions of P2 amplitudes at electrodes of the superior row, pronounced at electrodes farther from the midline. Additionally, this effect was stronger over the right hemisphere, and could also be observed at the lower row electrodes P10 and PO10. In detail, we observed reduced P2 amplitudes following $S1_A$ as compared to $S1_B$ for 90/10% for the superior row of electrodes of both hemispheres and for 70/30% S2s (at PO7, P8, and PO8), and reduced amplitudes following $S1_B$ as compared to $S1_A$ for 30/70% S2s for both the superior and inferior rows of electrodes of the right hemisphere except for electrode O10, and for 10/90% S2s for the superior electrodes of both hemispheres as well as for the inferior electrodes of the right hemisphere except for electrode O10, all $ps < .05$. Identity-specific adaptation effects, as described by the difference between $S1_M$ and the mean of $S1_A$ and $S1_B$ at morph level 50/50%, were observed at P8 and PO8, $t(21) = -2.29$, $p = .033$, $d = -.35$, and $t(21) = -3.80$, $p = .001$, $d = -.44$, respectively. We also found categorical adaptation of the P2 response, which was similar to that of N170, though smaller in magnitude, and restricted to inferior electrodes [interaction of row and S1 condition: $F(4,84) = 25.51$, $p = .001$, $\varepsilon_{HF} = .71$, $\eta^2_p = .55$].[5]

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[5] Note that we also applied the same analyses as for P2 to the N250r mean amplitudes in a time window of 230-280 msec. The patterns were identical [except that N250r showed an additional difference between $S1_M$ and the mean of $S1_A$ and $S1_B$ at morph level 50/50% for O2 electrode, $t(21) = -2.49$, $p = .021$, $d = -0.24$], suggesting that both components essentially capture the same effect in the present experiment. Accordingly, we decided to report only the results for the earlier of both components - the P2. Nevertheless, we will refer to the N250r in the Discussion section.

To assess the topography of the relevant effects, current source density (CSD) maps (see Fig. 6) were obtained using spherical spline interpolation (Perrin et al., 1989). The difference waves for identity-specific PR effects (calculated by the subtraction of the ERP curves of the $S1_B$ condition from those of $S1_A$ condition) displayed a clear occipito-parieto-temporal distribution of gradient changes in the P2 time window. Just like the behavioural PR effect, the magnitude of the ERP PR effect also decreased with increasing S2 ambiguity, with no observable difference between $S1_A$ and $S1_B$ conditions for the ambiguous, 50/50% S2s (see Fig. 6 first row, middle map). Although the difference between $S1_A$ and $S1_B$ conditions does not show a clear lateralization for the unambiguous S2 stimuli (i.e., 90/10% and 10/90%) the effect seems to be lateralized to the right hemisphere for the more ambiguous 70/30% and 30/70% morph levels. This is indicated by a marginally significant interaction of hemisphere, electrode, S1 condition and S2 morph level, $F(32,672) = 1.39$, $p = .077$, $\eta^2_p = .06$, in the main ANOVA for the P2 mean amplitudes. Similar to the PR effect, the identity-specific adaptation effect (calculated as the subtraction of the ERP curve of the $S1_M$ condition minus that of the mean of $S1_A$ and $S1_B$ conditions) was visible as high voltage gradients at occipito-parieto-temporal sites only over the right hemisphere and only for the ambiguous, 50/50% S2s (see Fig. 6 second row, middle map). In contrast to both PR and identity-specific adaptation effects, category-specific adaptation (calculated as the subtraction of the ERP curve of the $S1_N$ condition minus that of the mean of all other S1 conditions; see Fig. 6 third row) showed somewhat different and more widespread occipito-parieto-temporal topographies. This effect was visible over all S2 morph levels, with somewhat stronger gradients over the right than over the left hemisphere. The different distribution of CSD maps in the three comparisons suggests a different cortical source for category-specific adaptation as compared to the identity-specific PR and AE. This analysis supports further the conclusions of our conventional ERP analyses, that revealed category-specific adaptation effects only over electrodes of the inferior occipito-temporal areas and showing both PR and identity-specific adaptation over more superior, parieto-occipital electrode sites.

Correlation analyses did not show any relationship between behavioural and ERP PR measures for any analysed time window, or for behavioural and ERP adaptation measures for the P1 and N170 components, all ps > .10. By contrast, we found a positive correlation between behavioural adaptation and the ERP adaptation effect, as calculated by $S1_M$ minus the mean of $S1_A$ and $S1_B$, for the superior electrodes of the right hemisphere for the P2

component, $r(20) = .663$, $p = .001$.[6] At the same time, there was no significant correlation of this ERP effect with behavioural PR, all ps > .1. This analysis confirmed that the identity-specific adaptation effects are related to the signal reduction at a relatively later time window at around 230 msec, located over the right occipito-temporal electrodes.
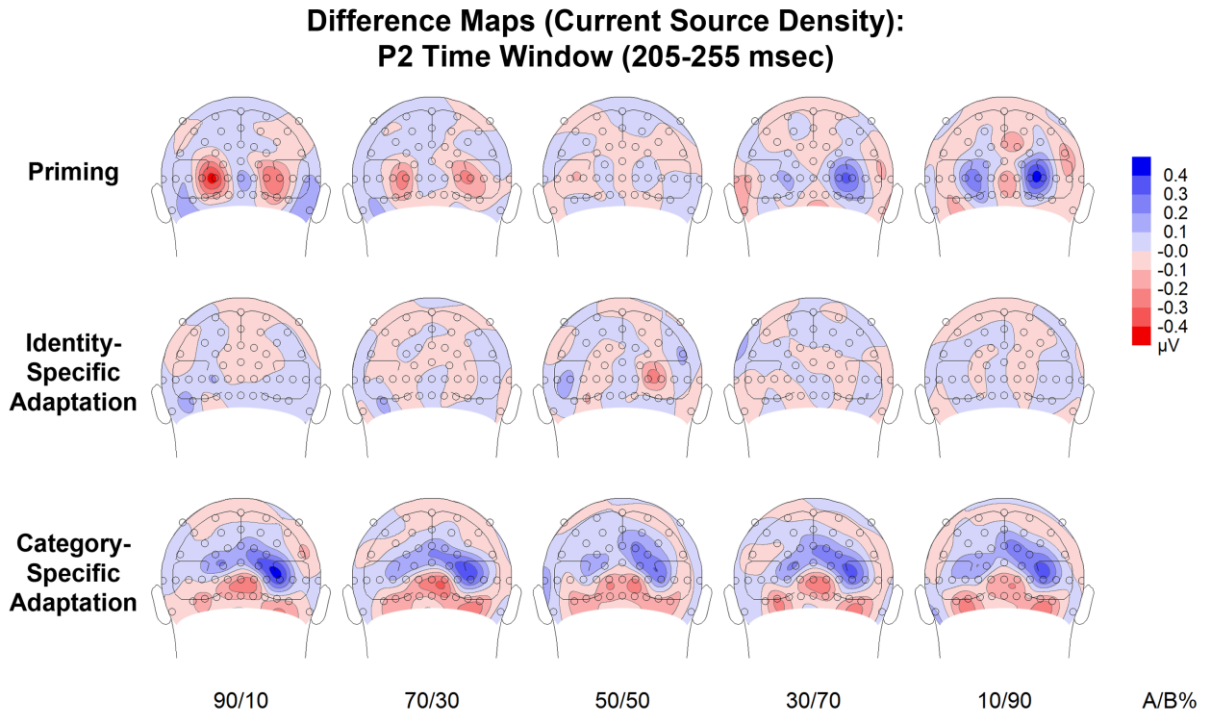
Figure 6. Topographical CSD maps for PR (difference between $S1_A$ and $S1_B$ conditions), identity-specific adaptation (difference between $S1_M$ and the mean of $S1_A$ and $S1_B$ conditions), and category-specific adaptation (difference between $S1_N$ and the mean of all other S1 conditions) at each S2 morph level for the P2 time window (205-255 msec). All maps were created using spherical spline interpolation and show a 110 degrees equidistant projection from a back view perspective (including electrode positions).

Unexpectedly, we also found a positive correlation between our behavioural adaptation and ERP PR measures for N170 over the left hemisphere, $r(20) = .670$, $p = .001$, and for P2 at the superior and inferior electrode rows over the left hemisphere, $r(20) = .568$, $p = .006$, and $r(20) = .489$, $p = .021$, respectively.[7] This increase of behavioural adaptation with increasing ERP PR was not an arbitrary effect, due to the high noise level of the accuracy data, because correlating the absolute difference in accuracy data between $S1_A$ and $S1_B$ conditions with the

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[6] For N250r, there was also a positive correlation of behavioural adaptation and the identity-specific ERP adaptation effect ($S1_M$ minus mean of $S1_A$ and $S1_B$) for the superior electrodes of the right hemisphere for the P2 component, $r(20) = .458$, $p = .032$. Additionally, we observed a negative correlation between both effects for the inferior electrode cluster in this time window, $r(20) = -.656$, $p = .001$, supporting a difference between the sources of signals recorded over superior and inferior electrode clusters.

[7] For N250r, this positive correlation between our behavioural adaptation and ERP PR measure was also observed for the superior electrodes over the left hemisphere, $r(20) = .470$, $p = .027$.

corresponding ERP differences at single morph levels did not lead to any significant correlation.

Discussion

In Experiment 2, we investigated the electrophysiological correlates of repetition PR and AEs for face identity within the same paradigm. As in Experiment 1, the behavioural data revealed a strong adaptation effect at the ambiguous S2 morph level, following presentation of identity A S1s, ambiguous S2s were more often perceived as identity B, and vice versa. Although there was a small PR effect in classification performance, the response time effect that was observed in Experiment 1 did not reach significance in Experiment 2; we only observed a small numerical effect in this direction.

In ERPs, we found a strong categorical adaptation effect around 150-200 msec post-stimulus, corresponding to the N170 ERP component (Kloth et al., 2010; Kovács et al., 2006; Zimmer and Kovács, 2011b): the ERP amplitudes were reduced for S2s of each tested morph level following face S1s as compared to noise S1s. We also found amplitude reductions for S2 faces following identity-congruent S1s as compared to other S1 stimuli that started already at around 90 msec after stimulus onset. These effects were weaker in the N170 time range and were the most pronounced 200 msec after stimulus onset. The late effect is in line with previous ERP studies of PR that typically report effects in the time range of 200-300 msec, i.e. the N250r (Schweinberger et al., 2002b, 2004). We will extend on this point in the General Discussion part.

Identity-specific adaptation effects, expressed as a difference between $S1_M$ and the mean of $S1_A$ and $S1_B$, were observed for the superior electrode row over the right hemisphere. Our correlation analyses revealed that from around 200 msec on, these differences are related to the behavioural AEs, in that larger differences in the ERPs went with larger behavioural effects. Our correlation analyses also revealed a somewhat unexpected relationship between ERP PR and behavioural adaptation. As, to our knowledge, there is no study reporting a similar correlation, the interpretation of this finding remains somewhat speculative at present. It is possible that if the ERP effects are particularly specific for repetition of the original identities, adaptation of the neuronal populations encoding these identities lead to higher behavioural aftereffects. However, further research will be necessary to clarify this issue.

General Discussion

The present study revealed that short-term repetition PR and AEs for face identity could be induced within a single paradigm using the same timing parameters and task. In performance data, repetition PR was observed as faster response times for identity-congruent S1-S2 pairs. We also found clear identity-specific and contrastive aftereffects for ambiguous S2 identities, which are in line with the notion of categorical processing of familiar face identity (Beale and Keil, 1995; Rotshtein et al., 2005). A recent study by Hills et al. (2010) reported a series of experiments on the influence of different adaptor types on face identity aftereffects. These results support the idea that such aftereffects involve a shift of the category boundary along a morphing continuum, induced by adaptation to one of the endpoints of the continuum. It needs to be noted that the present findings are broadly consistent with, but should not be taken as a proof for, categorical perception of facial identity. This is because the hallmark of categorical perception is the demonstration of better discrimination between two stimuli that straddle a category boundary, compared with two stimuli of comparable physical dissimilarity that fall within the same category. In the context of face perception, such a pattern of results has been consistently obtained in several studies (Beale and Keil, 1995; Campanella et al., 2000; Rotshtein et al., 2005; Young et al., 1997).

Although the S1 conditions (i.e., identity A, B, C, 50/50% A/B or noise) were blocked in our experiments, there were 14 different identities tested in each block, along their respective morphing continuum. Therefore, we cannot exclude the possibility that adaptation effects for certain identities interfered with each other. However, the observed strong AE suggests that any such interference, if present at all, must have been small and unsystematic. This would be in line with the idea that there are specific representations of each unique identity in the human brain (sometimes termed "face recognition units", Burton et al., 1990; for a more current account of mental representations of familiar faces, see Burton et al., 2011). Note, however, that there must be a mechanism of updating such identity-specific representations by current perceptual encounters (Bruce, 1994), implying that these representations can be adapted selectively. A view of adaptation in which contrastive aftereffects reflect the updating of long-term representations of specific faces may be contrasted with a traditional "perceptual" view of adaptation (e.g., Webster and MacLin, 1999). The representational view of face adaptation receives support by demonstrations of long-term effects of adaptation across days or even weeks (e.g., Carbon and Ditye, 2011; Carbon and Ditye, 2012; Carbon et al., 2007). Determining whether perceptual or memory processes drive the observed AEs is clearly beyond the scope of this paper, but attempts to specify potential mechanisms

underlying repetition-related effects are currently being made (e.g., Huber, 2008; Rieth and Huber, 2010). The results of other studies suggest that face identity is coded relative to a perceptual norm (Leopold et al., 2001; Rhodes and Jeffery, 2006). Following this logic, the lack of interference of the different adaptor identities could have been due to the fact that AE induced by relatively short adaptation periods are more transient in nature (Rhodes et al., 2007). Since our paradigm did not test whether the AE induced by an S1 would survive for longer than the presentation of the following S2, both perceptual and representational explanations of the present AE remain possible in principle.

It is important to note that, in the present study, repetition PR and AEs were never observed simultaneously for the same S2 stimuli. Accordingly, the two phenomena appear to be based on different mechanisms. There are different possibilities for how such mechanisms could be implemented at the neural level (Grill-Spector et al., 2006). In a recent study Hills et al. (2010) suggest that AEs and PR might occur at the same loci in the face recognition system. They based this conclusion on the fact that they found cross-modal aftereffects for visual and acoustic adaptors, analogous to similar effects observed for PR (Föcker et al., 2011; Schweinberger et al., 1997). However, in the absence of any available neurophysiological evidence, such a suggestion remains difficult to test.

Our analyses of ERPs revealed clear categorical adaptation effects when comparing ERPs elicited by S2 faces following face S1s and noise S1s. Similar to other findings of categorical adaptation (Amihai et al., 2011; Kloth et al., 2010; Kovács et al., 2006), these effects were pronounced in the N170 time range. Moreover, we observed the first markers of categorical adaptation already at around 90-140 msec (for related similar findings, cf. Schweinberger et al., 2007), and we observed strong effects for the later components, P2 and N250r. Interestingly, these later effects were only found for more inferior occipito-temporal electrodes over both hemispheres. In a recent study on face distortion aftereffects, Zimmer and Kovács (2011b) also found categorical adaptation for P1 and N170 ERP components, as well as for later time-periods. The authors argued that this effect might be related to the desensitization of a general face-processing mechanism by a repeated exposure to face stimuli as compared to the Fourier phase randomized "baseline".

Alongside this unspecific, general face adaptation effect, we also found a neural correlate of the identity-specific adaptation-related aftereffect on the ERP at around 200-280 msec post-stimulus onset. For the ambiguous S2 stimuli, the larger the difference of this ERP component between $S1_M$ and the mean of $S1_A$ and $S1_B$ was, the bigger the behavioural aftereffect was. Although we are not aware of any study reporting a similar effect, there are

recent findings by Burkhardt et al. (2010) showing a relation between ERP signals at around 190-260 msec and objective, as well as subjective face distortion effects. Note that face distortion aftereffects are thought to be related to face identity processing (e.g., Carbon et al., 2007) as well. Altogether, our results suggest that ERPs at around 200-300 msec, recorded over superior occipito-temporal sites, represent face identity processing, comparable to findings in studies of PR (Bindemann et al., 2008; Schweinberger et al., 2002b, 2004).

Similar to the findings of identity-specific adaptation, the identity-specific ERP PR effect was also reflected by modulations at time windows corresponding to the P1 and N170 components and was the most pronounced at around 200 msec over superior occipito-temporal recording sites. Previous studies have reported similar, but small face repetition effects in the P1 and N170 time windows already (Campanella et al., 2000; Guillaume & Tiberghien, 2001). In addition, Caharel et al. (2002) found familiarity related modulations of the N170 component and suggested that the processed information at this time window is sufficient for the categorization of faces on an individual level (see also Caharel et al., 2006). This idea seems to be also supported by other reports of neural correlates of self PR (Jemel et al., 2005), and a study by Kloth et al. (2006), who found increments of the electromagnetic M170 component for test faces primed by personally familiar faces as compared to famous or unfamiliar faces.

Nevertheless, the observation of very early identity-specific ERP modulations seems at odds with a large body of results suggesting that neither PR (e.g., Bindemann et al., 2008; Schweinberger et al., 2002b), nor face familiarity per se (Eimer, 2000) is able to modulate the N170 component. Such studies suggest that identity processing begins later than the time-window of N170. Alternatively, the identity-specific modulation of N170 could also reflect the structural encoding of the faces (Sagiv & Bentin, 2001) that might have been different for the S2 faces following (highly) similar S1 faces as compared to more dissimilar S1 faces in our study. At present, the most likely account for the early ERP correlates of PR in the P1 and N170 time-windows may be that these components reflect relatively low-level visual similarities of S1 and S2. This remains a possibility because the S1 stimuli of our study were always the original faces that were also used to create the S2 morph continua. However, the fact that S1 and S2 were always different in size reduces the likelihood of any effect of (pixelwise) similarity (for a review on the effect of similarity on the electrophysiology of face processing, see Rossion and Jacques, 2008) and excludes a retinotopic locus for this effect (for similar arguments, see Bindemann et al., 2008). Importantly, the most pronounced identity-specific ERP effects were observed from around 200 msec onwards. This is in line

with findings that suggest later components, such as the N250r, as the primary ERP reflections of identity processing (Bindemann et al., 2008; Gosling and Eimer, 2011; Schweinberger et al., 2002b, 2004).

Interestingly, the PR-related identity-specific ERP attenuations were observed in the absence of a clear behavioural PR in RTs in Experiment 2, although RTs are thought of as a strong marker of PR (see, e.g., Bindemann et al., 2008; Ellis et al., 1987; Schweinberger et al., 2002a, 2002b). In some contexts ERPs have been suggested to be more sensitive than behavioural measures (see, e.g., Guillaume et al., 2009 for the case of repetition PR, or Carbon et al., 2005 for the case of face illusions). Nevertheless, it may be noted that there was a significant, though small, PR effect in Experiment 2 in accuracy data, and a numerical PR effect in RTs as well. Therefore, the ERP PR effects could be related to behavioural PR as observed in both experiments: Both effects (1) depend on identity congruence of S1 and S2, (2) are the most pronounced for unambiguous S2s, and (3) are not present for ambiguous S2 stimuli. The PR effects reported in earlier studies (Bindemann et al., 2008; Schweinberger et al., 2002b, 2004) might reflect the extremes of the effect that we observed, as in these cases, N250r modulations were typically induced by identity repetition.

The most intriguing difference between PR and AEs in this study is the fact, that they are never observed simultaneously on the same S2s. Analyses of electrophysiological, as well as behavioural data revealed that PR was present at the unambiguous morph levels, whereas AEs were only observed at the ambiguous morph levels. This confirms the notion of PR and AE as different phenomena that could be implemented by the same neuron populations. This idea is also supported by the presence of a superior occipito-temporal right-hemispheric electrode cluster showing identity-specific adaptation as well as PR effects at around 200-300 msec post-stimulus onset. Since categorical adaptation is also observed in this time window, but over a different and more inferior scalp location, it is possible that identity-specific processing runs in parallel to general object categorization mechanisms.

But what determines whether face PR or AEs are induced in a stimulus repetition paradigm? A recent study on object perception (Daelli et al., 2010) reported adaptation effects for short (50 msec) and PR-like effects for longer (3100 msec) S1-S2-intervals. In our study PR and AEs were both induced under the same timing parameters. At the very least, this suggests that timing is not the only factor that determines the balance between PR and adaptation. Our results suggest that it is rather S2 ambiguity and/or the similarity of S1 and S2 that determines whether PR or AEs are induced.

S1-S2 similarity was often investigated in previous PR paradigms and was reported to be insensitive to certain stimulus changes (e.g., stretching the image; see Bindemann et al., 2008) while, to our knowledge, similar data regarding AEs is not available as yet. Other stimulus changes related to the similarity of S1 and S2 (e.g., using different images of the same persons as S1 and S2) are known to reduce both PR (Bindemann et al., 2008; Ellis et al., 1987) and AEs (Hills et al., 2010). Nevertheless, the role of similarity in PR and AEs might be different. While in PR studies, similarity is typically considered as the direct difference between S1 and S2 (for example same image vs. different image of a person), in AE studies, similarity is determined by two factors. On the one hand, the adaptor images and the images that were used to create the S2 continuum can be same or different images of a person, leading to a different similarity of S1 and S2, and on the other hand, the target images are typically morphs between two identities, also changing S1-S2 similarity (e.g., Hills et al., 2010). Using morphing as the only manipulation of the stimuli, our study suggests a potential role of S1-S2 similarity and/or S2 ambiguity in determining whether PR or AE is observed. Unfortunately, disentangling the influence of S2 ambiguity from that of S1-S2 similarity is not straightforward, and will require further research.

In conclusion, the present study is the first to simultaneously assess repetition PR and AEs for face identity as well as their electrophysiological correlates within a single paradigm. Our results show that face PR and aftereffects are both present in the same paradigm, but are never observed together for the same test stimuli. This indicates that exclusive mechanisms might underlie both PR and aftereffects. We also suggest that object-category and identity processing might run in parallel during face processing. Finally, our data also implicate that S2 ambiguity and/or the similarity of S1 and S2 are the necessary factors that determine whether PR or adaptation occur. Future research will be necessary to conclude between these possibilities.

Acknowledgements

Reference list

Amihai I, Deouell LY, and Bentin S. Neural adaptation is related to face repetition irrespective of identity: A reappraisal of the N170 effect. *Experimental Brain Research*, 209(2): 193-204, 2011.

Anstis S, Verstraten FAJ, and Mather G. The motion aftereffect. *Trends in Cognitive Sciences*, 2(3): 111-117, 1998.

Beale JM and Keil FC. Categorical effects in the perception of faces. *Cognition*, 57(3): 217-239, 1995.

Bindemann M, Burton AM, Leuthold H, and Schweinberger SR. Brain potential correlates of face recognition: Geometric distortions and the N250r brain response to stimulus repetitions. *Psychophysiology*, 45(4): 535-544, 2008.

Brainard DH. The psychophysics toolbox. *Spatial Vision*, 10(4): 433-436, 1997.

Brooks BE, Rosielle LJ, and Cooper EE. The priming of face recognition after metric transformations. *Perception*, 3(3): 297-313, 2002.

Bruce V. Stability from variation - The case of face recognition. *Quarterly Journal of Experimental Psychology, 47*(1), 5-28, 1994.

Burkhardt A, Blaha LM, Jurs BS, Rhodes G, Jeffery L, Wyatte D, DeLong J, and Busey T. Adaptation modulates the electrophysiological substrates of perceived facial distortion: Support for opponent coding. *Neuropsychologia*, 48(13): 3743-3756, 2010.

Burton AM, Bruce V, and Johnston RA. Understanding face recognition with an interactive activation model. *British Journal of Psychology*, 81: 361-380, 1990.

Burton AM, Jenkins R, and Schweinberger SR. Mental representations of familiar faces. *British Journal of Psychology*, 102: 943-958, 2011.

Caharel S, Fiori N, Bernard C, Lalonde R, and Rebai M. The effects of inversion and eye displacements of familiar and unknown faces on early and late-stage ERPs. *International Journal of Psychophysiology*, 62(1): 141-151, 2006.

Caharel S, Poiroux S, Bernard C, Thibaut F, Lalonde R, and Rebai M. ERPs associated with familiarity and degree of familiarity during face recognition. *International Journal of Neuroscience*, 112(12): 1499-1512, 2002.

Campanella S, Hanoteau C, Depy D, Rossion B, Bruyer R, Crommelinck M, and Guerit JM. Right N170 modulation in a face discrimination task: An account for categorical perception of familiar faces. *Psychophysiology*, 37(6): 796-806, 2000.

Carbon CC and Dikye T. Face adaptation effects show strong and long-lasting transfer from lab to more ecological contexts. *Frontiers in Perception Science*, 3: 1-6, 2012. doi: 10.3389/fpsyg.2012.00003

Carbon CC and Ditye T. Sustained effects of adaptation on the perception of familiar faces. *Journal of Experimental Psychology-Human Perception and Performance, 37*(3), 615-625, 2011.

Carbon CC, Schweinberger SR, Kaufmann JM, and Leder H. The Thatcher illusion seen by the brain: An event-related brain potentials study. *Cognitive Brain Research, 24*(3), 544-555, 2005.

Carbon CC, Strobach T, Langton SRH, Harsanyi G, Leder H, and Kovács G. Adaptation effects of highly familiar faces: Immediate and long lasting. *Memory & Cognition*, 35(8): 1966-1976, 2007.

Cave CB. Very long-lasting priming in picture naming. *Psychological Science*, 8(4): 322-325, 1997.

Clifford CWG. Perceptual adaptation: Motion parallels orientation. *Trends in Cognitive Sciences*, 6(3): 136-143, 2002.

Cziraki C, Greenlee MW, and Kovács G. Neural correlates of high-level adaptation-related aftereffects. *Journal of Neurophysiology*, 103(3): 1410-1417, 2010.

Daelli V, van Rijsbergen NJ, and Treves A. How recent experience affects the perception of ambiguous objects. *Brain Research*, 1322: 81-91, 2010.

Davies-Thompson J, Gouws A, and Andrews TJ. An image-dependent representation of familiar and unfamiliar faces in the human ventral stream. *Neuropsychologia*, 47(6): 1627-1635, 2009.

Durgin FH and Proffitt DR. Visual learning in the perception of texture: Simple and contingent aftereffects of texture density. *Spatial Vision*, 9(4): 423-474, 1996.

Eimer M. Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, 111(4): 694-705, 2000.

Ellis AW, Young AW, Flude BM, and Hay DC. Repetition priming of face recognition. *Quarterly Journal of Experimental Psychology*, 39(2): 193-210, 1987.

Föcker J, Hölig C, Best A, and Röder B. Crossmodal interaction of facial and vocal person identity information: An event-related potential study. *Brain Research*, 1385: 229-245, 2011.

Frisby J. *Seeing: Illusion, Brain and Mind.* Oxford: Oxford University Press, 1979.

Gauthier I, Tarr MJ, Moylan J, Skudlarski P, Gore JC, and Anderson AW. The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, 12(3): 495-504, 2000.

Gosling A and Eimer M. An event-related brain potential study of explicit face recognition. *Neuropsychologia*, 49(9): 2736-2745, 2011.

Grill-Spector K, Henson R, and Martin A. Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, 10(1): 14-23, 2006.

Guillaume C, Guillery-Girard B, Chaby L, Lebreton K, Hugueville L, Eustache F, and Fiori N. The time course of repetition effects for familiar faces and objects: An ERP study. *Brain Research*, 1248: 149-161, 2009.

Guillaume F and Tiberghien G. An event-related potential study of contextual modifications in a face recognition task. *Neuroreport*, 12(6): 1209-1216, 2001.

Henson RNA. Neuroimaging studies of priming. *Progress in Neurobiology*, 70(1): 53-81, 2003.

Hills PJ, Elward RL, and Lewis MB. Cross-modal face identity aftereffects and their relation to priming. *Journal of Experimental Psychology-Human Perception and Performance*, 36(4): 876-891, 2010.

Huber DE. Immediate priming and cognitive aftereffects. *Journal of Experimental Psychology-General, 137*(2), 324-347, 2008.

Huynh H and Feldt LS. Estimation of the box correction for degrees of freedom from sample data in randomized block and split-plot designs. *Journal of Educational Statistics*, 1(1): 69-82, 1976.

Jemel B, Pisani M, Rousselle L, Crommelinck M, and Bruyer R. Exploring the functional architecture of person recognition system with event-related potentials in a within- and cross-domain self-priming of faces. *Neuropsychologia*, 43(14): 2024-2040, 2005.

Jenkins R, Beaver JD, and Calder AJ. I thought you were looking at me - Direction-specific aftereffects in gaze perception. *Psychological Science*, 17(6): 506-513, 2006.

Jiang F, Blanz V, and O'Toole AJ. Probing the visual representation of faces with adaptation - A view from the other side of the mean. *Psychological Science*, 17(6): 493-500, 2006.

Kanwisher N, McDermott J, and Chun MM. The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17(11): 4302-4311, 1997.

Kloth N, Dobel C, Schweinberger SR, Zwitserlood P, Bolte J, and Junghofer M. Effects of personal familiarity on early neuromagnetic correlates of face perception. *European Journal of Neuroscience*, 24(11): 3317-3321, 2006.

Kloth N and Schweinberger SR. The temporal decay of eye gaze adaptation effects. *Journal of Vision*, 8(11): 1-11, 2008.

Kloth N, Schweinberger SR, and Kovács G. Neural correlates of generic versus gender-specific face adaptation. *Journal of Cognitive Neuroscience*, 22(10): 2345-2356, 2010.

Kovács G, Cziraki C, Vidnyanszky Z, Schweinberger SR, and Greenlee MW. Position-specific and position-invariant face aftereffects reflect the adaptation of different cortical areas. *Neuroimage*, 43(1): 156-164, 2008.

Kovács G, Zimmer M, Banko E, Harza I, Antal A, and Vidnyanszky Z. Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cerebral Cortex, 16*(5): 742-753, 2006.

Kovács G, Zimmer M, Harza I, and Vidnyanszky Z. Adaptation duration affects the spatial selectivity of facial aftereffects. *Vision Research*, 47(25): 3141-3149, 2007.

Krekelberg B, Boynton GM, and van Wezel RJA. Adaptation: From single cells to BOLD signals. *Trends in Neurosciences*, 29(5): 250-256, 2006.

Leopold DA, O'Toole AJ, Vetter T, and Blanz V. Prototype-referenced shape encoding revealed by high-level after effects. *Nature Neuroscience*, 4(1): 89-94, 2001.

Leopold DA, Rhodes G, Müller, KM, and Jeffery L. The dynamics of visual adaptation to faces. *Proceedings of the Royal Society B-Biological Sciences*, 272(1566): 897-904, 2005.

Näsänen R. Spatial frequency bandwidth used in the recognition of facial images. *Vision Research*, 39(23): 3824-3833, 1999.

Perrin F, Pernier J, Bertrand O, and Echallier JF. Spherical splines for scalp potential and current-density mapping. *Electroencephalography and Clinical Neurophysiology*, 72(2): 184-187, 1989.

Rhodes G and Jeffery L. Adaptive norm-based coding of facial identity. *Vision Research*, 46(18): 2977-2987, 2006.

Rhodes G, Jeffery L, Clifford CWG, and Leopold DA. The timecourse of higher-level face aftereffects. *Vision Research*, 47(17): 2291-2296, 2007.

Rhodes G, Jeffery L, Watson TL, Clifford CWG, and Nakayama K. Fitting the mind to the world: Face adaptation and attractiveness aftereffects. *Psychological Science*, 14(6): 558-566, 2003.

Rhodes G, Jeffery L, Watson TL, Jaquet E, Winkler C, and Clifford CWG. Orientation-contingent face aftereffects and implications for face-coding mechanisms. *Current Biology*, 14(23): 2119-2123, 2004.

Rieth CA and Huber DE. Priming and Habituation for Faces: Individual Differences and Inversion Effects. *Journal of Experimental Psychology-Human Perception and Performance, 36*(3), 596-618, 2010.

Rossion B and Jacques C. Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage*, 39(4): 1959-1979, 2008.

Rotshtein P, Henson RNA, Treves A, Driver J, and Dolan RJ. Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience*, 8(1): 107-113, 2005.

Sagiv N and Bentin S. Structural encoding of human and schematic faces: Holistic and part-based processes. *Journal of Cognitive Neuroscience*, 13(7): 937-951, 2001.

Schweinberger SR, Herholz A, and Stief V. Auditory long-term memory: Repetition priming of voice recognition. *Quarterly Journal of Experimental Psychology*, 50(3): 498-517, 1997.

Schweinberger SR, Huddy V, and Burton AM. N250r: A face-selective brain response to stimulus repetitions. *Neuroreport*, 15(9): 1501-1505, 2004.

Schweinberger SR, Kloth N, and Jenkins R. Are you looking at me? Neural correlates of gaze adaptation. *Neuroreport*, 18(7): 693-696, 2007.

Schweinberger SR, Pickering EC, Burton AM, and Kaufmann JM. Human brain potential correlates of repetition priming in face and name recognition. *Neuropsychologia*, 40(12): 2057-2073, 2002a.

Schweinberger SR, Pickering EC, Jentzsch I, Burton AM, and Kaufmann JM. Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. *Cognitive Brain Research*, 14(3): 398-409, 2002b.

Schweinberger SR, Zäske R, Walther C, Golle J, Kovács G, and Wiese H. Young without plastic surgery: Perceptual adaptation to the age of female and male faces. *Vision Research*, 50(23): 2570-2576, 2010.

Webster MA, Kaping D, Mizokami Y, and Duhamel P. Adaptation to natural facial categories. *Nature*, 428(6982): 557-561, 2004.

Webster MA and MacLin OH. Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review*, 6(4): 647-653, 1999.

Yamashita JA, Hardy JL, De Valois KK, and Webster MA. Stimulus selectivity of figural aftereffects for faces. *Journal of Experimental Psychology-Human Perception and Performance*, 31(3): 420-437, 2005.

Young AW, Rowland D, Calder AJ, Etcoff NL, Seth A, and Perrett DI. Facial expression megamix: Tests of dimensional and category accounts of emotion recognition. *Cognition, 63*(3), 271-313, 1997.

Zäske R, Schweinberger SR, Kaufmann JM, and Kawahara H. In the ear of the beholder: Neural correlates of adaptation to voice gender. *European Journal of Neuroscience*, 30(3): 527-534, 2009.

Zhao L and Chubb C. The size-tuning of the face-distortion after-effect. *Vision Research*, 41(23): 2979-2994, 2001.

Zimmer M and Kovács G. Position specificity of adaptation-related face aftereffects. *Philosophical Transactions of the Royal Society B-Biological Sciences, 366*(1564), 586-595, 2011a.

Zimmer M and Kovács G. Electrophysiological correlates of face distortion after-effects. *Quarterly Journal of Experimental Psychology*, 64(3): 533-544, 2011b.

3.2 Adaptor identity modulates adaptation effects in familiar face identification and their neural correlates

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Abstract

Adaptation-related aftereffects (AEs) show how face perception can be altered by recent perceptual experiences. Along with contrastive behavioural biases, modulations of the early event-related potentials (ERPs) were typically reported on categorical levels. Nevertheless, the role of the adaptor stimulus per se for face identity-specific AEs is not completely understood and was therefore investigated in the present study. Participants were adapted to faces (S1s) varying systematically on a morphing continuum between pairs of famous identities (identities A and B), or to Fourier phase randomized faces, and had to match the subsequently presented ambiguous faces (S2s; 50/50% identity A/B) to one of the respective original faces. We found that S1s identical with or near to the original identities led to strong contrastive biases with more identity B responses following A adaptation and vice versa. In addition, the closer S1s were to the 50/50% S2 on the morphing continuum, the smaller the magnitude of the AE was. The relation between S1s and AE was, however, not linear. Additionally, stronger AEs were accompanied by faster reaction times. Analyses of the simultaneously recorded ERPs revealed categorical adaptation effects starting at 100 ms post-stimulus onset, that were most pronounced at around 125 - 240 ms for occipito-temporal sites over both hemispheres. S1-specific amplitude modulations were found at around 300 - 400 ms. Response-specific analyses of ERPs showed reduced voltages starting at around 125 ms when the S1 biased perception in a contrastive way as compared to when it did not. Our results suggest that face identity AEs do not only depend on the physical similarity of S1 and S2, but also on the ambiguity of S1. Furthermore, short-term plasticity of face identity processing might work in parallel to object-category processing, and is reflected in the first 400 ms of the ERP.

Keywords: face perception, adaptation, identity, ERP, plasticity

Introduction

Human faces are a highly relevant stimulus class carrying manifold social signals, such as a person's identity, emotional state, gender, or age. Nevertheless, our perception of a given face is not necessarily identical at different points in time, as preceding visual experiences can influence it. The adaptation-related aftereffect (AE) is one such phenomenon, where prolonged exposure (i.e., adaptation) to a stimulus leads to contrastive biases in the perception of a subsequently presented stimulus. AEs have been described previously for lower level visual information such as line-orientation [1] or motion [2], but also for high-level information, including various characteristics of faces, among them a person's identity [3-6], gender [7-10], ethnicity, emotional expression [10], gaze [11,12], and age [13].

In a recent study on face identity perception, Hills et al. [3] showed that adaptation to one familiar identity biases perception of a face morphed between this and another familiar identity towards the not adapted identity. Interestingly, the amount of AE depended on the type of the adaptor: adaptation to one of the faces that were used to create the morphs led to higher AEs than adaptation to different pictures of the same identities, while the strongest AEs were found for adaptation to artist drawn caricatures. Previous studies have also shown that AEs are influenced by adaptor and test stimulus presentation times [5,14]. Longer adaptation and shorter test presentation increased the strength of AE. However, other studies suggest that AEs are relatively insensitive to variations of the adaptors, such as in contrast, colour, or size [15], viewpoint, inversion, or vertical stretching [6].

In all of these studies, AEs were typically induced by effective adaptors, such as the veridical or original faces of given identities, strong emotional expressions, or heavy distortions of faces. Some studies also found that adaptation to a face that is neutral on the adapted dimension does not lead to AEs, for example for facial distortions [16] or for facial identity [4]. Furthermore, "different image" adaptors [e.g., 3], if included at all, were only used to rule out image-specific AEs. As of yet, a parametric study of the influence of the adaptor stimulus per se on the strength of AE has, to our knowledge, never been made.

Face AEs were often observed with modulations of event-related potentials (ERPs), and two groups of effects can be separated in the literature. Category-specific adaptation, especially of the N170 ERP component (or of its magnetic equivalent, the M170), was observed as reduced amplitudes for test faces following adaptation to faces as compared to stimuli of a different category [7,8,17-20]. Some studies also reported distortion-specific modulations of ERPs for test faces after adaptation to distorted faces [17,21]. Compared to categorical adaptation effects on the N170, the time windows of those specific effects

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appeared more variable. Zimmer and Kovács [17] showed that N170 was additionally reduced after adaptation to distorted as compared to undistorted faces, whereas Burkhardt et al. [21] found the earliest effect after a similar manipulation in a later P250 component. Somehow at odds with findings of N170 being insensitive to the repetition of facial identity [19,22,23] or to familiarity per se [24], recent studies also reported a sensitivity of the N170 ERP to the identity of unfamiliar faces in an adaptation paradigm, but without addressing behavioural aftereffects [e.g., 25].

A different line of experiments used functional magnetic resonance imaging (fMRI) to investigate the suppression of the blood oxygen level dependent (BOLD) signal in AE paradigms [26,27]. Cziraki et al. [26] found face-specific response suppression in the fusiform face area [FFA; 28] for composite face/hand stimuli after face adaptation, and this suppression was stronger in trials in which adaptation successfully biased perception away from the adaptor category. In an fMRI study on expression and identity AEs, Furl et al. [29] found similar response-specific effects in the medial temporal lobe, but not in the FFA or occipital face area [OFA; 30]. The functional mechanisms underlying such activation differences are still under discussion [for a review, see 31]. Furthermore, Rotshtein et al. [32] made an attempt to investigate categorical perception of face identity [33] without prior adaptation, to test the role of FFA and OFA in face recognition. They found that the inferior occipital gyrus showed sensitivity for the (physically driven) similarity of the stimuli, whereas the right fusiform gyrus responded to identity changes, implicating its role in identity recognition.

In a recent study on identity AEs [34], we asked how adaptation influences the perception of faces varying on morph continua between pairs of familiar identities. Clear AEs were only observed for ambiguous test stimuli if the adaptor was one of the original faces, while there was no AE following 50/50% morphs or Fourier phase randomized faces. Simultaneously recorded ERPs showed clear categorical adaptation for the N170, P2 and N250 components, as well as identity-specific adaptation effects for the P2 and N250, which were correlated with behavioural AEs. These results suggested an influence of ambiguity and/or (physical) similarity of the stimuli for AEs. However, as the design of Walther et al. [34] focused on relating AEs and priming to each other, it did not allow to draw specific conclusions about the role of adaptor similarity or ambiguity for AEs alone. Hence, in the present study, we investigated the stimulus-driven mechanisms behind the influence of the adaptor on the perception of the following test stimulus in an S1-S2 paradigm similar to Walther et al. [34]. Varying the identity of the adaptor (S1) parametrically on a morphing

continuum, while keeping the test stimulus (S2) constant at an ambiguous level, we found a contrastive bias on the perception of S2 faces. Furthermore, we hypothesized that if S1-S2 similarity was the only factor that affects AEs then a linear relationship between S1 morph level and classification performance should be observable, whereas S1 ambiguity might lead to a rather stepwise function assuming categorical perception of familiar face identities [see, e.g., 32,33]. In Figure 1 we present the hypothetical data according to both models. In fact, the magnitude of AEs was systematically influenced by the S1 morph level, and the data pattern suggested a role both of the similarity between adaptor and test stimuli, and of the ambiguity of the adaptors. Simultaneously recorded ERPs showed that S1 morph level affected brain responses in two relatively late time windows around 300 - 400 ms. In earlier time windows, especially around 125 - 240 ms, we observed categorical adaptation and response-specific effects.
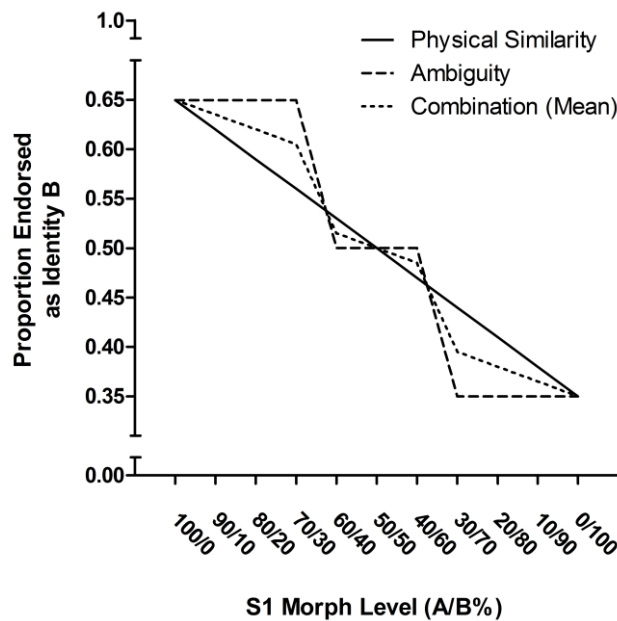
Figure 1. Hypothetical classification performance. Curves reflect the expected accuracy data (proportion endorsed as identity B) for $S2_{50/50\%}$ faces following the different S1 adaptors assuming that S1-S2 similarity, ambiguity, or a combination of both drives aftereffects. The maximal size of aftereffect and the ambiguous area of the ambiguity curve were estimated on the basis of prior results [34]. For the latter, interpolation of data from the noise adaptation condition suggested that only S2s between 40/60% and 60/40% identity A/B showed classification performance close to chance level (i.e., between 40% and 60% classification performance, criterion set arbitrarily). The curve for the combination of S1 similarity and ambiguity was approximated by the mean of the other two curves.

Materials and Methods

Participants

Twenty-two right-handed students of the University of Jena (12 female) with a mean age of 23.3 years and a range of 20 to 27 years contributed data. All participants had normal or corrected to normal vision, gave written informed consent and received course credit for their participation. Data from five additional participants had to be excluded from the analysis due to technical problems ($N = 3$) or extensive EEG artifacts and drifts ($N = 2$). The experiment was carried out in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of the Friedrich-Schiller-University of Jena.

Stimuli

Stimuli comprised 28 famous faces (14 female) collected from the public domain of the world-wide web. We formed 14 same-gender pairs consisting of two unique identities (A and B) with as little associative relationship between the two members of the pairs as possible. For each of these 14 pairs, we created a morphing continuum between identities A and B (Sierra software Morph™ , version 2.5) with eleven morph levels (corresponding to 10% steps, $S1_{100/0\%}$ to $S1_{0/100\%}$). These morphs, as well as Fourier phase randomized versions of faces ($S1_{N(oise)}$) that were unique for each A-B pair, were used as first stimuli (S1s). $S1_N$ served as a control stimulus matched on low level visual information and was created by MATLAB 7.6 (MathWorks Inc.) using an algorithm similar to Näsänen [35]. The second, target stimulus (S2) was always the ambiguous, 50/50% A/B morph of the identity pair that was presented as S1. Beforehand, images were prepared using Adobe Photoshop CS2 (Adobe Systems Inc.). Excessive hairstyles were cropped and faces were aligned to the same pupil position. Next, images were converted to greyscale and set to similar luminance and contrast values subjectively. Where appropriate, strands of hair, paraphernalia or extensive make-ups were manually removed. Final images measured 531 x 704 pixels. E-prime 2.0 software was used for stimulus presentation on a CRT monitor. S2 faces were presented at maximum visual angles of approximately 7.2 x 5.2 degrees, and S1 faces at 9.0 x 6.5 degrees, on a grey background. The mean luminance of the faces was 15 cd/m² [measurement procedure as described in 34]. S1 stimuli were presented 25% larger than S2 faces to prevent effects based on retinal position.

Procedure

Participants were seated in a dimly lit chamber 90 cm in front of the screen. A chin rest was used to reduce head movements during data recording to a minimum. Participants had to fixate the S1 stimulus, and to match the following S2 face to one of its original identities (A or B).

Experimental trials (see Fig. 2) started with a variable fixation period of 700 - 1000 ms, after which the S1 was shown for 3000 ms. After an 1000 ms blank screen, the S2 was presented for 400 ms. Subsequently, participants had to match the morphed S2 face via button press (2-AFC) to one of its original identities (A or B, corresponding to $S1_{100/0\%}$ and $S1_{0/100\%}$), which were presented side by side on the choice screen for 1500 ms (positioned randomly, with identity A being presented on the left side for half of the trials, stimulus size: 7.2 x 5.2 degrees). A 10.8 degrees distance from image-centre to image-centre was used to prevent spatial overlap between the S2 and the faces of the choice-screen. Responses were recorded during the presentation of the choice screen, and the message "Bitte schneller reagieren!" ("Please respond faster!") was displayed for 1000 ms if no response occurred in this time window.

The experiment consisted of two practice phases and an experimental phase. The experimental phase comprised 504 trials in three blocks (168 trials/block). Stimuli from all 14 A/B pairs were presented once per block in each of the 12 S1 conditions. Within blocks, stimulus order was random. The assignment of celebrities to labels A and B in each face pair was counterbalanced across participants. Participants were allowed to take a user-terminated rest every 56 trials. Trial procedure of the practice phases was similar to that of the experimental phase, except that different stimuli were presented that were not used in the experimental phase. Both practice phases comprised a representative portion of S1 conditions (i.e., $S1_{80/20\%}$, $S1_{50/50\%}$, $S1_{20/80\%}$, and $S1_N$). In practice phase 1 (16 trials), unambiguous S2 stimuli and feedback were used to familiarize participants with the matching task, whereas stimulation in practice phase 2 (12 trials) was analogous to that in the experimental phase, i.e., 50/50% A/B morphs were used as S2, and no feedback was given. The total experimental time was about 62 min.
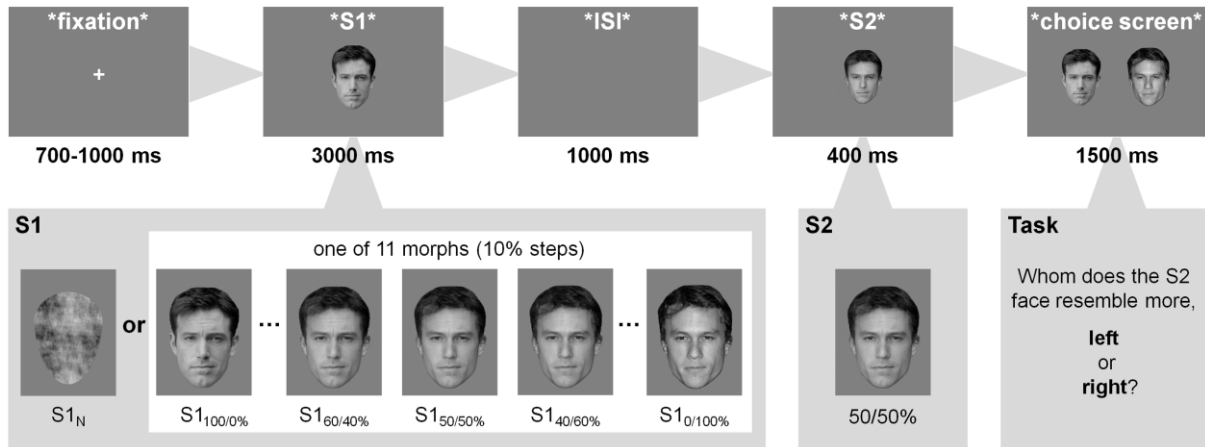
Figure 2. Trial structure of the experiment. Sample images belong to one of the 14 identity A/B pairs that were used in the experiment. Note that $S1_{50/50\%}$ and $S2_{50/50\%}$ are identical images, and that the expressions in asterisks are for illustration only and were not presented on the screen. The original images of identity A (Ben Affleck) and identity B (Heath Ledger) were obtained from http://wallpaper-s.org/72__Ben_Affleck,_Actor.htm (last access: 04/17/2013) and http://24.media.tumblr.com/tumblr_m1z1hcXtCM1qbps4ao1_500.jpg (last access: 04/17/2013), respectively.

Event-related Potential Recordings

The electroencephalogram (EEG) was recorded using a 64-channel Biosemi Active II system (Biosemi, Amsterdam, The Netherlands) at electrode positions Fp1, FT9, AF3, F1, F3, F5, F7, FT7, TP9, FC3, FC1, C1, C3, C5, T7, TP7, PO9, CP3, CP1, P1, P3, O9, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, Fpz, Fp2, FT10, AF4, Afz, Fz, F2, F4, F6, F8, FT8, TP10, FC4, FC2, FCz, Cz, C2, C4, C6, T8, TP8, PO10, CP4, CP2, P2, P4, O10, P8, P10, PO8, PO4 and O2 (according to the extended international 10/20 system). Note that the Biosemi system uses a combined ground/reference (CMS/DRL) circuit (cf. to http://www.biosemi.com/faq/cms&drl.htm). In addition, the horizontal electrooculogram (EOG) was recorded from the outer canthi of both eyes, and the vertical EOG bipolarly from above and below the left eye. The sampling-rate was 512 Hz (bandwidth: DC to 120 Hz). Offline we created 1200-ms-long epochs starting 200 ms before S2 onset. Ocular artifact correction was computed automatically with BESA 5.1.8.10 (MEGIS Software GmbH, Graefelfing, Germany) for all signals, and a recalculation to average reference was applied. Thresholds for artifact rejection were 100 μV for amplitude, 75 μV for gradient, and 0.1 μV for low signal. Trials with missing responses were excluded as well. On average, 39 trials per condition (i.e., ~93% of all trials) were used for the analyses (range: 38 - 40 trials per condition). Finally, we calculated event-related potentials (ERPs) by averaging the trials within each condition for each channel and participant. We additionally calculated ERPs depending on the response of the participants to S2 and the S1 identity [cf., e.g., 26]: for

unambiguous S1s (corresponding to $S1_{100/0\%}$, $S1_{90/10\%}$, $S1_{80/20\%}$, $S1_{20/80\%}$, $S1_{10/90\%}$, and $S1_{0/100\%}$) we averaged all trials where the response was incongruent with the respective S1 identity (i.e., when adaptation biased perception away from the identity of the S1), as well as all trials with congruent responses (i.e., when adaptation did not lead to a contrastive bias of perception of the $S2_{50/50\%}$). Because there were about twice as many trials with successful compared to unsuccessful adaptation, we randomly included only every second trial with successful adaptation for this analysis, to achieve comparable trial numbers in both conditions ($M = 76$ trials/condition; range: 71 to 81 trials per condition). ERPs were digitally filtered with a 0.3 Hz high-pass (zero-phase shift, 6 dB/octave) and a 40 Hz low-pass filter (zero phase shift, 12 dB/octave). As we were interested in the role of S1 for the processing of S2 in the current study ERPs for S1 were not analysed.

Behavioural Data Analysis

ANOVAs with repeated measures on S1 condition (11; $S1_{100/0\%}$ to $S1_{0/100\%}$ in 10% steps) were performed for S2 accuracies (in proportion endorsed as identity B) and S2 reaction times (RTs). Epsilon corrections for heterogeneity of covariance according to Huynh and Feldt (1976) were used throughout, where appropriate. Errors of omission (no key press) and trials with reaction times (RTs) faster than 200 ms were excluded from the analyses (in total, 0.7% of all experimental trials). To assess the character of the respective psychometric curves, we carried out polynomial contrast analyses with the ANOVAs. Regarding our hypothesis, a linear trend would reflect the influence of (physical) S1-S2 similarity on AEs, whereas the influence of S1 ambiguity should be manifested in higher order trends in general, and fourth order trends in particular (cf. Fig. 1). In addition, the difference between subsequent S1 morph levels, as well as between each face S1 condition and the chance level (0.5, i.e., 50%), were evaluated using t-tests (paired-samples and one-sample, respectively; two-sided). Paired-samples t-tests (two-sided) were used to determine if there was a significant difference between $S1_{50/50\%}$ and $S1_N$ for accuracies and RTs. For accuracy data, $S1_N$ was also compared to chance level using a one-sample t-test (two-sided). Post-hoc t-tests were not corrected for multiple comparisons. Only significant results or important trends are reported.

ERP Data Analysis

We calculated mean amplitudes in the response to S2 for P1 (100 - 150 ms), N170 (125 - 175 ms), P2 (190 - 240 ms), and N250 (250 - 300 ms) time windows, as well as for two consecutive later time windows (300 - 350 ms and 350 - 400 ms) for each condition, electrode, and participant separately. With the exception of the two later time windows, for

which no clear peaks were identifiable, time windows were centered on the respective peaks of the grand average across all conditions and participants at representative electrodes. In all following analyses, the topographic factors hemisphere (left vs. right) and electrode position (except for P1, which we only measured at O1 and O2) were included. N170 was quantified at P7/8, P9/10, PO7/8, and PO9/10. P2 and N250, as well as the two later time windows, were measured at P7/8, P9/10, PO7/8, PO9/10, O1/2, and O9/10. Note that the two later time windows are simply fixed 50-ms time segments that do not correspond to prominent peaks in the waveform, and thus any interpretation relative to known components should be considered with caution. For all ANOVAs, Epsilon corrections for heterogeneity of covariance according to Huynh and Feldt (1976) were used throughout, where appropriate. Post-hoc t-tests were not corrected for multiple comparisons. Topographic effects will only be reported when in interaction with the experimental variables.

To analyse *categorical adaptation effects*, we calculated the means across all face S1 conditions in every time window and compared these to the respective $S1_N$ condition via ANOVAs with repeated measures on hemisphere, electrode, and S1 category (face vs. noise). Significant (or marginally significant) interactions of S1 category and topographic factors were tested post-hoc by comparing face S1s and noise S1s at each electrode separately (paired-samples t-tests, two-sided).

To assess *adaptation effects depending on S1 morph level*, repeated-measures ANOVAs including the factors hemisphere, electrode, and S1 condition (11; excluding $S1_N$) were carried out for each component/time window. If the main ANOVA yielded an at least marginally significant interaction of S1 condition with a topographic factor, separate ANOVAs with repeated measures on S1 condition (11) and polynomial contrast analyses were carried out for each electrode of the respective overall analysis. If the effect of S1 condition was significant, we compared $S1_{100/0\%}$ and $S1_{0/100\%}$ to $S1_{50/50\%}$ with paired-samples t-tests (two-sided). To allow further comparisons to another recent study from our lab [34], we also tested the difference between $S1_{50/50\%}$ and the mean of $S1_{100/0\%}$ and $S1_{0/100\%}$ conditions in such cases in the same way.

For the analyses of *response-specific effects*, new mean amplitudes were calculated for the respective conditions. We used the same time windows and electrodes as given above, and ANOVAs with repeated measures on hemisphere, electrode position (except for P1), and response congruence (congruent vs. incongruent) were conducted. Significant (or marginally significant) interactions of response congruence and topographic factors were tested post-hoc with paired-samples t-tests (two-sided).

Results

Behavioural Data

Varying the identity of S1 determined the participants' responses to S2 as suggested by the significant main effect of S1 condition in the ANOVA for classification data ($F(10,210) = 48.88$, $p < .001$, $\varepsilon_{HF} = .220$, $\eta^2_p = .699$). The more similar the S1 was to one of the original identities, the stronger the classification of the ambiguous S2 face was biased towards the opposite identity and, therefore, the stronger was the contrastive aftereffect (see Fig. 3A). Polynomial contrast analyses revealed a strong linear trend ($F(1,21) = 77.28$, $p < .001$, $\eta^2_p = .786$), but also significant quadratic ($F(1,21) = 7.33$, $p = .013$, $\eta^2_p = .259$), fourth order ($F(1,21) = 10.46$, $p = .004$, $\eta^2_p = .333$), and ninth order trends ($F(1,21) = 5.23$, $p = .033$, $\eta^2_p = .199$), as well as marginally significant fifth and seventh order trends ($F(1,21) = 4.17$, $p = .054$, $\eta^2_p = .166$, and $F(1,21) = 3.29$, $p = .084$, $\eta^2_p = .136$, respectively). Note that the observed data pattern suggests that both S1-S2 similarity and S1 ambiguity affects AEs (cf. Fig. 1). The comparison of each S1 morph level with chance level confirmed that the previous presentation of the ambiguous $S1_{60/40\%}$ and $S1_{50/50\%}$ faces did not lead to perceptual biases ($ps > .05$), whereas all other S1 morph levels led to a classification performance significantly different from chance (all $ps < .05$). The comparison of S2s following subsequent morph levels (see Table 1) showed differences between all subsequent pairs except for S1s near the unambiguous, as well as the most ambiguous S1 morph levels. Therefore, perception of the ambiguous S2 seems to be influenced by certain S1 morph levels in much the same way, indicating a step-wise shape of the curve.

The ANOVA for S2 RTs showed a main effect of S1 condition ($F(10,210) = 10.82$, $p < .001$, $\varepsilon_{HF} = .885$, $\eta^2_p = .340$), that was best described by a strong quadratic trend ($F(1,21) = 41.63$, $p < .001$, $\eta^2_p = .665$; see Fig. 3B). This suggests that the closer the S1 morph was to one of the original identities, the faster the responses to the ambiguous S2 were. The polynomial contrast analyses revealed also fourth order ($F(1,21) = 12.40$, $p = .002$, $\eta^2_p = .371$), and sixth order trends ($F(1,21) = 5.78$, $p = .026$, $\eta^2_p = .216$), as well as marginally significant ninth and tenth order trends ($F(1,21) = 4.05$, $p = .057$, $\eta^2_p = .162$, and $F(1,21) = 3.20$, $p = .088$, $\eta^2_p = .132$, respectively).

The $S1_N$ condition, that was introduced as an additional control, was neither significantly different from chance ($t(21) = -1.30$, $p = .207$), nor from the $S1_{50/50\%}$ condition, ($t(21) = -0.85$, $p = .403$), for S2 classification data. Nevertheless, there was a marginally significant difference between $S1_N$ and $S1_{50/50\%}$ for S2 RTs, suggesting that the slowest responses were observed following $S1_N$ ($t(21) = -1.83$, $p = .082$).

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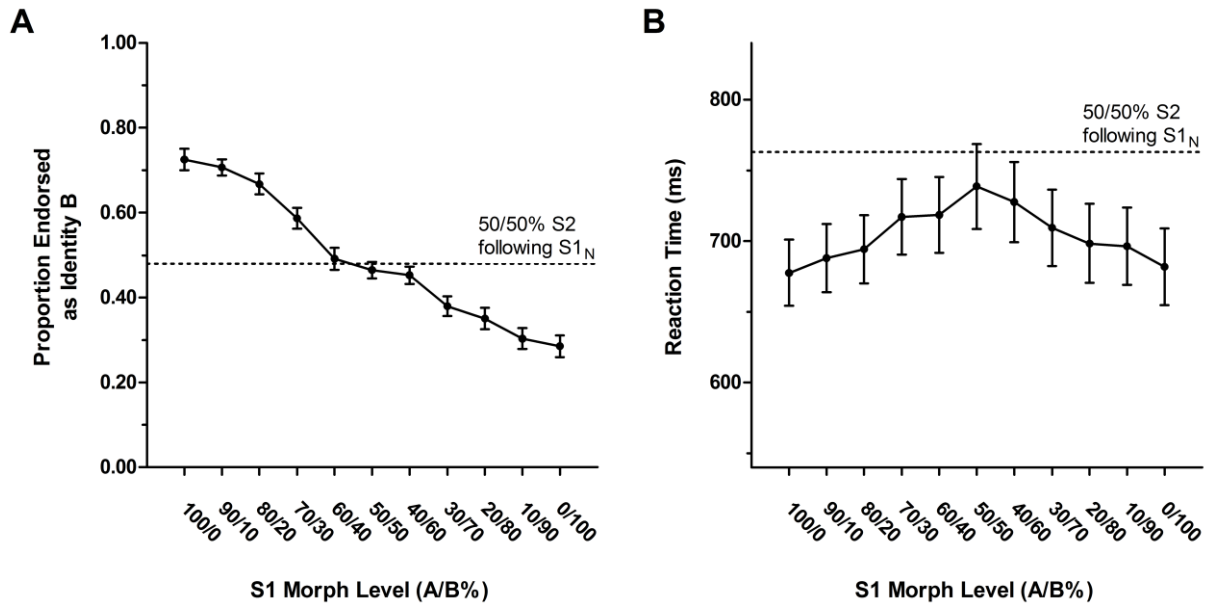
Figure 3. Behavioural data. A: Accuracy data (proportion endorsed as identity B) for $S2_{50/50\%}$ faces following the different S1 adaptors. B: Reaction times (in ms) for $S2_{50/50\%}$ faces following the different S1 adaptors. Error bars show ±1 standard error of the mean (SEM).

Table 1

t-tests of differences in the proportion of S2 being endorsed as identity B between subsequent S1 morph levels

Difference	*M*	*SD*	*t*(21)	*p*
$S1_{100/0\%}$ - $S1_{90/10\%}$	0.02	0.09	1.00	.328
$S1_{90/10\%}$ - $S1_{80/20\%}$	0.04	0.09	2.10	**.048**
$S1_{80/20\%}$ - $S1_{70/30\%}$	0.08	0.12	3.26	**.004**
$S1_{70/30\%}$ - $S1_{60/40\%}$	0.10	0.08	5.28	**.000**
$S1_{60/40\%}$ - $S1_{50/50\%}$	0.03	0.12	0.99	.332
$S1_{50/50\%}$ - $S1_{40/60\%}$	0.01	0.12	0.50	.623
$S1_{40/60\%}$ - $S1_{30/70\%}$	0.07	0.07	5.05	**.000**
$S1_{30/70\%}$ - $S1_{20/80\%}$	0.03	0.06	2.42	**.025**
$S1_{20/80\%}$ - $S1_{10/90\%}$	0.05	0.06	3.58	**.002**
$S1_{10/90\%}$ - $S1_{0/100\%}$	0.02	0.07	1.20	.244

*Note:* Significant *p*-values are in boldface.

ERP Data

Categorical adaptation effects. To assess categorical adaptation, i.e. adaptation related to generic face exposure [7], we averaged the S2 ERPs of the eleven S1 conditions where S1 was a face, and then contrasted this average with the $S1_N$ condition (see also the difference between all face S1s and $S1_N$ in Fig. 4). The first component reflecting categorical adaptation was the P1, quantified by a main effect of S1 category ($F(1,21) = 13.46$, $p = .001$, $\eta^2_p = .391$). Irrespective of hemisphere, the mean amplitudes of P1 were larger for S2s following face S1s as compared to $S1_N$. Importantly, the most prominent categorical adaptation effects were observed for the N170 and the P2 ERP components. Both components showed significant main effects of S1 category ($F(1,21) = 15.11$, $p = .001$, $\eta^2_p = .418$, and $F(1,21) = 29.20$, $p < .001$, $\eta^2_p = .582$, for N170 and P2, respectively), which were qualified by interactions of electrode and S1 category ($F(3,63) = 10.08$, $p < .001$, $\varepsilon_{HF} = .738$, $\eta^2_p = .324$, and $F(5,105) = 7.05$, $p = .002$, $\varepsilon_{HF} = .434$, $\eta^2_p = .251$, for N170 and P2, respectively). Corresponding to prior findings [e.g., 17, see their Figs. 3A and 3B], adaptation to face S1s led to smaller N170 amplitudes and larger P2 amplitudes than adaptation to $S1_N$ over most of the occipito-temporal electrodes. Post-hoc tests for N170 revealed significant differences between S2s following face S1s and $S1_N$ at P9, PO9, P8, P10, and PO10 ($ps < .05$), as well as PO8 ($t(21) = 1.73$, $p = .099$). These differences were significant at all analysed electrodes for P2 ($ps < .05$), except for O2 ($t(21) = 1.54$, $p = .138$). N250 also showed categorical adaptation reflected by an interaction of electrode and S1 category ($F(5,105) = 7.53$, $p < .001$, $\varepsilon_{HF} = .609$, $\eta^2_p = .264$). N250 mean amplitudes were significantly larger (i.e., less positive) for S2s following face S1s as compared to $S1_N$ at P7, PO7, and O1 (all $ps < .05$), as well as O2 ($t(21) = -1.76$, $p = .093$), suggesting somewhat more pronounced effects over superior occipito-temporal sites. Finally, we also found significantly smaller (i.e., less positive) mean amplitudes for S2s following face S1s as compared to $S1_N$ irrespective of electrode in the analyses of the two later time windows, as shown by main effects of S1 category in the 300 - 350 ms and 350 - 400 ms time windows ($F(1,21) = 13.71$, $p = .001$, $\eta^2_p = .395$, and $F(1,21) = 8.15$, $p = .009$, $\eta^2_p = .280$, respectively). Topographical difference maps for the 125 - 175 ms time window (corresponding to the N170 ERP component; see Fig. 5A) suggested that categorical adaptation was most pronounced over occipito-temporal regions of both hemispheres, confirming the results of mean amplitudes analyses.

Adaptation effects depending on S1 morph level. We found no effect of S1 condition for P1, N170, and N250 ERP components. Although there was a marginally significant interaction of electrode and S1 condition in the analyses of P2 ($F(50,1050) = 1.52$, $p = .063$,

$\varepsilon_{HF} = .432$, $\eta^2_p = .068$), its pattern was rather unsystematic. When tested separately only the P10 electrode showed an effect of S1 condition ($F(10,210) = 2.03$, $p = .033$, $\eta^2_p = .088$), which was fitted best by cubic and fourth order trends ($F(1,21) = 5.02$, $p = .036$, $\eta^2_p = .193$, and $F(1,21) = 10.06$, $p = .005$, $\eta^2_p = .324$, respectively). In contrast to the effects observed for the earlier components, there were prominent modulations of S2 ERPs by S1 condition in both the 300 - 350 ms and 350 - 400 ms time windows at occipito-temporal sites (see Fig. 6 and Figs. S1 - S3 of Supporting Information), as shown by significant main effects of S1 condition ($F(10,210) = 2.33$, $p = .013$, $\eta^2_p = .100$, and $F(10,210) = 4.20$, $p < .001$, $\eta^2_p = .167$, respectively). These effects were further qualified by a significant interaction of electrode and S1 condition in the 300 - 350 ms time window ($F(50,1050) = 1.79$, $p = .010$, $\varepsilon_{HF} = .510$, $\eta^2_p = .079$), and a marginally significant interaction of electrode and S1 condition in the 350 - 400 ms time window ($F(50,1050) = 1.50$, $p = .062$, $\varepsilon_{HF} = .474$, $\eta^2_p = .067$). However, the effects of S1 condition were qualitatively similar in both time windows and observable at several electrodes, as revealed by post-hoc ANOVAs (see Tables 2 and 3). In general, the closer the S1 face was to one of the original faces, the larger (less negative) the S2 mean amplitudes were. This pattern was confirmed by strong quadratic trends in the data, but sometimes modified by additional linear or higher order trends (see Tables 2 and 3). Furthermore, post-hoc t-tests showed significant differences between $S1_{100/0\%}$ and $S1_{50/50\%}$ at PO7, PO9, O1, and PO8 ($ps < .05$) in the 300 - 350 ms time window, and significant differences at PO7, PO9, and O1 ($ps < .05$), as well as a trend at O2 ($t(21) = 1.91$, $p = .070$), in the 350 - 400 ms time window. $S1_{0/100\%}$ and $S1_{50/50\%}$ differed significantly at PO7, O1, and PO8 ($ps < .05$) in the 300 - 350 ms time window, while in the 350 - 400 ms time window, there were only trends for such a difference at O1 and O2 ($t(21) = 1.83$, $p = .081$, and $t(21) = 1.72$, $p = .099$, respectively). The difference between $S1_{50/50\%}$ and the mean of $S1_{100/0\%}$ and $S1_{0/100\%}$ was significant at PO7, O1, and PO8 ($ps < .05$) in the 300 - 350 ms time window, while in the 350 - 400 ms time window, this difference was significant at PO7 ($t(21) = -2.34$, $p = .029$) and O1 ($t(21) = -2.48$, $p = .022$), and marginally significant at O2 ($t(21) = -2.02$, $p = .056$). Note that the latter difference seems to rely too much on a symmetric modulation of ERPs by S1 condition and is therefore not optimal in the context of the present experiment. Together with the topographical effects, revealed by the main ANOVAs, the post-hoc results suggest that S1 morph level dependent adaptation effects are somewhat less pronounced over more temporal electrodes, especially in the 300 - 350 ms time window.

Response-specific effects. We found first hints for effects of the congruence of S1 and the behavioural response to the S2 (see Methods section) in the N170 time window (see Fig.

7). N170 mean amplitudes were larger when perception was biased away from the S1, i.e., the response was incongruent to the S1, as described by a significant interaction of electrode and response congruence ($F(3,63) = 4.33$, $p = .029$, $\varepsilon_{HF} = .525$, $\eta^2_p = .171$). Post-hoc tests showed trends at PO9 and PO10 ($t(21) = -1.97$, $p = .062$, and $t(21) = -1.76$, $p = .094$, respectively). For P2, mean amplitudes were significantly smaller (i.e., relatively more negative) for incongruent responses, i.e., when adaptation biased perception away from the identity of the adaptor, as indicated by an interaction of electrode and response congruence ($F(5,105) = 6.02$, $p = .001$, $\varepsilon_{HF} = .660$, $\eta^2_p = .223$). Post-hoc tests showed significant differences between conditions with congruent and incongruent responses at PO9, P10, and PO10 (all $ps < .05$), as well as a trend at P8 ($t(21) = -1.97$, $p = .062$), indicating slightly larger effects over the right hemisphere. Although there was no interaction of hemisphere and response congruence in the overall ANOVA, a slight right lateralization of the occipito-temporal effects was also suggested by topographical difference maps for the P2 time window (see Fig. 5B). Response-specific effects were also observed in the N250 time window, again as a significant interaction of electrode and response congruence ($F(5,105) = 7.03$, $p < .001$, $\varepsilon_{HF} = .786$, $\eta^2_p = .251$). The N250 mean amplitudes were larger (i.e., less positive/more negative) for S2 faces following incongruent responses as compared to congruent responses at P9, PO9, P8, and P10 ($ps < .05$), as well as at PO10 ($t(21) = -2.01$, $p = .058$). In the two later time windows, mean amplitudes were lower (i.e., less positive/more negative) for S2 faces following incongruent when compared to congruent responses. This was quantified by a significant interaction of electrode and response congruence ($F(5,105) = 4.91$, $p = .007$, $\varepsilon_{HF} = .508$, $\eta^2_p = .189$) in the 300 - 350 ms time window, and significant interactions of hemisphere and response congruence, as well as electrode and response congruence in the 350 - 400 ms time window ($F(1,21) = 5.31$, $p = .032$, $\eta^2_p = .202$, and $F(5,105) = 3.24$, $p = .038$, $\varepsilon_{HF} = .494$, $\eta^2_p = .133$, respectively). Post-hoc tests revealed that the amplitude reduction for incongruent responses was significant at P9, PO9, and P10 ($ps < .05$), and marginally significant at P8 ($t(21) = -1.81$, $p = .085$) in the 300 - 350 ms time window, as well as at PO9, P8, and P10 ($ps < .05$) in the 350 - 400 ms time window, with an additional, but opposed trend at PO7 ($t(21) = 1.88$, $p = .074$).
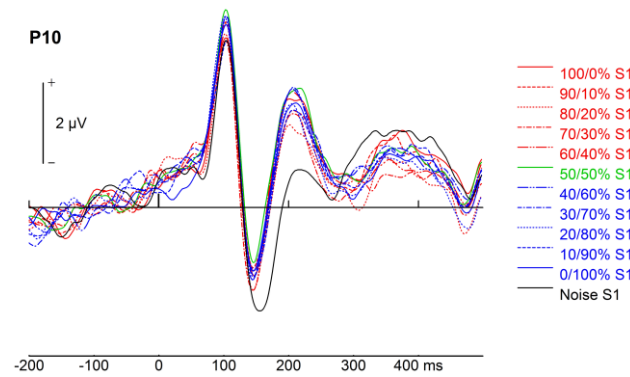
Figure 4. Sample ERPs. ERPs for 50/50% S2 faces following the eleven S1 morphs at P10 electrode, plotted from -200 to 500 ms. Note that the choice screen onset was at 400 ms.
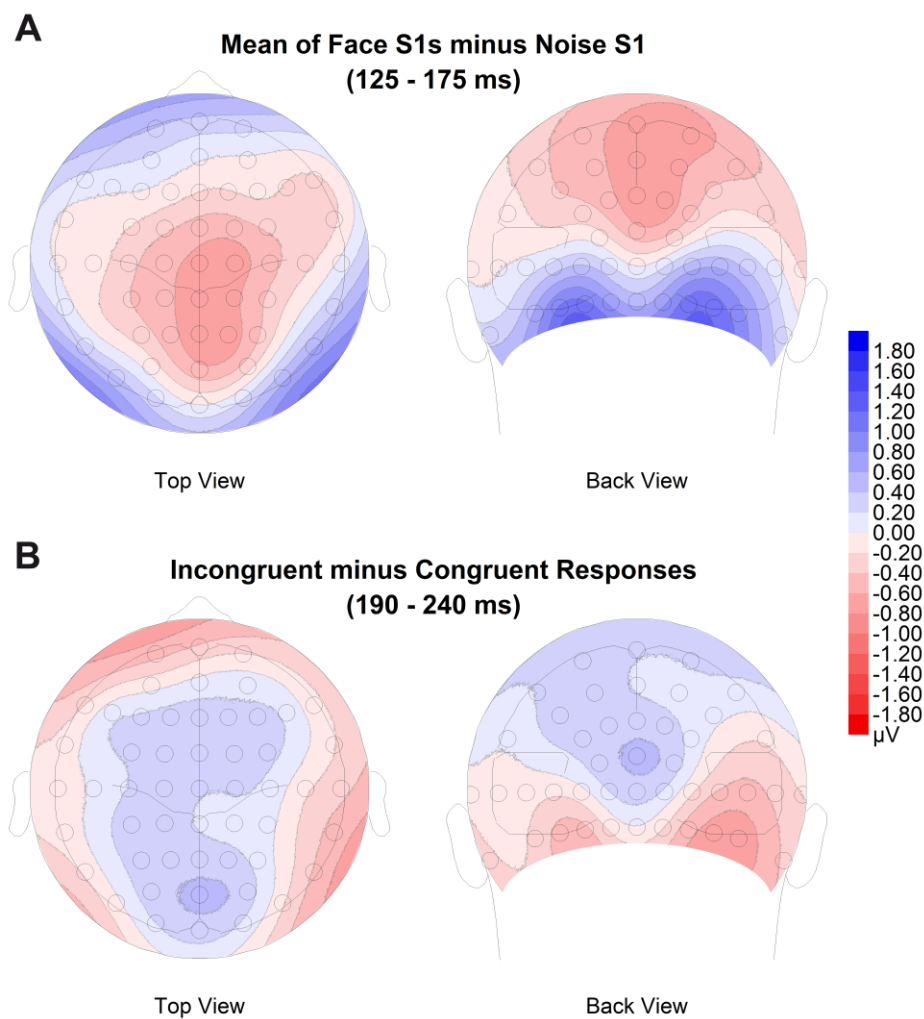
Figure 5. Topographical difference maps. A: ERPs to S2 preceded by face S1s minus those preceded by the Noise S1 ($S1_N$; 125 - 175 ms). B: Trials with incongruent minus congruent responses (190 - 240 ms). All maps were created using spherical spline interpolation and show a 110 degrees equidistant projection from a top and back view perspective (including electrode positions).
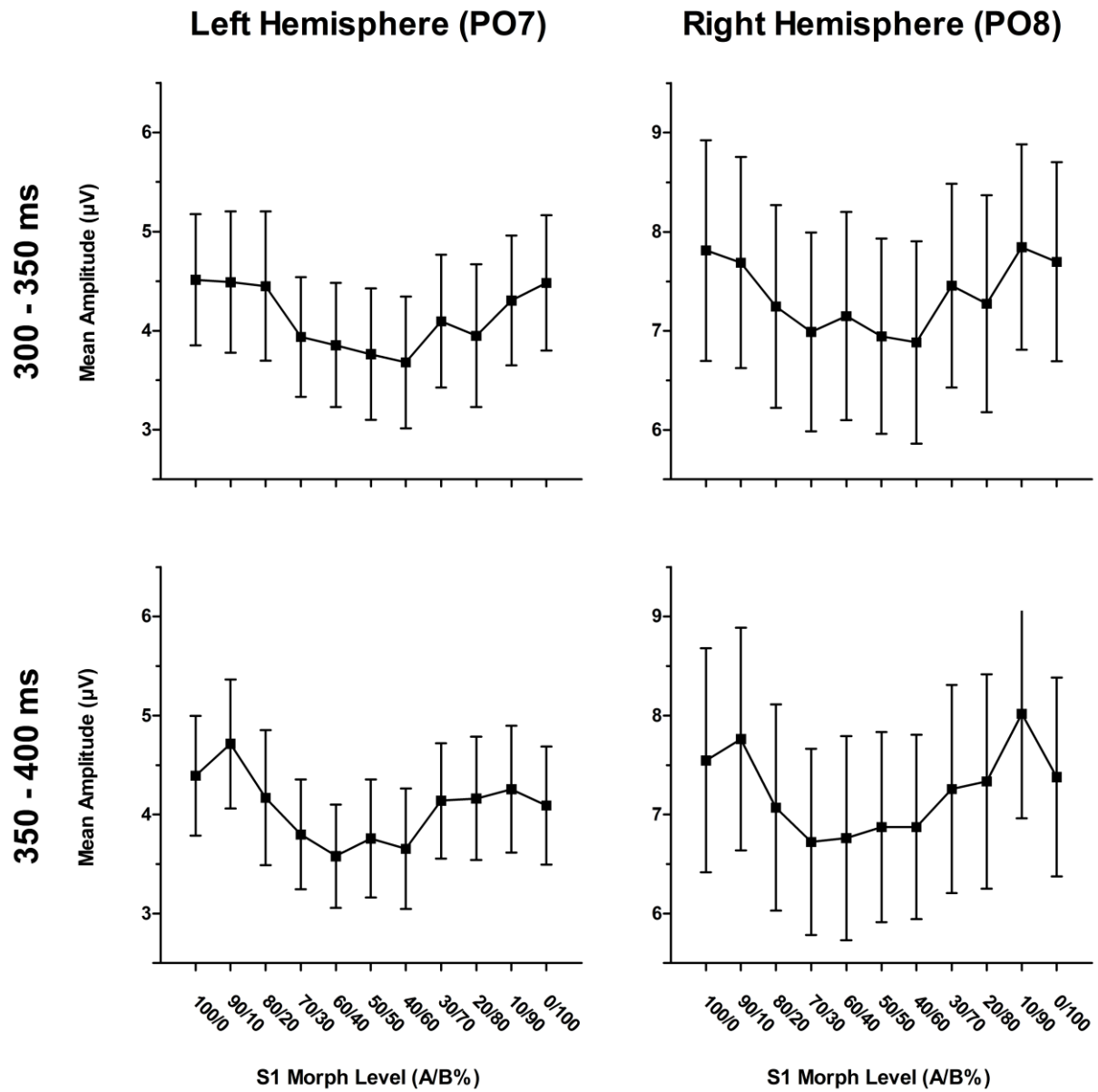
Figure 6. ERP effect of S1 condition. Mean amplitudes (300 - 350 ms and 350 - 400 ms) for $S2_{50/50\%}$ faces following the eleven S1 morphs for one representative electrode pair (PO7 and PO8). Error bars show ±1 standard error of the mean (SEM).
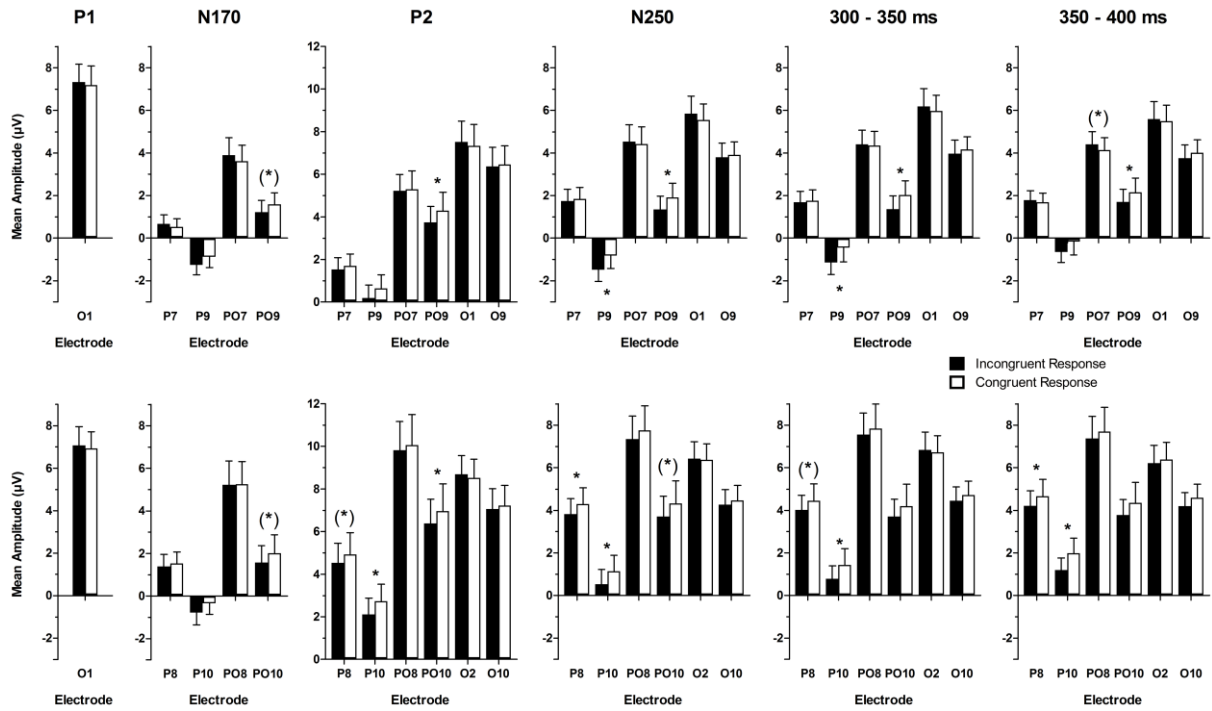
Figure 7. Response-specific effects. Mean amplitudes of trials with incongruent (i.e., adaptation biased perception of S2 away from the identity of the S1) and congruent responses (i.e., adaptation did not lead to a contrastive bias of perception of the S2$_{50/50\%}$) for all analysed components and electrodes over left (top row) and right hemisphere (bottom row). Significant differences between incongruent and congruent responses and trends are marked: (*) - $p < .10$; * - $p < .05$. Error bars show ±1 standard error of the mean (SEM).

Table 2

Post-hoc ANOVA with repeated measures on S1 condition (11) at each of the occipito-temporal electrodes in the 300 - 350 ms time window

Electrode	Main Effect of S1 Condition	Polynomial Contrasts
P7	$F(10,210) = 1.97$, $p = .053$, $\varepsilon_{HF} = .795$, $\eta^2_p = .086$	Quadratic: $F(1,21) = 7.66$, $p = .012$, $\eta^2_p = .267$
PO7	$F(10,210) = 2.37$, $p = .011$, $\eta^2_p = .102$	Quadratic: $F(1,21) = 27.21$, $p < .001$, $\eta^2_p = .564$
PO9	$F(10,210) = 2.02$, $p = .032$, $\eta^2_p = .088$	Quadratic: $F(1,21) = 7.63$, $p = .012$, $\eta^2_p = .267$
O1	$F(10,210) = 3.06$, $p = .001$, $\eta^2_p = .127$	Quadratic: $F(1,21) = 21.56$, $p < .001$, $\eta^2_p = .507$
P8	$F(10,210) = 2.23$, $p = .029$, $\varepsilon_{HF} = .778$, $\eta^2_p = .096$	Quadratic: $F(1,21) = 5.84$, $p = .025$, $\eta^2_p = .218$
		4th Order: $F(1,21) = 5.54$, $p = .028$, $\eta^2_p = .209$
PO8	$F(10,210) = 2.73$, $p = .004$, $\eta^2_p = .115$	Quadratic: $F(1,21) = 16.67$, $p < .001$, $\eta^2_p = .443$

Note: The analysed electrodes were P7, P9, PO7, PO9, O1, O9, P8, P10, PO8, PO10, O2, and O10. Only (marginally) significant S1 condition effects and significant polynomial trends are reported.

Table 3

Post-hoc ANOVA with repeated measures on S1 condition (11) at each of the occipito-temporal electrodes in the 350 - 400 ms time window

Electrode	Main Effect of S1 Condition	Polynomial Contrasts
P7	$F(10,210) = 2.38$, $p = .011$, $\eta^2_p = .102$	Linear: $F(1,21) = 5.03$, $p = .036$, $\eta^2_p = .193$
PO7	$F(10,210) = 3.13$, $p = .003$, $\varepsilon_{HF} = .803$, $\eta^2_p = .130$	Quadratic: $F(1,21) = 28.14$, $p < .001$, $\eta^2_p = .573$
		4th Order: $F(1,21) = 9.99$, $p = .005$, $\eta^2_p = .322$
PO9	$F(10,210) = 3.42$, $p < .001$, $\eta^2_p = .140$	Quadratic: $F(1,21) = 12.57$, $p = .002$, $\eta^2_p = .369$
		Cubic: $F(1,21) = 5.15$, $p = .034$, $\eta^2_p = .197$
O1	$F(10,210) = 2.73$, $p = .004$, $\eta^2_p = .115$	Quadratic: $F(1,21) = 13.57$, $p = .001$, $\eta^2_p = .393$
O9	$F(10,210) = 3.16$, $p = .002$, $\varepsilon_{HF} = .838$, $\eta^2_p = .131$	Quadratic: $F(1,21) = 7.25$, $p = .014$, $\eta^2_p = .257$
		Cubic: $F(1,21) = 4.44$, $p = .047$, $\eta^2_p = .175$
		4th Order: $F(1,21) = 9.03$, $p = .007$, $\eta^2_p = .301$
P8	$F(10,210) = 2.53$, $p = .007$, $\eta^2_p = .107$	Quadratic: $F(1,21) = 7.24$, $p = .014$, $\eta^2_p = .256$
		4th Order: $F(1,21) = 5.34$, $p = .031$, $\eta^2_p = .203$
PO8	$F(10,210) = 3.39$, $p = .001$, $\varepsilon_{HF} = .796$, $\eta^2_p = .139$	Quadratic: $F(1,21) = 10.60$, $p = .004$, $\eta^2_p = .335$
		4th Order: $F(1,21) = 4.45$, $p = .047$, $\eta^2_p = .175$
		6th Order: $F(1,21) = 9.88$, $p = .005$, $\eta^2_p = .320$
PO10	$F(10,210) = 2.42$, $p = .009$, $\eta^2_p = .103$	Quadratic: $F(1,21) = 14.40$, $p = .001$, $\eta^2_p = .407$
		6th Order: $F(1,21) = 4.84$, $p = .039$, $\eta^2_p = .187$
O2	$F(10,210) = 3.40$, $p < .001$, $\eta^2_p = .139$	Quadratic: $F(1,21) = 11.86$, $p = .002$, $\eta^2_p = .361$
		4th Order: $F(1,21) = 7.35$, $p = .013$, $\eta^2_p = .259$
		6th order: $F(1,21) = 6.35$, $p = .020$, $\eta^2_p = .232$
O10	$F(10,210) = 2.19$, $p = .019$, $\eta^2_p = .095$	Quadratic: $F(1,21) = 11.46$, $p = .003$, $\eta^2_p = .353$
		4th Order: $F(1,21) = 4.59$, $p = .044$, $\eta^2_p = .179$

Note: The analysed electrodes were P7, P9, PO7, PO9, O1, O9, P8, P10, PO8, PO10, O2, and O10. Only (marginally) significant S1 condition effects and significant polynomial trends are reported.

Discussion

In the present study, we investigated the effect of parametric manipulation of S1 identity by morphing on AEs in familiar face perception. We replicated the findings of typical adaptation studies in showing contrastive biases in the perception of ambiguous faces after adaptation to veridical S1 faces [3,6], as well as the lack of such effects following adaptation to ambiguous S1 morphs [4,10,34]. Additionally, the strength of AEs was influenced by the S1 morph level systematically, in that AEs were smaller for S1s closer to the most ambiguous morph and stronger for S1s closer to the original faces. Conforming to our hypotheses, the observed linear and non-linear components of the influence of S1 morph level suggest that both the ambiguity of the adaptor stimuli as well as the adaptor-target similarity affect face identity AEs. This conclusion is supported by the comparison of accuracy differences between S1 pairs with 10% physical dissimilarity on our morphing continuum as well.

In analogy to studies of other face AEs, the observed effects of the current study might involve high-level representations of face identities, that were adapted selectively depending on the perceived identity of the S1 [6]. This idea is linked to studies showing that face identity is perceived categorically [32,33]. Although we could not test for categorical perception explicitly in our design (the target face was always the same 50/50% ambiguous face), the non-linear contributions to the effect of S1 morph level suggest that categorical perception of the S1 might indeed be involved in AEs. AEs were stronger for S1s lying away from the boundary between two identities, while virtually no AE was observed for S1s close to the category boundary. Note that, although the linear trend in the effect of S1 morph level suggests the involvement of lower-level processes in the observed AEs as well, a merely retinotopic locus of AEs was ruled out by introducing a size change from S1 to S2 in the present study [see, e.g., 36]. Although separating high- and low-level contributions to face AEs is rather difficult, an account combining categorical perception with opposite AEs [37] could be helpful to further investigate the involvement of physical similarity and high-level identity information in face identity AEs.

RTs were also modulated by the identity of S1, in that participants responded faster following S1s near or equal to one of the original identities as compared to ambiguous S1s. Larger biases in the perception of target faces were therefore associated with faster RTs, possibly because the percept after effective adaptation was less ambiguous and easier to classify. Such an effect can be seen in extension to studies describing the benefits on discrimination performance associated with face adaptation [38,39]. Furthermore, a recent computational modeling study of adaptation-related aftereffects [40] also suggested that a

higher amount of adaptation leads to faster RTs for face stimuli. Additionally, we found a marginal RT benefit of face adaptation as compared to noise adaptation, but no image-specific priming effect for 50/50% morphs, that was described earlier in a similar gender discrimination study by Kovács et al. (unpublished data).

In the present study, we found categorical adaptation effects in ERPs which are broadly consistent with those reported in other studies [8,17,19,34]. In detail, ERPs over occipito-temporal recording sites were different if S1 was a face or a noise stimulus and this effect was most pronounced in the N170 and P2 time windows. However, a degree of categorical adaptation was already seen in the P1 component. Although some studies suggested that object category might be processed in such an early time window [e.g., 41], this is controversial [42] and a number of recent studies state that face category processing does not occur before the N170 time window [e.g., 18,19]. In comparison to the earlier effects, the N250 effects of the present study were rather weak and seemed limited to the more superior electrodes over the left hemisphere, whereas categorical adaptation was more pronounced in both the 300 - 350 ms and 350 - 400 ms time windows. In a recent study on the neural correlates of face AEs and priming [34], we observed similar effects of N170, P2, and N250, but the design of that study did not allow us to analyse later time windows. As studies on categorical adaptation typically focused on earlier ERP components [e.g., 8,19] as well, our study is the first to show that later S2 ERPs can be modulated by the category of S1. However, further research is needed to validate this finding. Also note that in our previous study [34], we observed categorical adaptation on the N250 as less positive/more negative mean amplitudes for S2s following noise S1s over more inferior occipito-temporal electrodes, whereas in the present study, more positive/less negative amplitudes for S2s following $S1_N$ were observed over the more superior occipito-temporal recording sites. The differences between the present categorical adaptation effects on P1 and N250 and those reported earlier [34] might be due to different carry-over adaptation effects between trials, possibly introduced by the randomization of face and noise S1 trials. Altogether, the categorical effects observed in the present study suggest that the processing of stimulus category takes place in a relatively long time interval, encompassing the early ERP components, such as P1 and N170, as well as the P2, N250, and the time between 300 and 400 ms post stimulus.

In ERPs, our analyses also revealed effects of the manipulation of S1 identity (i.e., S1 morph level) in two relatively late time windows (300 - 350 ms and 350 - 400 ms) at occipito-temporal sites. Here, S2 mean amplitudes were more positive following unambiguous S1s as compared to ambiguous S1s. As the relationship between S1 morph level and amplitude is not

linear, but quadratic, the signals did not seem to be modulated by the mere physical similarity of S1 and S2, but rather reflect the identity ambiguity of the S1 stimulus. This might be related to the activation of an identity-specific area in right fusiform gyrus that was described by Rotshtein et al. [32]. Nevertheless, future research will have to confirm this finding and its interpretation, that has to remain somewhat speculative at present. We did not observe any systematic effects of S1 identity manipulation for earlier ERPs on the S2, such as the N250r, that is thought to be the first component reflecting individual face recognition [23,43]. A possible reason for this might be that the N250r effects of the previous studies were typically measured as an increased negativity for familiar faces following images of the same as compared to a different identity, whereas in the present study the ambiguous S2 test face was not a familiar or identifiable face. Although some studies reported N170 modulations by facial identity [e.g., 25], early components such as P1 and N170 were often described as insensitive to short term repetition priming for familiar face identities [19,23,44] and face familiarity per se [24]. Nevertheless, one might ask why the manipulation of S1 morph level, that involved a gradual physical change from one S1 image to another, failed to modulate pictorial encoding or structural encoding stages of face processing, as reflected by P1 and N170, respectively [for a review, see 45]. However, our S1 stimuli were equalized in lower-level properties such as relative size, luminance, and contrast (see Materials and Methods section), and therefore, the differences introduced by morphing may have been too subtle to affect these processes selectively. Finally, the present non-existent or unsystematic early ERP effects of S1 condition could reflect a power problem related to the moderate number of trials. That said, the systematic and significant late ERP effects of S1 condition between 300 and 400 ms would seem to argue against such a general power problem.

With the large number of unambiguous S1s used, we were also able to analyse trials where participants' response to S2 was incongruent to the S1 (i.e., adaptation successfully biased perception away from the adaptor identity) as compared to trials where perception was congruent to the S1 (i.e., adaptation did not lead to repelling aftereffects). Besides effects on N170, N250, and later time-windows, there was a prominent reduction of P2 mean amplitudes when adaptation lead to contrastive AEs as compared to when it did not. This effect could be related to studies showing increased suppression of the fMRI signal in trials where adaptation biased perception of an ambiguous test face away from the adaptor [26,29], and suggests that amplitude modulations by adaptation to a specific face identity are related to perceptual decisions about ambiguous faces as measured with behaviour. The P2 is also thought to reflect task difficulty [46]. However, a novel study by Banko et al. [47] showed that it rather

reflects increased perceptual processing demands, related to the presence of stimulus noise. In the present study, the decrease of P2 amplitude was specific to the response given while stimulation and task were identical and might therefore also reflect a lower difficulty of the decision when adaptation led to contrastive AEs as compared to when it did not. The results of other recent studies [48-50] suggested that a decrease in P2 amplitude is associated with decreasing typicality, or increased distinctiveness, of a test face in reference to a face space [51]. Note that the present results of the P2 are perfectly consistent with those recent findings, if one assumes that adaptation elicits a transient shift of the centre of face space towards the adaptor [e.g., 16] in those trials in which adaptation successfully elicited contrastive AEs. We hold that in those trials (compared to trials where adaptation did not lead to a contrastive bias), the very same ambiguous S2 likely has been perceived as more distinctive and characteristic of the respective celebrity. Accordingly, those recent effects of caricaturing on the P2 and the present reduction of the P2 component during successful adaptation trials may reflect highly related phenomena in high-level face perception.

As qualitative differences between the processing of familiar and unfamiliar faces were sometimes suggested [52], it is unclear whether the effects observed in the present study and other studies on face identity AEs [e.g., 3,6] would generalize to unfamiliar face perception. For example, faces which are more readily recognized might lead to stronger maximal AEs via stronger activations of high-level representations of the individual faces in the face processing network, possibly reflected by modulations of the later ERP time windows. A recent study by Laurence and Hole [53] reported no difference in face distortion AEs between famous and unfamiliar faces, while reduced AEs were found only for the own face of the participants, suggesting only a moderate influence of familiarity on such configural AEs. Additionally, we observed clear behavioural AEs using a very similar paradigm to that of the present study with experimentally familiarized faces (unpublished data), although during this familiarization, faces were only shown from one perspective for several seconds. As, to our knowledge, there is no data on the role of familiarity for face identity AEs as of yet, such that further studies are needed to clarify this issue.

In conclusion, our results revealed that face identity AEs are modulated (1) by parametric manipulation of S1 identity, and also (2) not just by physical similarity, but also by the ambiguity of the S1 adaptors. Furthermore, our data suggest a benefit of adaptation to unambiguous S1s for response speed. ERPs revealed systematic correlates of short-term plasticity of face identity processing within the first 400 ms following S2 onset. Especially the later parts of these effects seemed to reflect the influence of S1 ambiguity rather than physical

similarity. Finally, we also observed categorical adaptation during this time window, suggesting that the processing of stimulus category and identity may partially overlap in time.

Acknowledgements

References

1. Clifford CWG, Wenderoth P, Spehar B (2000) A functional angle on some after-effects in cortical vision. Proc Biol Sci 267: 1705-1710.

2. Anstis S, Verstraten FAJ, Mather G (1998) The motion aftereffect. Trends Cogn Sci 2: 111-117.

3. Hills PJ, Elward RL, Lewis MB (2010) Cross-modal face identity aftereffects and their relation to priming. J Exp Psychol Hum Percept Perform 36: 876-891.

4. Leopold DA, O'Toole AJ, Vetter T, Blanz V (2001) Prototype-referenced shape encoding revealed by high-level after effects. Nat Neurosci 4: 89-94.

5. Rhodes G, Jeffery L, Clifford CWG, Leopold DA (2007) The timecourse of higher-level face aftereffects. Vision Res 47: 2291-2296.

6. Hole G (2011) Identity-specific face adaptation effects: Evidence for abstractive face representations. Cognition 119: 216-228.

7. Kloth N, Schweinberger SR, Kovács G (2010) Neural correlates of generic versus gender-specific face adaptation. J Cogn Neurosci 22: 2345-2356.

8. Kovács G, Zimmer M, Banko E, Harza I, Antal A, et al. (2006) Electrophysiological correlates of visual adaptation to faces and body parts in humans. Cereb Cortex 16: 742-753.

9. Kovács G, Zimmer M, Harza I, Vidnyanszky Z (2007) Adaptation duration affects the spatial selectivity of facial aftereffects. Vision Res 47: 3141-3149.

10. Webster MA, Kaping D, Mizokami Y, Duhamel P (2004) Adaptation to natural facial categories. Nature 428: 557-561.

11. Jenkins R, Beaver JD, Calder AJ (2006) I thought you were looking at me - Direction-specific aftereffects in gaze perception. Psychol Sci 17: 506-513.

12. Kloth N, Schweinberger SR (2008) The temporal decay of eye gaze adaptation effects. J Vis 8: 4.1-11.

13. Schweinberger SR, Zäske R, Walther C, Golle J, Kovács G, et al. (2010) Young without plastic surgery: Perceptual adaptation to the age of female and male faces. Vision Res 50: 2570-2576.

14. Leopold DA, Rhodes G, Muller KM, Jeffery L (2005) The dynamics of visual adaptation to faces. Proc Biol Sci 272: 897-904.

15. Yamashita JA, Hardy JL, De Valois KK, Webster MA (2005) Stimulus selectivity of figural aftereffects for faces. J Exp Psychol Hum Percept Perform 31: 420-437.

16. Webster MA, MacLin OH (1999) Figural aftereffects in the perception of faces. Psychon Bull Rev 6: 647-653.

17. Zimmer M, Kovács G (2011) Electrophysiological correlates of face distortion after-effects. Q J Exp Psychol 64: 533-544.

18. Ganis G, Smith D, Schendan HE (2012) The N170, not the P1, indexes the earliest time for categorical perception of faces, regardless of interstimulus variance. Neuroimage 62: 1563-1574.

19. Amihai I, Deouell LY, Bentin S (2011) Neural adaptation is related to face repetition irrespective of identity: A reappraisal of the N170 effect. Exp Brain Res 209: 193-204.

20. Harris A, Nakayama K (2007) Rapid face-selective adaptation of an early extrastriate component in MEG. Cereb Cortex 17: 63-70.

21. Burkhardt A, Blaha LM, Jurs BS, Rhodes G, Jeffery L, et al. (2010) Adaptation modulates the electrophysiological substrates of perceived facial distortion: Support for opponent coding. Neuropsychologia 48: 3743-3756.

22. Bindemann M, Burton AM, Leuthold H, Schweinberger SR (2008) Brain potential correlates of face recognition: Geometric distortions and the N250r brain response to stimulus repetitions. Psychophysiology 45: 535-544.

23. Schweinberger SR, Pickering EC, Jentzsch I, Burton AM, Kaufmann JM (2002) Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. Cogn Brain Res 14: 398-409.

24. Eimer M (2000) Event-related brain potentials distinguish processing stages involved in face perception and recognition. Clin Neurophysiol 111: 694-705.

25. Caharel S, d'Arripe O, Ramon M, Jacques C, Rossion B (2009) Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: Evidence from the N170 ERP component. Neuropsychologia 47: 639-643.

26. Cziraki C, Greenlee MW, Kovács G (2010) Neural correlates of high-level adaptation-related aftereffects. J Neurophysiol 103: 1410-1417.

27. Kovács G, Cziraki C, Vidnyanszky Z, Schweinberger SR, Greenlee MW (2008) Position-specific and position-invariant face aftereffects reflect the adaptation of different cortical areas. Neuroimage 43: 156-164.

28. Kanwisher N, McDermott J, Chun MM (1997) The fusiform face area: A module in human extrastriate cortex specialized for face perception. J Neurosci 17: 4302-4311.

29. Furl N, van Rijsbergen NJ, Treves A, Dolan RJ (2007) Face adaptation aftereffects reveal anterior medial temporal cortex role in high level category representation. Neuroimage 37: 300-310.

30. Gauthier I, Tarr MJ, Moylan J, Skudlarski P, Gore JC, et al. (2000) The fusiform "face area" is part of a network that processes faces at the individual level. J Cogn Neurosci 12: 495-504.

31. Grill-Spector K, Henson R, Martin A (2006) Repetition and the brain: Neural models of stimulus-specific effects. Trends Cogn Sci 10: 14-23.

32. Rotshtein P, Henson RNA, Treves A, Driver J, Dolan RJ (2005) Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. Nat Neurosci 8: 107-113.

33. Beale JM, Keil FC (1995) Categorical effects in the perception of faces. Cognition 57: 217-239.

34. Walther C, Schweinberger SR, Kaiser D, Kovács G (2012) Neural correlates of priming and adaptation in familiar face perception. Cortex: , http://dx.doi.org/10.1016/j.cortex.2012.08.012.

35. Näsänen R (1999) Spatial frequency bandwidth used in the recognition of facial images. Vision Res 39: 3824-3833.

36. Rhodes G, Jeffery L, Watson TL, Jaquet E, Winkler C, et al. (2004) Orientation-contingent face aftereffects and implications for face-coding mechanisms. Curr Biol 14: 2119-2123.

37. Jaquet E, Rhodes G, Hayward WG (2007) Opposite aftereffects for Chinese and Caucasian faces are selective for social category information and not just physical face differences. Q J Exp Psychol 60: 1457-1467.

38. Oruc I, Barton JJS (2011) Adaptation improves discrimination of face identity. Proc Biol Sci 278: 2591-2597.

39. Rhodes G, Watson TL, Jeffery L, Clifford CWG (2010) Perceptual adaptation helps us identify faces. Vision Res 50: 963-968.

40. Theodoni P, Kovács G, Greenlee MW, Deco G (2011) Neuronal adaptation effects in decision making. J Neurosci 31: 234-246.

41. Thierry G, Martin CD, Downing P, Pegna AJ (2007) Controlling for interstimulus perceptual variance abolishes N170 face selectivity. Nat Neurosci 10: 505-511.

42. Rossion B, Jacques C (2008) Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. Neuroimage 39: 1959-1979.

43. Schweinberger SR, Huddy V, Burton AM (2004) N250r: A face-selective brain response to stimulus repetitions. Neuroreport 15: 1501-1505.

44. Schweinberger SR, Pickering EC, Burton AM, Kaufmann JM (2002) Human brain potential correlates of repetition priming in face and name recognition. Neuropsychologia 40: 2057-2073.

45. Schweinberger SR (2011) Neurophysiological correlates of face recognition. In: Calder AJ, Rhodes G, Johnson MH, Haxby JV, editors. The Oxford Handbook of Face Perception. Oxford: University Press. pp. 345-366.

46. Philiastides MG, Ratcliff R, Sajda P (2006) Neural representation of task difficulty and decision making during perceptual categorization: A timing diagram. J Neurosci 26: 8965-8975.

47. Banko EM, Gal V, Kortvelyes J, Kovács G, Vidnyanszky Z (2011) Dissociating the effect of noise on sensory processing and overall decision difficulty. J Neurosci 31: 2663-2674.

48. Schulz C, Kaufmann JM, Walther L, Schweinberger SR (2012) Effects of anticaricaturing vs. caricaturing and their neural correlates elucidate a role of shape for face learning. Neuropsychologia 50: 2426-2434.

49. Schulz C, Kaufmann JM, Kurt A, Schweinberger SR (2012) Faces forming traces: Neurophysiological correlates of learning naturally distinctive and caricatured faces. Neuroimage 63: 491-500.

50. Kaufmann JM, Schweinberger SR (2012) The faces you remember: Caricaturing shape facilitates brain processes reflecting the acquisition of new face representations. Biol Psychol 89: 21-33.

51. Valentine T (1991) A unified account of the effects of distinctiveness, inversion, and race in face recognition. Q J Exp Psychol A 43: 161-204.

52. Megreya AM, Burton AM (2006) Unfamiliar faces are not faces: Evidence from a matching task. Mem Cognit 34: 865-876.

53. Laurence S, Hole G (2011) The effect of familiarity on face adaptation. Perception 40: 450-463.

Supporting Information
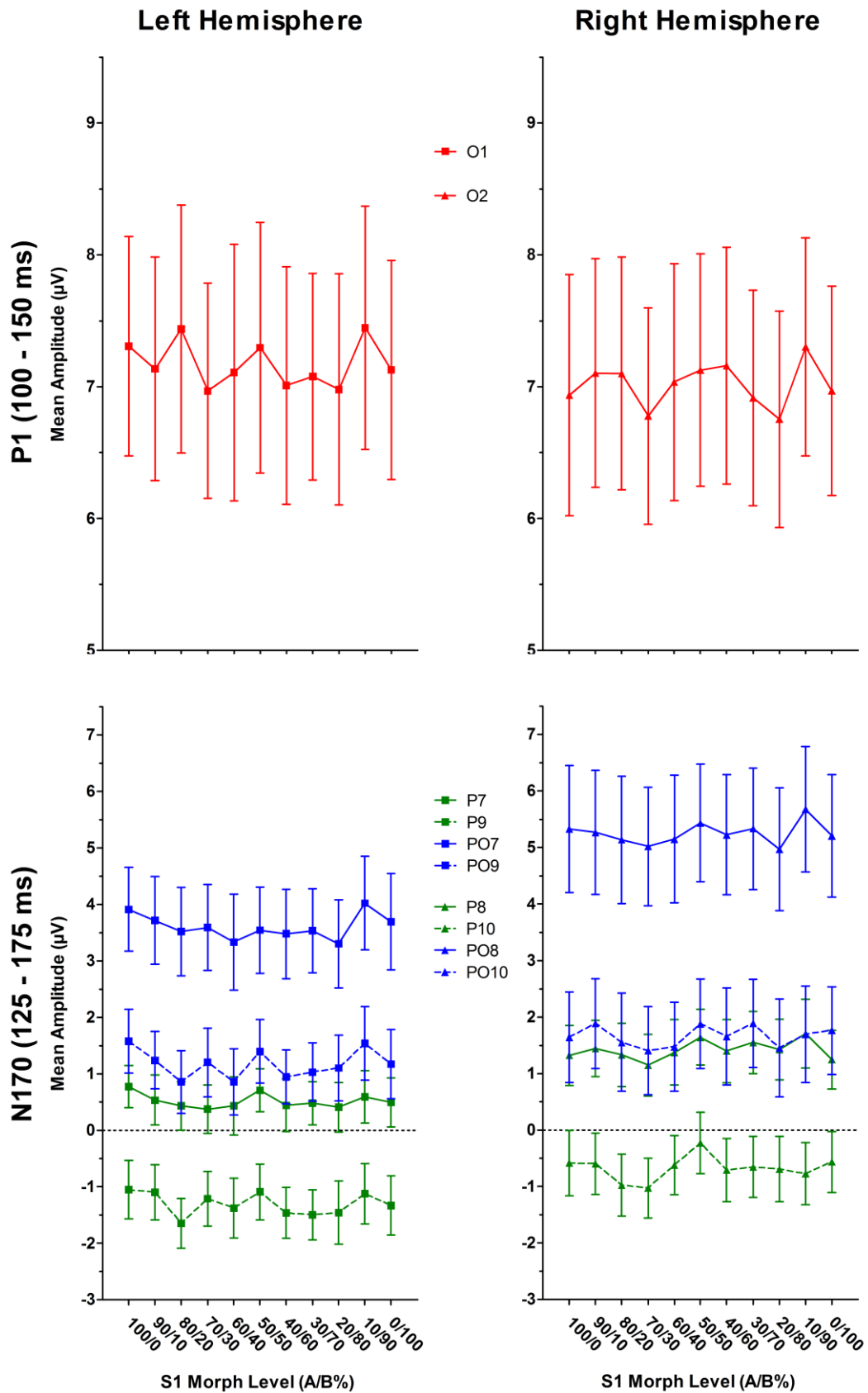
Figure S1. ERP effect of S1 condition on the P1 and N170 components. Mean amplitudes for $S2_{50/50\%}$ faces following the eleven S1 morphs at all analysed electrodes for P1 (100 - 150 ms) and N170 (125 - 175 ms) time windows. Error bars show ±1 standard error of the mean (SEM).
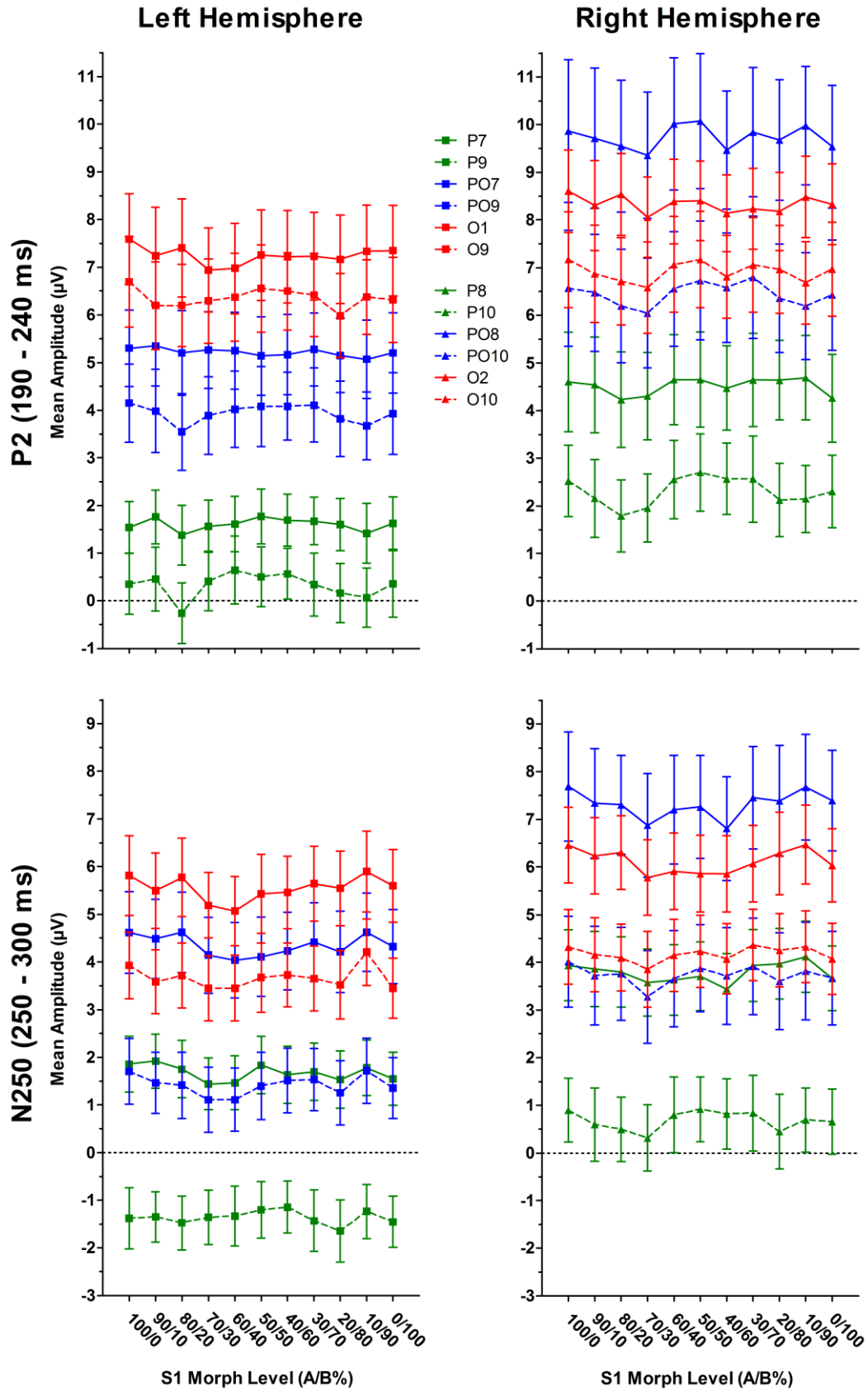
Figure S2. ERP effect of S1 condition on the P2 and N250 components. Mean amplitudes for $S2_{50/50\%}$ faces following the eleven S1 morphs at all analysed electrodes for P2 (190 - 240 ms) and N250 (250 - 300 ms) time windows. Error bars show ±1 standard error of the mean (SEM).
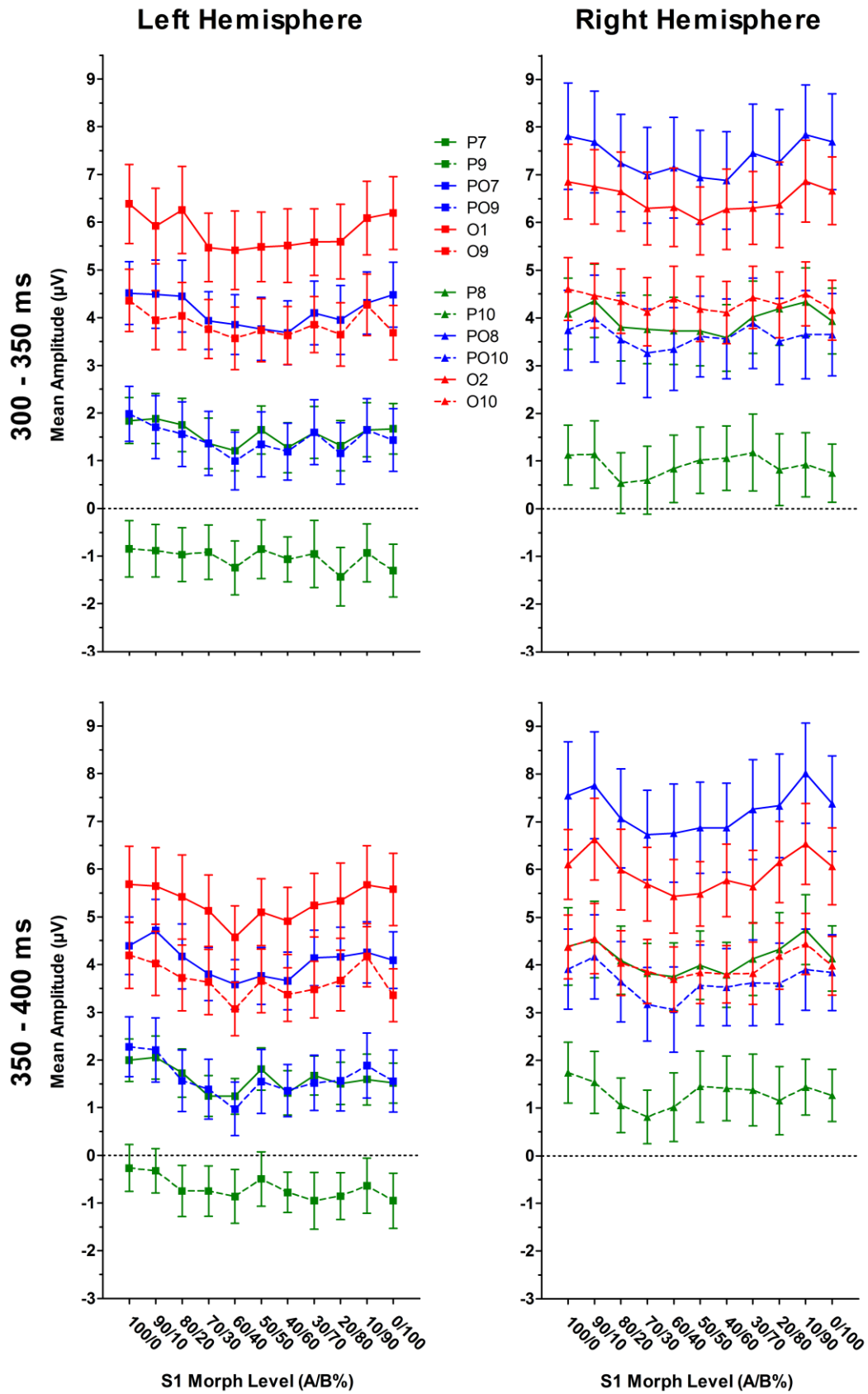
Figure S3. ERP effect of S1 condition in the late time windows. Mean amplitudes for $S2_{50/50\%}$ faces following the eleven S1 morphs at all analysed electrodes for the 300 - 350 ms and 350 - 400 ms time windows. Error bars show ±1 standard error of the mean (SEM).

3.3 Dissociating the neural bases of repetition priming and adaptation in the human brain for faces

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Abstract

The repetition of a given stimulus leads to the attenuation of the functional magnetic resonance imaging (fMRI) signal when compared to unrepeated stimuli, a phenomenon called fMRI adaptation or repetition suppression (RS). Previous studies related the RS of the fMRI signal behaviourally both to improved performance for the repeated stimulus (priming, PR) and to shifts of perception away from the first stimulus (adaptation-related aftereffects, AE). Here we used identical task (gender discrimination), trial structure (S1: 3000 ms, ISI: 600 ms, S2: 300 ms) and S2 stimuli (androgynous faces) to test how RS of the face-specific areas of the occipito-temporal cortex relates to PR and AE. By varying S1 we could induce PR (significantly faster reaction times when S1 and S2 were identical when compared to different images) as well as gender-specific AE (an increased ratio of male responses if S1 was a female face when compared to ambiguous faces or to Fourier-randomized noise (FOU) images). Presenting any face as S1 led to significant RS of the BOLD signal in the fusiform (FFA) and occipital face areas (OFA) as well as of the lateral occipital cortex (LO) of both hemispheres when compared to FOU, reflecting stimulus category-specific encoding. Primed trials, on the other hand, led to a signal reduction only in bilateral FFA. Our results show that PR and AE can be elicited for the same stimuli and depend on the similarity of S1 and S2. Further, the results suggest differential neural mechanisms of category-specific processing and image repetition PR.

Keywords: fMRI, priming, adaptation, faces

Introduction

Repeating a certain stimulus has several consequences both on the behaviour of a subject as well as on the neural responses. Behaviourally the prior presentation of a related or identical stimulus can lead to faster and more accurate responses for a given target. This effect is termed as priming (PR) and is studied extensively for both low (Magnussen 2000) and high-level stimuli, such as faces. In the latter case, PR effects were typically investigated for familiarity or identity decisions in long-term (e.g., Ellis et al. 1987; Ellis et al. 1996) and immediate repetition contexts (e.g., Schweinberger et al. 2002; Brooks et al. 2002; Bindemann et al. 2008). In addition, in various paradigms the preceding stimulus (the adaptor) has been shown to bias the decisions about a target, leading to contrastive adaptation-related aftereffects (AEs; Clifford et al. 2007; Thompson and Burr 2009). Such AEs have been found for a wide range of stimuli from oriented lines (Campbell and Maffei 1971; Clifford 2002) and moving patterns (Sekuler and Ganz 1963; Anstis et al. 1998) to high-level visual stimuli such as faces (e.g., Webster and MacLin 1999; for a review, see Webster and MacLeod 2011). In such paradigms of AE for example, the gender classification of an androgynous face was found to be biased towards male decisions following prolonged adaptation to a female face and towards female decisions following adaptation to a male face (Kloth et al. 2010; Kovács et al. 2006, 2007; Webster et al. 2004). Despite the clear differences in their behavioural outcomes, currently both PR and AEs are associated with similar neural effects, predominantly with a reduction of neural activation for the repeated stimulus when compared to a non-repeated one, a phenomenon termed as repetition suppression (RS).

Although PR effects can also be observed for the repetition of semantically related non-identical stimuli, in the current study we focus on the case of image repetition PR where the identical stimulus is repeated, since there is evidence that both phenomena rely on different neural processes (Schweinberger et al. 1995). For the repetition of identical stimuli, several extracellular single-cell studies showed RS of the neural response in the monkey brain (Gross et al. 1972; Miller et al. 1991; Desimone 1996). Later, the neural effects of stimulus repetition have also been studied extensively in human subjects using functional magnetic resonance imaging (fMRI). The blood oxygen level dependent (BOLD) signals of the extrastriate visual areas have been shown to decrease for repeated when compared to non-repeated stimulation, a phenomenon currently considered as the neuroimaging equivalent of the RS observed on single-cell level. This phenomenon has become known as fMRI adaptation (fMRIa) and is currently widely applied in the field of cognitive neurosciences (for reviews see Grill-Spector

and Malach 2001;Grill-Spector et al. 2006; Krekelberg et al. 2006) to infer neural stimulus tuning by manipulating the adaptor stimuli and monitoring the changes of response attenuation in very different behavioural paradigms (Kourtzi and Kanwisher 2001; Grill-Spector et al. 2006; Malach 2012). However, due to the large variety of applied designs it is not yet clear how RS and certain behavioural effects relate to each other. Moreover, although several models have been suggested in the past to explain the neural mechanisms of fMRIa and RS (DeBaene and Vogels 2010; Grill-Spector et al. 2006; Sawamura et al. 2006), it is also unclear as yet if a single, unified model can explain the response attenuation of different cortical areas elicited by various methods.

As for paradigms related to PR, the repetition of an identical stimulus leads to RS of the BOLD signal in extrastriate regions of the visual cortex (Buckner et al. 1998; Koutstal et al. 2001; Henson 2003). This RS is usually the most pronounced for immediate stimulus repetitions (Sayres and Grill-Spector 2006), but has also been shown after longer delays, even after several days (van Turennout et al. 2001). For face stimuli, repeated presentation of a certain face elicits reduced BOLD signals in the face selective cortical regions (Henson et al. 2002; Andrews and Ewbank 2004; Summerfield 2008), such as the occipital face area (OFA; Gauthier et al. 2000) and the fusiform face area (FFA; Kanwisher et al. 1997), but also in the object-selective lateral occipital cortex (LO; Malach et al. 1995). These regions have been connected to different functions within the face-processing network (Haxby et al. 2000), the FFA being associated with face processing at a configurational level (Kanwisher et al. 1998), which is supported by RS not being disrupted by low-level changes in this region (Andrews and Ewbank 2004) or by changes in other aspects of the faces such as their expression (Winston et al. 2004). A study using morph continua between two famous faces (Rotshtein et al. 2005) could show that RS in the FFA was only present if the category boundary between the two presented stimuli was crossed, reflecting the neural basis for the effect of categorical perception of face identity (Beale and Keil 1995). In contrast to this, in this study RS in OFA was largely driven by physical changes in the stimuli, regardless of the location of the individual stimuli in the morph continuum (Rotshtein et al. 2005). The authors could also show that anterior regions of the face-processing network reflect greater sensitivity for identity changes (i.e. greater BOLD-signal differences for pairs lying within one identity and pairs crossing the categorical boundary) for faces that were more familiar to the subjects. Indeed, RS has been shown to depend on face familiarity: while reduced responses in face-selective regions can be observed for familiar faces, enhanced responses can be observed for unfamiliar stimuli (Henson et al. 2000). Although most of these studies of RS did not employ

behavioural measures of processing efficiency (such as faster reaction times for primed vs. unprimed conditions), it is suggested that this RS of the BOLD signal is related to the behaviourally observed effects in repetition PR paradigms (for a review see Henson 2003). Nevertheless, most of the times it is not straightforward to link behavioural PR and RS causally (see Buracas et al. 2005 for the general problem of linking fMRI responses to behaviour) and so far only a few neuroimaging studies attempted to make such correlations. In fact, some studies raised doubts about RS being the neural equivalent of PR, as either RS was not specific for their "primed" conditions (Ganel et al. 2006) or its magnitude did not correlate with the amount of behaviourally observed effects (Sayres and Grill-Spector 2006).

Interestingly, AEs in face perception have been associated with RS in face-selective regions as well (Cziraki et al. 2010; Furl et al. 2007; Löffler et al. 2005). Gender adaptation has been shown to lead to lower BOLD signals in OFA and FFA when compared to control conditions using phase-randomized adaptors (Kovács et al. 2008). This result is consistent with the N170/M170 modulations in event-related potentials that have been observed following adaptation (Kovács et al. 2005; Kovács et al. 2007; Harris and Nakayama 2007) and is thought to reflect the structural encoding stages of face processing (Bentin et al. 1996; Rossion et al. 1999). Reduced activity in extrastriate body area (EBA; Downing et al. 2001) and FFA has also been found for face versus hand category adaptation experiments (Cziraki et al. 2010). In this study, face or hand adaptors biased the perception of ambiguous test stimuli in opposite directions: while hand adaptation led to RS in EBA, face adaptation led to RS in FFA, showing that adaptation aftereffects are category-specific on a neural level. In studies of face gender AEs, RS seems to be associated with the behavioural effect of biased gender perception: RS was shown to occur in conditions in which gender perception was altered due to prior adaptation (Kovács et al. 2008). However, a recent ERP study (Kloth et al. 2010) comparing the effects of gender-specific and face-specific adaptation failed to show a clear connection between N170 modulations and gender-specific adaptation: the same N170 modulations were found for test stimuli following any face adaptors (ambiguous as well as unambiguous) when compared to phase-randomized noise adaptors. This suggests that the N170 modulation effect is due to the adaptation to the category of faces, irrespective of gender and reflects the neural processes related to generic face configuration processing rather than gender-specific encoding mechanisms.

The similarity of findings from neuroimaging studies of PR and AEs is somewhat surprising because of the distinct behavioural implications of the two phenomena. Although there are studies that have tried to elicit PR and AEs in subjects' behaviour by manipulating

the temporal properties, predominantly the length of the inter-stimulus interval of their paradigms (motion AE: Kanai and Verstraten 2005; Pavan et al. 2009; high-level object AE: Daelli et al. 2010) no study has compared the fMRI correlates of PR and adaptation within the same subjects and paradigm as of yet. Such a comparison could shed light on the question, if RS, as it is associated with both behavioural phenomena, reflects different mechanisms or a common underlying system.

However, eliciting both effects within a single paradigm is not entirely straightforward due to the fundamental differences of commonly used PR and AE paradigms. First, the timing parameters between PR and AE studies differ: while PR paradigms typically employ short S1 (prime) durations or even masked presentation of the prime (Henson 2003; Sayres and Grill-Spector 2006), AE paradigms typically use longer S1 (adaptor) durations (although relatively shorter durations can lead to AEs as well; see Kovács 2007). Second, the behavioural tasks vary for studies of PR and AEs: tasks in typical PR studies are usually based on features necessary for recognition, which are suitable for quantifying processing efficiency (e.g. deciding if a person is a famous person or not), while for AEs the tasks always have to include the adapted stimulus feature in order to see the behavioural AE (e.g. deciding if a face is male or female after being adapted to a male or female face).

In a recent EEG study (Walther et al. 2012), we used a face identity adaptation paradigm, where we manipulated the ambiguity of the test stimulus on a continuum between two famous faces. For ambiguous test stimuli we observed behavioural AEs. However, if the test stimuli were less ambiguous (i.e. they were closer to the veridical adaptor faces) PR started to emerge. In addition to showing that both effects can be evoked within the same paradigm and subjects, we were able to identify ERP components that reflect PR and AEs separately. PR was already reflected by a modulation of components as early as 90 ms and being the most pronounced in the N250r range (Schweinberger et al. 2002). In contrast to this, category-specific adaptation effects were the largest on the N170 component while identity-specific adaptation effects emerged only at around 205-255 ms post-stimulus onset. These results suggested that exclusive, temporally separate mechanisms might underlie identity-specific PR and AE as well as category-specific adaptation processes.

In our current study, we used fMRI to disentangle brain regions mediating PR and AEs. We used a gender adaptation paradigm (Kovács et al. 2006, 2008) with familiar face stimuli to demonstrate that PR and adaptation to face category can be observed within the same subjects and paradigm simultaneously. However, in contrast to our previous experiment (Walther et al. 2012) we manipulated PR and AEs by changing the S1 image rather than the

S2 test stimulus. We were able to confirm that both PR and category-specific adaptation effects are related to the RS of face selective regions. In addition to that we show that the two behavioural phenomena PR and AE differ in their neural correlates and are therefore likely to employ different neural mechanisms and systems.

Materials and Methods

Subjects

Seventeen healthy university students participated in the experiment (mean age: 22.9 years, *SD*: 2.7 years, 11 female, all right-handed). All subjects had normal or corrected-to normal vision and provided their written consent. The experiment was carried out in accordance to the Declaration of Helsinki and approved by the Ethical Committee of the University of Regensburg.

Stimulation and Procedure

We collected images of 25 female and 25 male celebrities from the public domain of the world-wide web. The celebrities were selected to be well-known in Germany and therefore familiar to all subjects. Images were selected to be full-frontal and have a neutral expression. Next, we created 25 female-male stimulus pairs and for each pair we created the 50%/50% intermediate androgynous morph image, using Sierra Morph 2.5 (Sierra Home). Afterwards all images were converted into grayscale, fit behind a shield-mask (to avoid any heuristic-based decisions of the outer features, see Goshen-Gottstein and Ganel 2000 for a similar procedure) and subjectively equated for luminance and contrast using Adobe Photoshop CS5 (Adobe Systems, San Jose, CA, USA). All original male images were Fourier phase randomized using the algorithm of Näsänen (1999) which replaces the phase spectrum with random values (ranging from 0 to 360), leaving the amplitude spectrum of the image intact. These images were used as control ("Fourier") stimuli. All images (mean luminance: 18 cd/m²) were presented centrally and subtended a visual angle of 7° vertically and 6° horizontally. Stimuli were back-projected via an LCD video projector (JVC, DLA-G20, Yokohama, Japan, 72 Hz, 800 x 600 resolution) onto a translucent circular screen (30° diameter), placed inside the scanner bore at 63 cm from the observer. Stimulus presentation was controlled via Matlab (The MathWorks, Natick, MA, USA), using Psychtoolbox (Version 3.0.8). The experiment was composed of three runs of a gender decision task (similar to that of Kovács et al. 2008), presented in a random order. Subjects had to perform a two-alternative forced choice gender discrimination task, deciding if the androgynous target stimulus (S2,

presented for 300 ms) was male or female by pressing a button with either their index or middle finger. In each run (100 trials per run) the S2 could be preceded by different adaptor stimuli (S1), which were presented for 3000 ms. In the "Fourier run" (FOU), S1 was always a Fourier phase randomized image. In half of the trials this image was the Fourier phase randomized version of the male image used to create the S2 (FOU-S) while in another half it was the phase-randomized version of another, unrelated original male face (FOU-D). In the "androgynous run" (ANG), on half of the trials the S1 was the image of the same ambiguous androgynous face as the S2 (primed trial, ANG-S), while on the other half of the trials the S1 was an ambiguous image of another face pair (unprimed trial, ANG-D). In the "female run" (FEM), on half of the trials the S1 was the original female face that was used to create the ambiguous S2 (adaptation same trial, FEM-S), while on the other half of the trials the S1 was an original female face that was unrelated to the S2 (adaptation different trial, FEM-D). Note that despite the changes of S1, the S2, as well as the task of the subjects, was identical for every block. These three runs were designed in a way that FOU, where S1 was always the Fourier phase randomized version of S2, served as a control condition to estimate face category-specific effects (Kloth et al. 2010). ANG, where S1 was either identical to S2 or it was another androgynous face, was designed to elicit image repetition and image PR effects. Finally FEM was used for testing gender-specific adaptation effects (Kloth et al. 2010; Kovács et al. 2008). S1 and S2 were always separated by an inter-stimulus interval varying randomly between 400-800 ms and the trials were followed by a 1-3 s long inter-trial interval. To minimize local feature adaptation, the size of the S2 was reduced by 10% relative to S1, so that the S2 subtended a visual angle of 6.3° vertically and 5.4° horizontally. Each S2 image was repeated four times per block. For stimulus trial examples see Figure 1.

Parameters and Data Analysis

Imaging was performed using a 3-Tesla MR Head scanner (Siemens Allegra, Erlangen, Germany). For the functional series we continuously acquired images (34 slices, 10° tilted relative to axial, T2* weighted EPI sequence, TR = 2000 ms; TE = 30 ms; flip angle = 90°; 64 x 64 matrices; in-plane resolution: 3 x 3 mm; slice thickness: 3 mm). High-resolution T1-weighted images were acquired using a magnetization-prepared rapid gradient-echo sequence (MP-RAGE; TR = 2250 ms; TE = 2.6 ms; 1 mm isotropic voxel size) to obtain a 3D structural scan. Details of preprocessing and statistical analysis are given elsewhere (Kovács et al. 2008; Cziraki et al. 2010). Briefly, the functional images were realigned, normalized to the MNI-152 space, resampled to 2 x 2 x 2 mm resolution and spatially smoothed with a Gaussian kernel of 8 mm FWHM (SPM8, Wellcome Department of Imaging Neuroscience, London,

UK). Regions of interests (ROI) analysis was based on the results of a separate functional localizer run (480 s long, 20 s epochs of stimulation). For this localizer scan, blocks of faces (different from those used in the main experiment), nonsense-objects and their Fourier phase randomized versions were presented, interleaved with 20 s of blank periods (stimulus presentation rate: 2 Hz; 300 ms exposition time; 200 ms blank). MARSBAR 0.42 toolbox for SPM (Brett et al. 2002) was used for the ROI data analysis. One subject was excluded from the ROI analysis due to bad localizer data.
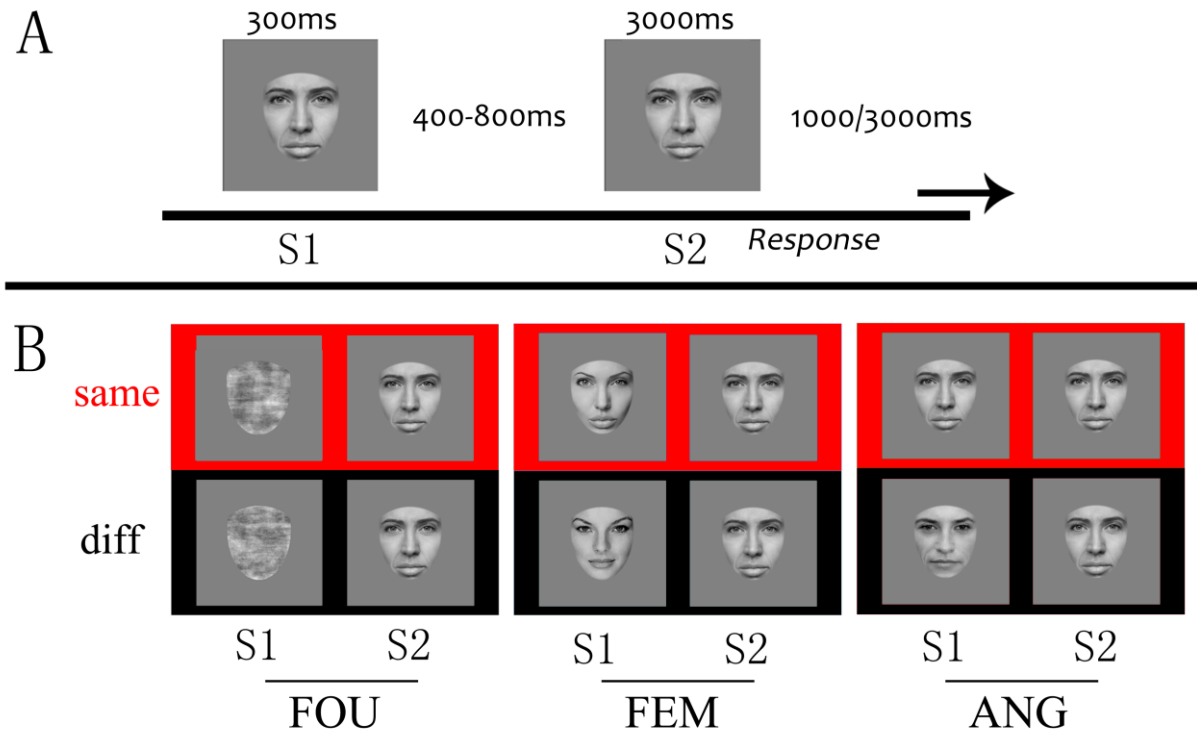
Figure 1. A: Timing parameters of a single trial. This example shows a ANG-S trial. B: Overview of all conditions used in the experiment. Note that the S2 is identical in every condition, while the S1 varies. In the SAME-condition, the S1 is related or identical to the S2 (see methods), in the DIFF-condition, the S1 is unrelated to the S1. FOU, ANG, and FEM were grouped in runs, while the SAME and DIFF trials were presented randomly during each run.

The location of face responsive areas was determined individually as areas responding more strongly to faces than to objects and to Fourier noise images in the functional localizer scans ($p_{uncorrected} < 10^{-6}$; $T = 4.86$, $df = 273$), FFA (average MNI coordinates ($\pm SE$): -40(1), -57(2), -19(1) and 41(1), 55(2), -17(1) for the left ($n = 14$) and right hemispheres ($n = 15$), respectively) and the OFA (average MNI coordinates ($\pm SE$): -41(1), -78(2), -12(1) and 43(1), -77(1), -12(1) for the left ($n = 14$) and right ($n = 13$) hemispheres). Areas selectively responding to objects were determined by similar functional localizer scans comparing the activity obtained for nonsense objects versus their Fourier randomized versions and faces

($p_{\text{uncorrected}} < 10^{-6}$; $T = 4.86$; $df = 273$), area LO: (average MNI coordinates (±SE): 36(2), -79(2), 7(2) and 37(2), -79(2), 4(2) for left ($n = 11$) and right ($n = 11$) hemispheres). The ROIs were selected individually on the single subject level from these thresholded T-maps. Areas matching our anatomical criteria and lying closest to the corresponding reference clusters (based on the results of the previous literature) were considered as their appropriate equivalents on the single subject level. A time series of the BOLD mean voxel signal within an 4 mm radius sphere around the local peak of the areas of interest was calculated and extracted from our event-related sessions using finite impulse response (FIR) models (Ollinger et al. 2001). The convolution of a reference hemodynamic response function with box-car functions, representing the onsets and durations of the experimental conditions, was used to define the regressors for a general linear model analysis. All trials were analysed and modeled at the onset of the S2 stimuli. The peak of the event-related averages at 6 s was used as an estimate of the magnitude of the response and was averaged across observers. In addition to the above described ROI analysis we also conducted a random-effects whole-brain analysis (with a threshold PFWE < .05) using the GLM model of the ROI analysis to search for additional areas, modulated by AE or PR. Finally, since recent studies suggest that in adaptation paradigms the cortical response can depend on the behavioural response of the subjects (Cziraki et al. 2010) we performed a second random-effects whole-brain analysis where subjects' decisions were also included in the GLM model as a regressor. For this analysis we split the data of FEM-S/FEM-D according to whether adaptation biased perception away from the gender of the adaptor in a certain trial, or whether it did not lead to such contrastive biases. Similarly we split the data of the ANG-S / ANG-D conditions as well into trials where the reaction times were shorter than the respective subject's median reaction time (i.e., PR was present) and trials where the reaction time was above this subject's median reaction time (i.e., no PR is manifest).

For the gender discrimination performance and for the reaction times we performed a two-way within subject ANOVA with run type (3; FOU, FEM, ANG) and trial type (2; same or different) as factors. In addition, we estimated the magnitude of AE using the following formula: $\text{Perf}_A = (\text{Perf}_{\text{FEM-S}} + \text{Perf}_{\text{FEM-D}}) / 2 - \text{Perf}_{\text{ANG-D}}$ where $\text{Perf}_{\text{FEM-S}}$, $\text{Perf}_{\text{FEM-D}}$, and $\text{Perf}_{\text{ANG-D}}$ are the % endorsed as male in the FEM-S, FEM-D, and ANG-D conditions, respectively. Similarly, the magnitude of PR was calculated by $\text{RT}_P = \text{RT}_{\text{ANG-D}} - \text{RT}_{\text{ANG-S}}$ where $\text{RT}_{\text{ANG-S}}$ and $\text{RT}_{\text{ANG-D}}$ are the average reaction times of the subjects for ANG-S and ANG-D, respectively. All post-hoc analyses were performed by Fisher LSD tests.
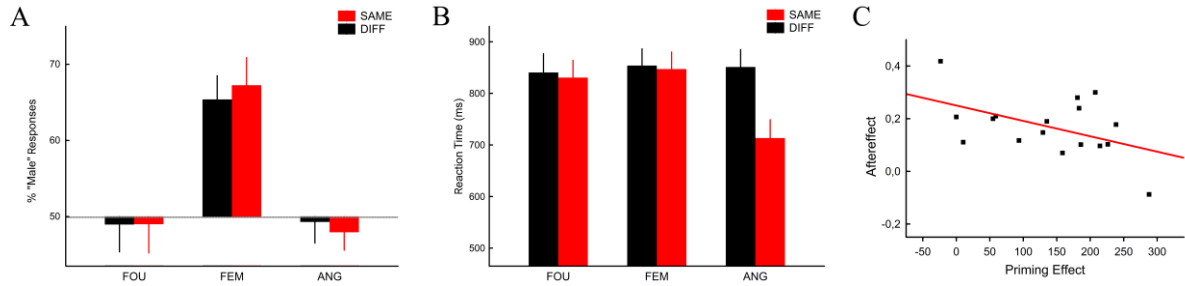
Results

Behavioral Results

Aftereffect. Subjects' gender discrimination performance (see Fig. 2A) depended significantly on the nature of the S1 (main effect of run: $F(2,32) = 23.71$, $p < .001$, without a significant main effect of trial-type or run x trial interaction) in the sense that the mean proportion of "male" responses was significantly higher for FEM-S and FEM-D when compared to the other conditions (where it was around 50% chance level). This shows that prior presentation of a female face biases the perception of an ambiguous androgynous face towards male responses and leads to gender-specific face aftereffects, confirming previous results (Kloth et al. 2010; Kovács et al. 2006, 2008). On the other hand, FEM-S and FEM-D were not significantly different ($p = .28$), suggesting that the identity of the adaptor stimulus has no effect on this bias of gender decision of the subjects. The same was true for FOU-S and FOU-D as well ($p = .98$). Finally, it is worth mentioning that the average gender decisions in the ANG-S and ANG-D conditions were not significantly different from the performance in the FOU-S or FOU-D conditions either ($p > .50$ for all comparisons). Since S1 was an androgynous face in both ANG-S and ANG-D this confirms previous data that suggest no aftereffects after the presentation of neutral stimuli (Webster and MacLin 1999).

Image repetition PR. We found a significant difference in reaction times (see Fig. 2B) between S1 conditions as well (main effect of run: $F(2,32) = 4.03$, $p = .03$; main effect of trial: $F(1,16) = 23.00$, $p < .001$; run x trial interaction: $F(2,32) = 36.23$, $p < .001$). The responses were significantly faster in ANG-S trials when compared to any other S1 condition ($p < .001$ for all comparisons), as shown by post-hoc tests. This suggests that repetition of the same stimulus (note that S1 and S2 were identical images in the ANG-S condition but S1 and S2 differed in size by approximately 10 %; see Methods) leads to shorter reaction times in the gender decision task, a manifestation of the behavioural PR effect. Further, there was no significant difference between any other condition ($p > .10$ for all comparisons of FOU-S, FOU-D, FEM-S, FEM-D and ANG-D).

Interestingly, we found a significant negative correlation between the magnitude of PR (RT_P; expressed as the reaction time difference between ANG-S and ANG-D; see Methods) and gender AE (the difference of proportion of "male" responses between FEM-S/FEM-D and FOU-S/FOU-D; see Methods; see Fig. 2C; $r = -.48$, $p = .05$). Subjects with larger PR showed weaker AE and vice versa. This suggests that the behavioural aftereffects and repetition PR effects are related to each other. This is so despite the fact that PR and AE are manifest after different S1 images (note that the AE is measured by comparing ANG-D vs.

FEM S1 trials while the PR is measured by comparing the reaction times of the ANG-S vs. ANG-D S1 trials).

Figure 2. Behavioural results. A: Gender responses as proportions of "male" classifications. Only in the FEM conditions responses are biased (towards more "male" classifications), while in all other conditions the proportion of male responses is around 50%. B: Reaction times. Reaction times were faster in the ANG-S condition, which reflects a behavioural priming effect. C: Correlation of priming and adaptation effect magnitudes. Subjects showing larger priming effects tended to show weaker adaptation effects and vice versa. Aftereffect magnitude was computed as the difference of FEM and ANG-D responses proportions, while priming effects were computed as the reaction time difference of ANG-D and ANG-S (see methods).

Neuroimaging Results

Region of interest analysis - category-specific adaptation. For quantifying RS, associated with the processing of stimulus category we focused on the difference between the FOU-S/D and the FEM-S/D conditions. We expected significant response reductions for the FEM-S and FEM-D conditions, similarly to previous findings of adaptation studies with peripheral faces (Kovács et al. 2008) and with other high-level stimuli (Cziraki et al. 2010). Figure 3A shows the results of this comparison for each ROI. We could observe significant adaptation-related response reductions in the left FFA (main effect of run: $F(2,26) = 12.43$, $p < .001$), right FFA (main effect of run: $F(2,28) = 9.63$, $p < .001$) and left OFA (main effect of run: $F(2,26) = 6.02$, $p = .007$). This was due to the fact that both FOU-S and FOU-D were significantly different from FEM-S as well as from FEM-D ($p < .01$ for all comparisons) in a way that responses to the FEM trials were lower than those to the FOU trials. For all these regions, however, post-hoc tests showed that the FOU-S and FOU-D conditions did not differ from each other ($p > .80$ for right and left FFA, $p = .22$ for left OFA). Similarly, FEM-S and FEM-D conditions evoked similar BOLD signals ($p > .10$ for all comparisons). The right OFA also showed a strong tendency for lower responses in the FEM when compared to FOU conditions ($F(2,24) = 2.81$, $p = .08$) and the same was true for right LO ($F(2,20) = 2.95$, $p = .07$). No main effect of block and therefore no indication of adaptation-related response reduction was found in the left LO. Altogether this comparison shows that our paradigm led to a significant face category-specific adaptation of the response in several areas of the

occipito-temporal cortex. This confirms previous findings with peripheral stimulus presentations (Kovács et al. 2008).

Region of interest analysis - gender-specific adaptation. The comparison of FOU with FEM illustrates the sensitivity of a given area to the category of face stimuli per se, suggesting "generic" face sensitivity, in a similar way to Kloth et al. (2010). However, we also found a significant response reduction for ANG-S and ANG-D trials in left and right FFA and in left OFA when comparing them to the FOU-S and FOU-D conditions ($p < .01$ for all comparisons). This indicates that the S1 being a face is sufficient for eliciting the effect. In order to test the more specific gender-related changes of the BOLD signal one should compare conditions where the stimuli are both faces but while one condition leads to specific AEs the other fails to do so. Hence, we also tested if there is a difference between the BOLD signal in the ANG-D condition (where S1 was an androgynous face, different from S2, that neither leads to bias of gender decisions, nor to reaction time benefits in our behavioural data; see Figs. 2A and B) when compared to that of the FEM-S/D conditions (where S1 is a female face, leading to AE). Similarly to previous findings for early ERP components (Kovács et al. 2006; Kloth et al. 2010) we did not find such a gender-specific response reduction in any of the areas.

Region of interest analysis - PR effects. For assessing the repetition PR effects, following previous neuroimaging studies (see Henson 2003), we were interested in the magnitude of RS when comparing a condition where S1 and S2 were identical images with a condition where S1 and S2 were of different faces. Thus we measured PR-related RS by comparing two conditions where S1 was an androgynous face, identical to (ANG-S) or different from (ANG-D) S2 (see Fig. 3B). We found a significant modulation of the BOLD signal bilaterally in the FFA (significant interaction of run x trial type: $F(2,26) = 5.76$, $p = .008$, and $F(2,28) = 4.55$, $p = .02$, for the left and right hemispheres, respectively), in that the responses of both left and right FFAs were weaker for ANG-S trials than for ANG-D trials ($p = .005$ and $p = .01$, for left and right hemispheres, respectively). Therefore, this modulation reflects the RS typically associated with stimulus-repetition-related PR (Grill-Spector et al. 2006). However, we did not find such effects in any other ROI of our study (no significant run x trial interaction for any other ROI).

Region of interest analysis - comparing PR and adaptation effects. As we were primarily interested in disentangling the two phenomena of PR and AEs, we also checked which regions show different responses for the ANG-S and FEM-S/FEM-D conditions. We found that the left FFA was the only ROI where responses to these conditions were different.

Both FEM-S and FEM-D elicited greater responses than ANG-S ($p < .001$ for both comparisons). This suggests that left, but not the right FFA might be differently involved in repetition PR- and gender AE-related mechanisms.
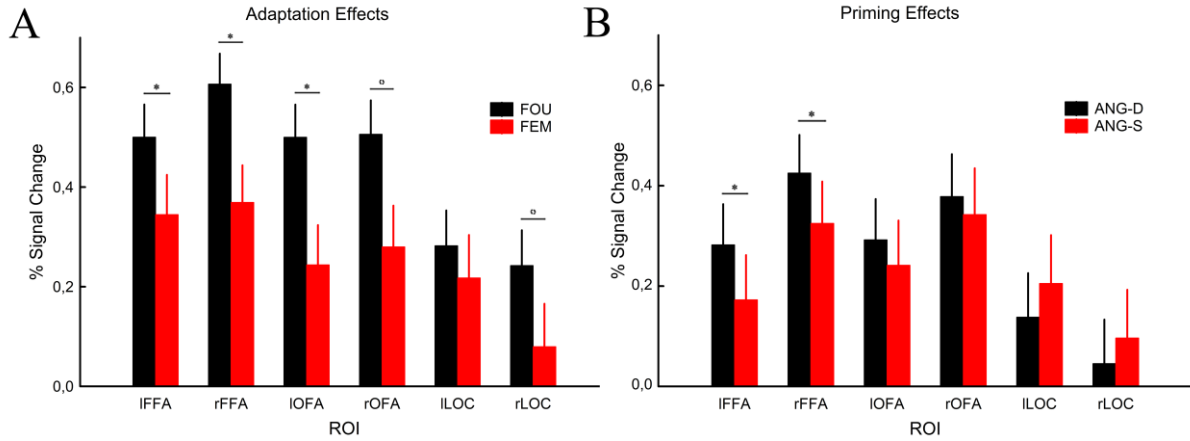
Figure 3. Adaptation (A) and priming (B) effects for each ROI. For the adaptation effects, FOU-S/FOU-D and FEM-S/FEM-D were merged (by computing the mean value) to common FOU and FEM conditions, respectively. Adaptation effects were observed in left and right FFA and left OFA. A significant priming effect could only be observed in the left and right FFA (*: $p < .01$, °: $p < .10$).

Whole-brain analysis. On the whole brain level (see Fig. 4A) we found a face category-specific effect, as revealed by the comparison of FOU conditions with all other conditions where S1 was a face (FEM-S/FEM-D and ANG-S/ANG-D), which can be seen in an extended region covering occipito-temporal parts of the visual cortex bilaterally. On the right side we found a cluster of 976 voxels ($p_{cluster} < .001$, $T_{peak} = 7.92$; peak coordinates: $x = 32$; $y = -82$; $z = 8$), and on the left side a cluster of 599 voxels ($p_{cluster} < .001$, $T_{peak} = 9.02$; peak coordinates: $x = -36$; $y = -86$; $z = 16$). This shows that large areas in the extrastriate cortex seem to contribute to face-repetition-related response reductions. No area showed response reduction related to PR (when tested by comparing ANG-D > ANG-S) on the whole-brain level. Interestingly however, we found a region that allowed to distinguish between image repetition PR- and face adaptation-related activations (expressed by the FEM > ANG-S contrast) in the whole-brain analysis (70 voxels; $p_{cluster} = .003$, $T_{peak} = 4.20$; peak coordinates: $x = -4$; $y = 28$; $z = 36$). This cluster is located in the anterior cingulate cortex (ACC) and it showed stronger activation in the FEM-S/FEM-D than in the ANG-S condition.

Since previous studies suggest that the neural activations during an adaptation paradigm depend on the perceptual bias of the subjects (Cziraki et al. 2010) we also performed a second whole-brain analysis with a re-estimated design that included the behavioural responses of the subjects as regressors as well. For this analysis we split the FEM trials on the basis whether

behavioural aftereffects were observed or not, and the ANG-S trials according to the effectiveness of PR (see Methods for details). With this analysis we could show that different brain regions are involved in the extent and success of the behavioural PR and adaptation outcomes, which also suggests different mechanisms underlying PR and AEs (see Fig. 4B). The trials leading to aftereffects were related to lower activations than those where adaptation led to no perceptual biases in three areas: 1) right middle frontal gyrus (135 voxels; $p_{cluster}$ = .034, T_{peak} = 5.68; peak coordinates: x = 42; y = 44; z = 24), 2) right inferior parietal lobe (173 voxels; $p_{cluster}$ = .010, T_{peak} = 5.42; peak coordinates: x = 52; y = -44; z = 42), and 3) the right medial frontal gyrus and right supplementary motor area (181 voxels; $p_{cluster}$ = .008, T_{peak} = 5.30; peak coordinates: x = 8; y = 12; z = 52). For trials with strong PR effects (i.e. shorter RTs than the median, see Methods) we found weaker activations than for trials without PR in the ACC (201 voxels; $p_{cluster}$ = .006, T_{peak} = 6.03; peak coordinates: x = 10; y = 22; z = 28), located close to the previously described medial frontal activation. The differential activations in these regions could indicate more efficient processing in the case of effective PR or AEs by reduced response conflicts.
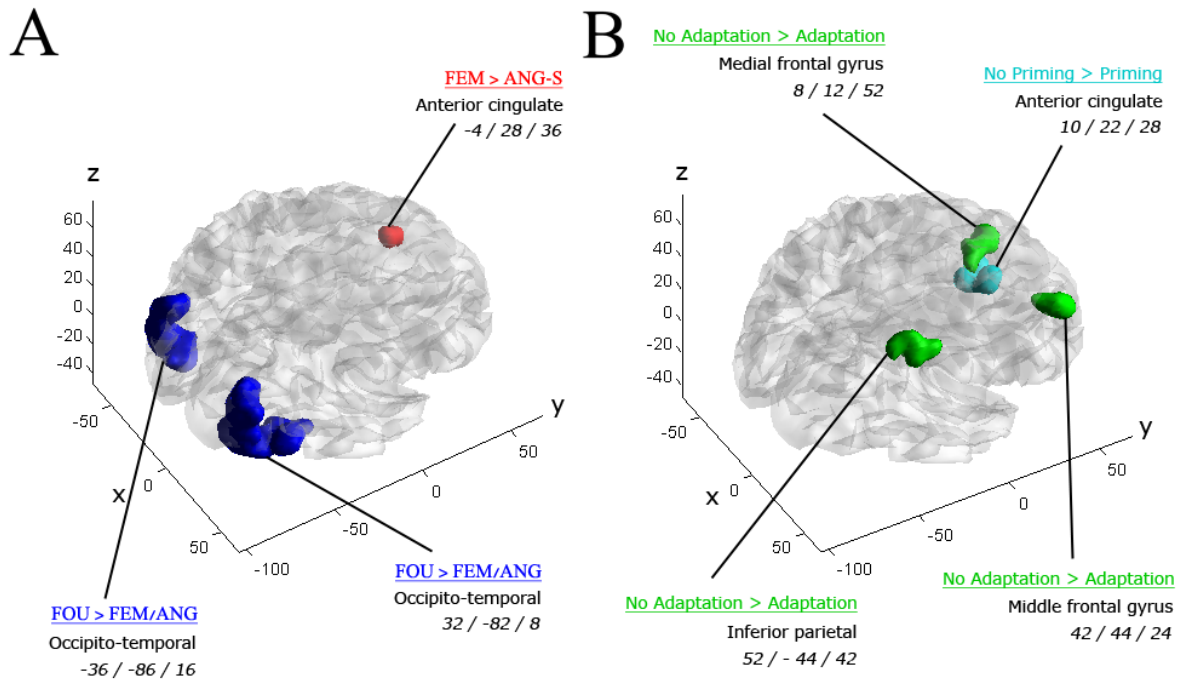
Figure 4. Results of the whole-brain analysis. A: Location of clusters showing response reduction related to face repetition (FOU > FEM/ANG; again FOU is the mean of FOU-S and FOU-D, FEM/ANG is the mean of FEM-S, FEM-D, ANG-S, and ANG-D) and a cluster showing differential responses for priming and adaptation (FEM > ANG-S). B: Clusters obtained from the split dataset. Three areas showed larger responses if adaptation was effective than if it was ineffective (No Adaptation > Adaptation) and one cluster showed larger activation for effective priming than for ineffective priming (No Priming > Priming).

Discussion

Our behavioural results show that repetition PR and face gender-specific AEs can be induced within the same paradigm and subjects. Using a gender decision task, PR was manifest in reduced reaction times when S1 and S2 were identical stimuli in the ANG-S as compared to any other condition. This novel effect of repetition of the same androgynous face might be - at least to some extent - related to findings of PR reported for veridical faces (for the case of familiarity decisions, see Ellis et al. 1997; and for the case of gender decisions, see Goshen-Gottstein and Ganel 2000). Several studies also suggested that there are image-specific and identity-specific contributions to PR effects in face perception (Schweinberger et al. 2002; Bindemann et al. 2008), the former playing a larger role in the present paradigm presumably. Gender-specific AEs (Webster et al. 2004) were observed as a male bias in gender perception following female adaptation (FEM-S/FEM-D) as compared to androgynous (ANG-S/ANG-D) or noise adaptation (FOU). This shows that we could specifically elicit behavioural PR and gender-specific AEs within the same subjects by manipulating solely the adaptor stimulus, while all other parameters remained constant. Interestingly, we found that the magnitude of the two behavioural effects was negatively correlated with each other: the fact that subjects with greater PR effects showed weaker AEs and vice versa reflects the differences between the underlying mechanisms or response strategies used.

Category-specific Adaptation

On a neural level we were able to show that both PR and adaptation effects are related to RS in the face-selective regions of the occipito-temporal cortex. We found that generic face category-specific adaptation effects (as assessed by a response reduction for the repetition of a face compared to the FOU condition) are reflected in RS in early and late regions of the object and face processing network (LOC, OFA, FFA). The RS we found when comparing FOU and FEM conditions was not specific for the biased perception on a behavioural level, as the same effect was also present when comparing FOU with ANG condition (where no decision shift was observed in gender classification). This unspecific nature of RS is also visible in the response reduction of large bilateral occipito-temporal regions observed in the whole-brain analysis when contrasting the FOU conditions and all other conditions. Therefore we suggest that the comparison of FOU and FEM conditions reflects a generic face category-specific effect in the sense that it is sensitive to the repetition of stimuli belonging to the category of faces.

Gender-specific Adaptation Effects

Similar to Kloth et al. (2010), who did not find any gender-specific AEs on early ERP components, we were not able to find large-scale RS related to gender-specific AEs in visual cortex. The reason behind the lack of such gender-specific adaptation effects is unclear. One possibility is that the neurons encoding the different genders (to a certain extent) differentially are intermixed with each other within the occipito-temporal areas. However, another, equally plausible reason can be that female- and male-specific neurons are spatially separated from each other, but only to such an extent that is not visible with current standard neuroimaging techniques. Since recent studies (Freeman et al. 2010) suggest that FFA encodes the gender of anothers' face, the gender-specific encoding of human faces will require further studies.

Image-PR-related Effects

PR effects (as assessed by the response reductions for the repetition of the same face when compared to any other face adaptor), on the other hand, were only observable in bilateral FFA. We did not observe any differences in the OFA when the adaptor was a face (ANG and FEM conditions), a finding that contradicts the results of Rotshtein et al. (2005), who found the OFA being selective to the physical image changes. If this was the case, we would have expected to find differences between the ANG-S and all other conditions, where the adaptor was a face, too. The lack of a neural effect of direct face repetition in OFA and LOC can be related to the temporal characteristics of the adaptor. In studies of AEs, the magnitude of RS has been shown to be related to the temporal dynamics of the adaptor. While in lower-level regions RS crucially depends on long-term exposure to the adaptor (Fang et al. 2005), higher-level regions attenuate their responses for short and long adaptor durations (Kovács et al. 2008). As we used 3000 ms S1 durations here, we could observe adaptation-related RS in FFA as well as in OFA. In typical PR studies, however, usually short S1 durations are used (Henson 2003). As yet there have been no neuroimaging studies that investigated PR effects for an immediate repetition PR task with longer S1 durations., comparable to that of the present study. Thus, it might be that for long S1 durations (as long as few seconds) PR effects are less pronounced and only detectable in higher-level regions, such as FFA. However, our recent ERP study (Walther et al. 2012) showed that PR effects were strongest on P2 and N250r (the latter being in line with findings from familiar face PR, see Schweinberger et al. 2002). Since the N250r is thought to originate from fusiform gyrus (Eger et al. 2005, Schweinberger et al. 2004), the largest PR effects should be expected in FFA, as observed in the present study.

Image Repetition PR versus Adaptation

The left FFA was the only area that allowed to disentangle the activations of the PR and AE conditions in that only this region showed a significantly smaller activation for the repeated image condition (ANG-S) when compared to FEM. In other words, the RS of the left FFA is the largest if the same identical image is presented twice, while in the right FFA the repetition of any face leads to similar RS. This suggests that the representation of the left FFA is more sensitive to the physical variations of the faces than that of the right FFA, a conclusion supported by prior results showing a primarily part-based representation of faces in left FFA (Harris and Aguirre 2010; but see Cooper et al. 2007, for a different conclusion). In addition to that, our whole-brain analysis also revealed that there are differences between PR- and AE-related activation in regions outside the visual cortex. We found that ACC is more strongly activated for the adapted when compared to the primed condition. This higher activation for adapted trials points towards higher decision efforts and uncertainty in the FEM conditions (maybe due to the perceptual AEs) when compared to the lower effort that is needed to make a decision in the primed trials, where the same stimulus is presented twice (Botvinick et al. 2004). However, recent studies suggest that adaptation can in fact also reduce decision uncertainty (Oruc and Barton 2011; Rhodes et al. 2010; Theodoni et al. 2012). Thus a direct comparison of decision difficulty during PR and AE trials requires further studies. Nevertheless, our findings suggest that there are cortical regions that show differential responses during the two perceptual phenomena, suggesting the recruitment of different neural mechanisms.

Our split-analysis also supports the view of different neural correlates for PR and AEs. If the two processes recruited the same neural systems, their outcome magnitude would likely be mediated by activation changes within the same areas. However, when we contrasted "effective" and "ineffective" PR or adaptation trials, we found different results. For PR, ACC showed greater activations for trials where PR did not lead to shorter RTs, a finding which has been related to response conflicts between prime and target in recent PR studies (D'Ostilio and Garraux 2012). Here, implicit categorization of the S1 as male or female can also lead to relatively longer reaction times in case the S2 is initially perceived as the opposite gender (although being physically the same). In the case of "ineffective" adaptation (in trials when adaptation did not lead to opposite aftereffects), activation was stronger than for "effective" adaptation in medial frontal regions. These regions previously have been connected to ambiguous decision making (Krain et al. 2006). Clearly, in the case of effective adaptation the ambiguity of stimuli is reduced by adaptation processes (Clifford 2007). In the case of a

"female" response after female adaptation, the ambiguity of the test stimulus may not be reduced sufficiently by adaptation. This is supported by the inferior parietal activation showing the same pattern (i.e. higher activation for unsuccessful when compared to successful adaptation), which can be interpreted as a reflection of higher decision uncertainty in trials where faces have been classified as female (Vickery and Jiang 2009). However, making a "female" decision in the adaptation block also requires larger cognitive control, since the more frequent "male" classification answer needs to be inhibited. This might be reflected in the higher activations in the medial frontal gyrus and the supplementary motor areas for "female" responses, which areas are associated with response inhibition (Sharp et al. 2010). These findings suggest that effective PR and adaptation lead to less investment of cognitive control (as reflected by lower activations in frontal regions), and are also in line with studies reporting behavioural benefits after face adaptation on classification performance (Oruc and Barton 2011; Rhodes et al. 2010) or response time measures (Walther et al. under revision). However, it seems that this benefit is related to different cortical circuits.

Altogether, our results show that it is possible to dissociate PR and adaptation-related neural activity, using the same paradigm within the same subjects. While category-specific adaptation effects are visible in most object and face selective regions, repetition PR effects are only present in bilateral FFA. Our findings suggest that PR and adaptation rely on different neural mechanisms.

Acknowledgements

References

Andrews TJ, Ewbank MP. Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *Neuroimage* 23: 905-913, 2004.

Anstis S, Verstraten FA, Mather G.The motion aftereffect. *Trends Cogn Sci* 2: 111-117, 1998.

Beale JM, Keil FC. Categorical effects in the perception of faces. *Cognition* 57: 217-239, 1995.

Bentin S, Allison T, Puce A, Perez E, McCarthy G. Electrophysiological studies of face perception in humans. *J Cogn Neurosci* 8: 551-565, 1996.

Bindemann M, Burton AM, Leuthold H, and Schweinberger SR. Brain potential correlates of face recognition: Geometric distortions and the N250r brain response to stimulus repetitions. *Psychophysiology* 45: 535-544, 2008.

Botvinick MM, Cohen JD, Carter CS. Conflict monitoring and anterior cingulate cortex: An update. *Trends Cogn Sci* 8: 539-546, 2004.

Brett M, Johnsrude IS, Owen AM. The problem of functional localization in the human brain. *Nat Rev Neurosci*, 3: 243-249, 2002.

Brooks BE, Rosielle LJ, and Cooper EE. The priming of face recognition after metric transformations. *Perception* 3: 297-313, 2002.

Buckner RL, Goodman J, Burock M, Rotte M, Koutstaal W, Schacter D, et al. Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron* 20: 285-296, 1998.

Buracas GT, Fine I, Boynton GM. The relationship between task performance and functional magnetic resonance imaging response. *J Neurosci* 25: 3023-3031, 2005.

Campbell FW, Maffei L. The tilt after-effect: A fresh look. *Vision Res* 11: 833-840, 1971.

Clifford CW. Perceptual adaptation: Motion parallels orientation. *Trends Cogn Sci* 6: 136-143, 2002.

Clifford CW, Webster MA, Stanley GB, Stocker AA, Kohn A, Sharpee TO, et al. Visual adaptation: Neural, psychological and computational aspects. *Vision Res* 47: 3125-3131, 2007.

Cooper TJ, Harvey M, Lavidor M, Schweinberger SR. Hemispheric asymmetries in image-specific and abstractive priming of famous faces: Evidence from reaction times and event-related brain potentials. *Neuropsychologia* 45: 2910-2921, 2007.

Cziraki C, Greenlee MW, Kovács G. Neural correlates of high-level adaptation-related aftereffects. *J Neurophysiol* 103: 1410-1417, 2010.

D'Ostilio K, Garraux G. Dissociation between unconscious motor response facilitation and conflict in medial frontal areas. *Eur J Neurosci* 35: 332-340, 2012.

Daelli V, Rijsbergen NJ van, Treves A. How recent experience affects the perception of ambiguous objects. *Brain Res* 1322: 81-91, 2010.

De Baene W, Vogels R. Effects of adaptation on the stimulus selectivity of macaque inferior temporal spiking activity and local field potentials. *Cerebral Cortex* 20: 2145-2165, 2010.

Desimone R. Neural mechanisms for visual memory and their role in attention. *Proc Natl Acad Sci USA* 93: 13494-13499, 1996.

Downing PE, Jiang Y, Shuman M, Kanwisher N. A cortical area selective for visual processing of the human body. *Science* 293: 2470-2473, 2001.

Eger E, Schweinberger SR, Dolan RJ, Henson RN. Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *Neuroimage* 26: 1128-1139, 2005.

Ellis AW, Young AW, Flude BM, Hay DC. Repetition priming of face recognition. *Quart J Exp Psychol A* 39: 193-210, 1987.

Ellis AW, Flude BM, Young A, Burton AM. Two loci of repetition priming in the recognition of familiar faces. *J Exp Psychol - Learn Mem Cogn* 22: 295-308, 1996.

Fang F, Murray SO, Kersten D, He S. Orientation-tuned FMRI adaptation in human visual cortex. *J Neurophysiol* 94: 4188-4195, 2005.

Farah MJ. Semantic and perceptual priming: How similar are the underlying mechanisms? *J Exp Psychol Hum Percept Perform* 15: 188-94, 1989.

Furl N, Rijsbergen NJ van, Treves A, Dolan RJ. Face adaptation aftereffects reveal anterior medial temporal cortex role in high level category representation. *Neuroimage* 37: 300-310, 2007.

Ganel T, Gonzalez CL, Valyear KF, Culham JC, Goodale MA, Köhler S. The relationship between fMRI adaptation and repetition priming. *Neuroimage* 32: 1432-1440, 2006.

Gauthier I, Tarr MJ, Moylan J, Skudlarski P, Gore JC, Anderson AW. The fusiform "face area" is part of a network that processes faces at the individual level. *J Cogn Neurosci* 12: 495-504, 2000.

Goshen-Gottstein Y, Ganel T. Repetition priming for familiar and unfamiliar faces in a sex-judgment task: Evidence for a common route for the processing of sex and identity. *J Exp Psychol Learn Mem Cogn* 26: 1198-1214, 2000.

Grill-Spector K, Henson RN, Martin A. Repetition and the brain: Neural models of stimulus-specific effects. *Trends Cogn Sci* 10: 14-23, 2006.

Grill-Spector K, Kushnir T, Edelman S, Avidan G, Itzchak Y, Malach R. Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron* 24: 187-203, 1999.

Grill-Spector K, Malach R. fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychol* 107: 293-321, 2001.

Gross CG, Rocha-Miranda CE, Bender DB. Visual properties of neurons in inferotemporal cortex of the macaque. *J Neurophysiol* 35: 96-111, 1972.

Harris A, Aguirre GK. Neural tuning for face whole and parts in human fusiform gyrus revealed by FMRI adaptation. *J Neurophysiol* 104: 336-345, 2010.

Henson RN. Neuroimaging studies of priming. *Prog Neurobiol* 70: 53-81, 2003.

Henson RN, Shallice T, Dolan R. Neuroimaging evidence for dissociable forms of repetition priming. *Science* 287: 1269-1272, 2000.

Henson RN, Shallice T, Gorno-Tempini ML, Dolan, RJ. Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cereb Cortex* 12: 178-186, 2002.

Itier RJ, Taylor MJ. Source analysis of the N170 to faces and objects. *Neuroreport* 15: 1261-1265, 2004.

Kanai R, Verstraten FA. Perceptual manifestations of fast neural plasticity: Motion priming, rapid motion aftereffect and perceptual sensitization. *Vision Res* 45: 3109-3116, 2005.

Kanwisher N, McDermott J, Chun MM. The fusiform face area: A module in human extrastriate cortex specialized for face perception. *J Neurosci* 17: 4302-4311, 1997.

Kanwisher N, Tong F, Nakayama K. The effect of face inversion on the human fusiform face area. *Cognition* 68: 1-11, 1998.

Kloth N, Schweinberger SR, Kovács G. Neural correlates of generic versus gender-specific face adaptation. *J Cogn Neurosci* 22: 2345-2356, 2010.

Kourtzi Z, Kanwisher N. Representation of perceived object shape by the human lateral occipital complex. *Science* 293: 1506-1509, 2001.

Koutstaal W, Wagner AD, Rotte M, Maril A, Buckner RL, Schacter DL. Perceptual specificity in visual object priming: Functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. *Neuropsychologia,* 39:184-99, 2001.

Kovács G, Cziraki C, Vidnyánszky Z, Schweinberger, SR., Greenlee MW. Position-specific and position-invariant face aftereffects reflect the adaptation of different cortical areas. *Neuroimage* 43: 156-164, 2008.

Kovács G, Zimmer M, Banko E, Harza I, Antal A, Vidnyánszky Z. Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cereb Cortex* 16: 742-753, 2006.

Kovács G, Zimmer M, Harza I, Antal A, Vidnyánszky Z. Position-specificity of facial adaptation. *Neuroreport* 16: 1945-1949, 2005.

Kovács G, Zimmer M, Harza I, Vidnyánszky Z. Adaptation duration affects the spatial selectivity of facial aftereffects. *Vision Res* 47: 3141-3149, 2007.

Krain AL, Wilson AM, Arbuckle R, Castellanos FX, Milham MP. Distinct neural mechanisms of risk and ambiguity: A meta-analysis of decision-making. *Neuroimage* 32: 477-484, 2006.

Krekelberg B, Boynton GM, van Wezel RJA. Adaptation: From single cells to BOLD. *Trends Cogn Sci* 29: 250-256, 2006.

Löffler G, Yourganov G, Wilkinson F, Wilson HR. fMRI evidence for the neural representation of faces. *Nat Neurosci* 8: 1386-1390, 2005.

Magnussen S. Low-level memory processes in vision. *Trends Neurosci* 3: 247-251, 2000.

Malach R. Targeting the functional properties of cortical neurons using fMR-adaptation. *Neuroimage* 62: 1163-1169,2012.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, et al. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc Natl Acad Sci USA* 92: 8135-8139, 1995.

Miller EK, Li L, Desimone R. A neural mechanism for working and recognition memory in inferior temporal cortex. *Science* 254: 1377-1379, 1991.

Näsänen R. Spatial frequency bandwidth used in the recognition of facial images. *Vision Res* 39: 3824-3833, 1999.

Ollinger JM, Shulman GL, Corbetta M. Separating processes within a trial in event-related functional MRI. *Neuroimage* 13: 210-217, 2001.

Oruc I, Barton JJS. Adaptation improves discrimination of face identity. *Proc Biol Sci* 278: 2591-2597, 2011.

Pavan A, Campana G, Guerreschi M, Manassi M, Casco C. Separate motion-detecting mechanisms for first- and second-order patterns revealed by rapid forms of visual motion priming and motion aftereffect. *J Vision* 9: 1-16, 2009.

Rhodes G, Watson TL, Jeffery L, Clifford CWG. Perceptual adaptation helps us identify faces. *Vision Res* 50: 963-968, 2010.

Rossion B, Delvenne JF, Debatisse D, Goffaux V, Bruyer R, Crommelinck M, et al. Spatio temporal localization of the face inversion effect: An event-related potentials study. *Biol Psychol* 50: 173-189, 1999.

Rotshtein P, Henson RN, Treves A, Driver J, Dolan RJ. Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nat Neurosci* 8: 107-13, 2005.

Sawamura H, Orban GA, Vogels R. Selectivity of neuronal adaptation does not match response selectivity: A single-cell study of the FMRI adaptation paradigm. *Neuron* 49: 307-318, 2006.

Sayres R, Grill-Spector K. Object-selective cortex exhibits performance-independent repetition suppression. *J Neurophysiol* 95: 995-1007, 2006.

Schweinberger SR, Huddy V, Burton AM. N250r – A face-selective brain response to stimulus repetitions. *Neuroreport* 15: 1501-1505, 2004.

Schweinberger SR, Pfütze E-M, Sommer W. Repetition priming and associative priming of face recognition. Evidence from event-related potentials. *J Exp Psychol: Learn Mem Cogn* 21: 722-736, 1995.

Schweinberger SR, Pickering EC, Jentzsch I, Burton AM, Kaufmann JM. Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. *Cogn Brain Res* 14: 398-409, 2002.

Sekuler RW, Ganz L. Aftereffect of seen motion with a stabilized retinal image. *Science* 139: 419 420, 1963.

Sharp DJ, Bonnelle V, De Boissezon X, Beckmann CF, James SG, Patel MC, et al. Distinct frontal systems for response inhibition, attentional capture, and error processing. *Proc Natl Acad Sci USA* 107: 6106-6111, 2010.

Summerfield C, Trittschuh EH, Monti JM, Mesulam MM, Egner T. Neural repetition suppression reflects fulfilled perceptual expectations. *Nat Neurosci* 11: 1004-1006, 2008.

Thompson P, Burr D. Visual aftereffects. *Curr Biol* 19: R11-R14, 2009.

Turennout M van, Ellmore T, Martin A. Long-lasting cortical plasticity in the object naming system. *Nat Neurosci* 3: 1329-1334, 2000.

Vickery TJ, Jiang YV. Inferior parietal lobule supports decision making under uncertainty in humans. *Cereb Cortex* 19: 916-925, 2009.

Walther C, Schweinberger SR, Kaiser D, Kovács G. Neural correlates of priming and adaptation in familiar face perception. *Cortex* (Sept 3, 2012), http://dx.doi.org/10.1016/j.cortex.2012.08.012

Webster MA, Kaping D, Mizokami Y, Duhamel P. Adaptation to natural facial categories. *Nature* 428: 557-561, 2004.

Webster MA, MacLeod DI. Visual adaptation and face perception. *Phil Trans R Soc B* 366: 1702-1725, 2011.

Webster MA, MacLin OH. Figural aftereffects in the perception of faces. *Psychon Bull Rev* 6: 647-653, 1999.

Winston JS, Henson RN, Fine-Goulden MR, Dolan RJ. fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *J Neurophysiol* 92: 1830-1839, 2004.

Young AW, Flude BM, Hellawell DJ, Ellis AW. The nature of semantic priming effects in the recognition of familiar people. *Br J Psychol* 85: 393-411, 1994.

4.   General Discussion

The studies reported in this thesis offer insights into the similarities and differences of face AEs and PR in familiar face perception on both behavioural and neural levels. In Study I, we established a new paradigm in which both effects could be induced in the perception of facial identity while keeping stimuli, timing, and task parameters constant. The results of Study I suggested that S2 ambiguity or S1-S2 similarity might determine whether AEs or PR is observed, and that exclusive mechanisms might underlie both AEs and PR. In Study II, we took a closer look at the role of these two factors for face identity AEs, and showed that AEs might not depend on physical similarity of S1 and S2 alone, but also on the ambiguity of the S1 stimuli with respect to the original face identities. In Studies I and II, simultaneously recorded ERPs helped to delineate the time course of identity-specific repetition effects. The ERP findings of Study I again suggested exclusive underlying mechanisms for both AEs and PR, while both studies revealed category-specific processes in parallel to identity-specific ones. Finally, in Study III we show that face gender AEs and image PR could be dissociated behaviourally, and fMRI revealed a dissociation between both effects in the left FFA, as well as widespread regions showing activation differences depending on stimulus category. While results of each single study are discussed in the main body of this thesis, the following sections try to shed some light on certain joint aspects and implications of the three studies.

4.1   Behavioural effects of adaptation and repetition priming

For ambiguous S2 faces following unambiguous S1s we observed behavioural AEs on the perception of facial identity (e.g., Hills et al., 2010; Hole, 2011) in Studies I and II, and face gender AEs in Study III (e.g., Kloth et al., 2010; Kovács et al., 2006; Webster et al., 2004). PR was found for identity congruent S1-S2 pairs (e.g., Bindemann et al., 2008; Schweinberger, Pickering, Jentzsch, et al., 2002) in Study I and image congruent S1-S2 pairs in Study III. As AEs and PR were never observed for the same stimuli in our studies, exclusive mechanisms might underlie both phenomena. This assumption is also supported by the dissociations of the neural responses associated with AEs and PR that were observed in our studies and which are detailed in a later section. The existence of different mechanisms for adaptation and PR has already been proposed by studies on the perception of words (Huber, 2008), objects (Daelli et al., 2010), and faces (e.g., Hills et al., 2010), but the nature of such mechanisms is still discussed.

In all three studies, both AEs and PR were observed despite a considerable size change from S1 to S2, rendering a low-level, i.e., retinotopic, locus of the effects unlikely (see, e.g,

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Rhodes et al., 2004). Therefore, our results might reflect processes involving higher level neural (face) representations, the activity of which was affected by prior stimulus presentations. In the case of AEs, it is thought that prior adaptation shifts the perceptual boundary of a given facial dimension in a multidimensional face space (Valentine, 1991) towards the adaptor. The involvement of higher level processes in AEs is also suggested by reports of face identity AEs following adaptation to geometrically distorted images (Hole, 2011) or a different image of the same person (Hills et al., 2010). However, Hills et al. (2010) also found that AEs were smaller following different adaptor images as compared to the same images that were used to create the continua, suggesting some image-specificity of the effects, which was also proposed by studies on face distortion AEs (Carbon & Ditye, 2012; Carbon et al., 2007). In consequence, some lower level contributions to the effects observed in our Studies I and II cannot be ruled out completely, as the adaptor images (S1s) were the original images of our morphing continua. In some contrast to this rather perceptual view on face AEs, PR was typically associated with higher level memory representations, such as FRUs (e.g., Bruce & Young, 1986). In a recent study on face identity AEs, Hills et al. (2010) made an interesting suggestion about how AEs and PR could be described within a common framework, i.e., Burton et al.'s IAC model (Burton et al., 1990). Hills et al. (2010) argued that AEs, in analogy to PR, could be observed at visual, FRU, and PIN levels of the IAC model and suggested a possible implementation, but they also put forward that the underlying mechanisms (which could not be specified) might be different.

In Study III, we used a gender classification paradigm to test the relatedness of AEs and PR on a facial dimension different than identity. Although we found that the results generally mirrored our findings on face identity AEs (Studies I and II), it is important to note that the observed effects might not necessarily reflect the same perceptual processes. Although the gender of a face is obviously linked to facial identity, gender can be determined equally well irrespective of whether a face is familiar or not (e.g., Ellis et al., 1990). Models of face perception (e.g., Bruce & Young, 1986; Burton et al., 1990) assume different functional units for the processing of facial identity and more general visual characteristics of faces such as gender. Such models also propose that PR is induced when familiar faces are repeated, and that it relies on existing representations of these faces in memory. This should be the case for the original famous identities in Study I, for which PR was found, but not necessarily for the gender ambiguous test faces in Study III. There is also a pathological hint for differences between face identity and gender processing, in that patients with impaired recognition of facial identity showed preserved recognition of facial gender (Tranel, Damasio, & Damasio,

1988). However, this view was challenged by studies proposing a single route for processing gender and identity of faces (Ganel & Goshen-Gottstein, 2002; Goshen-Gottstein & Ganel, 2000). Note that in our Study III, outer facial features and hair style were masked to prevent gender judgements based on simple heuristics and to force the processing of inner features of the faces (Goshen-Gottstein & Ganel, 2000). However, although Study III was designed to be more likely to involve a higher level face processing and to be better comparable to Studies I and II, the exact nature of these processes remains unclear as of yet.

In Studies I and III, we calculated correlations between behavioural AE and PR as a different method to assess their relatedness, but the results were quite divergent. In Study I, we did not observe a significant correlation of AE and PR, suggesting that these phenomena might be independent, at least on a behavioural level. However, Study III showed a negative correlation of both AE and PR and therefore proposed some relation between both phenomena. Still, this negative correlation also points to some difference in the underlying mechanisms. There are some possible explanations for this observation. First, the different experimental designs of Studies I and III made it necessary to calculate AE and PR differently for each study (see the respective Methods sections), so perhaps we did not capture exactly the same effects by our measurements. Second, different processes might underlie the analogous phenomena in both studies, as already discussed above. For example, the image-specific PR effect of Study III might involve more processing on lower perceptual levels than the identity-specific PR of Study I. Altogether, concluding a dependence or independence of AE and PR from the results of our correlation analyses is not straightforward. Future studies will be necessary to clear up this issue, as AE and PR were typically investigated in isolation in past studies, or, if measured in the same study, no correlation analyses were carried out (Daelli et al., 2010).

In our studies, many parameters that are thought to influence AEs and/or PR, such as timing, task, and stimulus set, were kept constant. Our results suggested two factors, which might determine whether AEs or PR were observed in an experiment, the first being related to ambiguity of the stimuli and the second being related to (physical) similarity of the stimuli. In all our studies, we were unable to disentangle both factors completely, as morphing inevitably manipulates both factors in conjunction. However, Study II used a special account to measure the roles of similarity and ambiguity for face identity AEs. Here, S1 faces were varied on a morphing continuum between two famous faces, and S2s were kept constant at an ambiguous level. In this paradigm, the different factors predict different data patterns for the relationship of S1 morph level and classification performance (cf. Fig. 1 of Study II): A linear relationship

would be expected when AEs are driven by physical similarity, whereas a step-wise pattern would indicate a role of ambiguity for AEs assuming categorical perception of familiar face identities (Beale & Keil, 1995; Rotshtein et al., 2005). In fact, we observed linear as well as non-linear relationships between S1 morph level and classification performance, suggesting that both similarity and ambiguity are important for face identity AEs. Therefore, our results extend on recent findings by Daelli et al. (2010), who suggested that AEs and PR in the perception of ambiguous objects could be induced by different S1-S2 delays. Here we could show that different timing is not crucial for the existence of either AE or PR, and that ambiguity and/or similarity might be important in this context.

First of all, we showed that S2 faces ambiguous in identity or gender can be subject to contrastive AEs when they are preceded by unambiguous S1 faces, but no such effects were observed for ambiguous S1 faces (see, e.g., Webster & MacLin, 1999). AEs were similarly large over a range of ambiguous S2 morph levels in Study I and a range of S1 morph levels in Study II, while they were non-existent at other morph levels. Furthermore, the effect of S1 ambiguity on AEs in Study II was quantified by certain significant non-linear polynomial contrasts, indicating an influence of ambiguity on AEs. However, linear contributions were there as well, suggesting an additional role of physical similarity of the stimuli. Interestingly, the emergence of PR effects seemed to rely on identity congruence of the most unambiguous S1s and S2s in Study I. Altogether, some of the experimental effects could be attributed to ambiguity, and rather seem to show an all-or-nothing character. This can be considered in analogy to the phenomenon of categorical perception (Beale & Keil, 1995; Rotshtein et al., 2005), where stimuli varying on a morph continuum are unequivocally perceived as one or the other end-point for all but a few very ambiguous morph levels.

The influence of similarity on face repetition-related effects was more often accounted for by the literature. As already described in the introduction, AEs as well as PR show a certain degree of image sensitivity, in that effects were smaller when "different" images were used as S1 and S2 (for the case of face AEs, see Carbon & Ditye, 2012; Carbon et al., 2007; Hills et al., 2010; and for the case of face PR, see Bindemann et al., 2008; Schweinberger et al., 2004; Schweinberger, Pickering, Jentzsch, et al., 2002). Moreover, in studies on the neural representation of facial expression a similar point was made to describe the observed identity congruence effects (Fox & Barton, 2007; Fox, Oruc, & Barton, 2008). In this context, Fox et al. (2008) proposed that AEs might decrease with increasing dissimilarity of the adaptor and test images, and argued that this might be the reason for the reduced AE when identity was incongruent between adaptation and test in their prior study (Fox & Barton, 2007). However,

in the Discussion section of our Study I, we argued that in PR studies, similarity is typically considered as a direct comparison between S1 and S2 images, whereas in studies on AEs, similarity may have two different sources, i.e., (1) the choice of S1 in relation to the original images used to create the morphing continuum, and (2) the morphing procedure itself. With respect to this, the arguments of Fox et al. (2008) seem to be restricted to point (1). This is because face AEs are typically not found for the case when S1 and S2 are most similar, i.e. identical, images. In line with other studies (e.g., Webster & MacLin, 1999), we could not observe any AEs for ambiguous test faces following the same ambiguous faces in the experiments reported here, and in Study I, PR, but no AE, was observed when S1 and S2 were identical unambiguous images. Our studies suggested a role of similarity and ambiguity for AEs and PR in some contradiction to the findings described above. AEs seemed to decrease with increasing similarity of S1 and S2 (Studies I and II) and were even reversed to PR (Study I) when similarity was manipulated by morphing alone.

Another interesting aspect of our data involved the reaction time measures. While the PR effects that we observed in Study I for identity congruent S1-S2 pairs are already well described in the literature (Bindemann et al., 2008; Schweinberger, Pickering, Jentzsch, et al., 2002), RT modulations by AEs have not been addressed extensively. In a recent study on auditory adaptation, Zäske, Schweinberger, Kaufmann, and Kawahara (2009) reported adaptation-related peak shifts of the RT curve in direction of the adaptor, and proposed that response uncertainty might have been altered by adaptation in these cases. Similar results were also obtained in our Study I, in that the maximal RT was shifted towards identity A following adaptation to identity A and vice versa for identity B. Although rarely described, this finding is not surprising. Assuming that adaptation shifts the perceived neutral or most ambiguous face on the morphing continuum towards the adaptor, and that it should be most difficult to match this ambiguous face to one of the original identities, different S2 morph levels should be perceived as most ambiguous and yield the slowest RTs depending on adaptation. Moreover, an interesting modulation of RTs by S1 morph level was observed in Study II. The closer the S1 was to one of the original face of the morphing continuum, the faster participants matched ambiguous test faces (50/50% identity A/B) to one of the original identities. This effect is well in line with reports of benefits of adaptation (Oruc & Barton, 2011; Rhodes, Watson, Jeffery, & Clifford, 2010; Theodoni, Kovács, Greenlee, & Deco, 2011), but also the RT peak shifts described above, additionally assuming that both the neutral (most ambiguous) morph level and the RT peak were shifted further on a (now hypothetical) S2 continuum, when the S1 led to a stronger contrastive bias on perception, as it

was the case for S1s closer to the original faces (see the classification performance data of Study II). Consequently, the RTs measured at the 50/50% morph level would be lower for larger distances between this morph level and the new neutral level, because the task is now easier to complete and response uncertainty is smaller. However, the RT modulations by AEs have one possible downside for the question of the relatedness of AE and PR. As PR is typically measured as an RT benefit, the stronger effects associated with AEs and the difficulty of the decision might have masked more subtle PR effects for more ambiguous stimuli in our studies. Unfortunately, our designs do not allow to exclude this possibility, although the pattern of ERP effects in Study I at least suggests that there were no electrophysiological PR effects on the most ambiguous morph level of Experiment 2, which was in turn the only morph level where AEs were observed behaviourally in this experiment. Perhaps future studies may help to disentangle the contributions of AEs and PR to RT measurements for more ambiguous test stimuli.

4.2 Neural effects of adaptation and repetition priming

In the present studies, a variety of neural effects possibly associated with AE or PR were observed. First of all, the comparison of S2 faces following face S1s and such following noise S1s revealed clear categorical adaptation for all test stimuli (e.g., Kovács et al., 2006; Zimmer & Kovács, 2011a). In ERPs (Studies I and II), occipito-temporal categorical adaptation effects were observed in all analysed ERP time windows beginning with N170 (Study I) or even P1 (Study II). Categorical adaptation effects were most pronounced on N170 and P2 and were observable over a wide range of electrodes. However, in the P2 and N250r time windows, categorical adaptation seemed restricted to inferior recording sites in Study I, and a similar topography was also visible in the N170 time window in data of Study II, suggesting that the brain source of these categorical adaptation effects might be more potent to project to the inferior occipito-temporal electrodes. The analyses of two later time windows in Study II revealed that category-specific differences changed polarity around the N250, and lingered on until 300 - 400 ms post stimulus. Interestingly, some ERP components, first and foremost the P2 (see, e.g., Burkhardt et al., 2010), also showed identity-specific effects in Studies I and II, that could be better observed over superior occipito-temporal regions. Altogether, our ERP data suggest that short-term plasticity of identity as well as categorical processing are reflected by the first 400 ms of the ERP, that both might run in parallel, and that they might rely on independent mechanisms possibly subserved by different neuron populations. The pattern observed for ERPs was also partly mirrored by the fMRI data of Study III. Here,

widespread categorical adaptation in FFA, OFA, and LO of both hemispheres (Cziraki et al., 2010; Kovács et al., 2008) stood in contrast to weaker specific effects of image repetition in both FFAs and non-existent gender-specific adaptation effects.

As described above, neural responses to the S2 faces were modulated by the category of the S1 stimulus, i.e., by whether a noise stimulus or a face was presented as S1. Such categorical effects were already observed in a variety of studies with different manipulations within the set of faces (Amihai et al., 2011; Kovács et al., 2008) as well as with different alternative categories such as noise stimuli (Cziraki et al., 2010; Kovács et al., 2008; Kovács et al., 2006), eggs (Amihai et al., 2011), or no visual, but auditory stimulation (Kloth et al., 2010). Altogether, this suggests that these effects reflect a general processing of stimulus category. The distributed occipito-temporal topographies of categorical effects in ERP voltage maps, especially in the N170 time range (see Results sections of Studies I and II), is also well in line with fMRI studies revealing that widespread areas along the visual stream, such as FFA, OFA, and LO (Cziraki et al., 2010; Kovács et al., 2008), show category-specific response modulations. Furthermore, categorical adaptation was observed already at around 100 - 150 ms in our Study II as well in later time windows (P2, N250, 300 - 350 ms, 350 - 400 ms) in Studies I and II. To my knowledge, there is no direct evidence for the relatedness of the categorical effects over the certain time windows, so it is not yet clear if different mechanisms contribute to these effects at different points in time or if the effects reflect one persistent process. Note, however, that visual inspection suggested a similarity of the topographical difference maps of noise minus face S1s over several ERP components (at least until around N250) in our studies. Together with the long time window over which categorical adaptation was observed in our studies, this favours the idea of a general, persistent process. Although this seems to be somewhat in contradiction to the notion of stimulus category processing being mostly done around or even before 150 ms after stimulus onset (e.g., Liu, Agam, Madsen, & Kreiman, 2009; Thorpe, Fize, & Marlot, 1996; VanRullen & Thorpe, 2001), a recent study by Rossion and Caharel (2011) constrains the interpretation of such early effects in the context of face perception by showing that here, the P1 ERP component most likely reflects the processing of low-level cues, whereas high-level face processing had its earliest reflection in the N170 time window. Our findings imply that it could be fruitful for future studies to consider categorical adaptation effects in a time interval longer than that used previously (e.g., Amihai et al., 2011; Ganis et al., 2012; Kovács et al., 2006). Another question that could be addressed in future studies is whether categorical adaptation effects are also modulated by the choice of the control stimulus. For example, noise adaptors (e.g.,

Kovács et al., 2008; Kovács et al., 2006; Zimmer & Kovács, 2011a) might show slightly different effects than more natural stimulus categories (Amihai et al., 2011). Interestingly, categorical effects partly differed between the blocked S1 presentations of Study I as compared to the randomized presentation of Study II. Therefore, the paradigm used might as well affect categorical adaptation effects. This might be explained by a different general face adaptation over the whole experiment if S1 conditions are presented randomly. This seems plausible, as some carry-over adaptation effects from previous trials can be expected (for an account for the temporal decay of adaptation effects, see Kloth & Schweinberger, 2008). Altogether, this suggests that the processing of stimulus category starts within the first 200 ms following stimulus onset, and that various cortical regions of higher and lower processing levels are involved.

Note that, as long as the neural reflections of adaptation and PR are still not clear (for a recent discussion in the case of PR, see Gotts et al., 2012), the categorical effects described here might as well be termed "categorical priming" in the sense that the (response irrelevant) categorization of the S2 as a face is facilitated (primed) if the preceding stimulus was also a face as compared to a noise pattern. Nevertheless, we decided to use the term categorical adaptation because this is how such effects are typically referred to in the literature (e.g., Amihai et al., 2011; Kloth et al., 2010; Kovács et al., 2008; Kovács et al., 2006; Zimmer & Kovács, 2011a).

In all of our studies, we also observed other, more specific effects, which were, at least in part, weaker than the categorical effects described above. In the case of PR, we observed clear ERP effects in Study I, which were most pronounced for the P2 and the following N250 time window. In both cases, test faces following identity congruent S1s showed more negative amplitudes as compared to the other conditions, with both effects being the same qualitatively. This suggests that both the P2 and N250 modulations might be related to a common difference in neural activations that is sustained over both time windows. Therefore, the P2 effects of our study might be considered as an early reflection of individual recognition, as initially proposed for the N250r (Bindemann et al., 2008; Schweinberger et al., 2004; Schweinberger, Pickering, Jentzsch, et al., 2002). Unfortunately, how these PR-related ERP modulations translate to the fMRI results of Study III is not straightforward. In Study III, image-specific PR was found in bilateral FFAs. Schweinberger, Pickering, Jentzsch, et al. (2002) found that the source of their N250r PR effects might well be on the fusiform gyrus, but they also acknowledged that the degree of an involvement of FFA was unclear. At the very least, this could suggest that the sources of both specific PR effects observed in our

studies might be in the same brain region, i.e., the fusiform gyrus. While the specific PR effects in our studies were relatively clear, specific adaptation effects were harder to detect. In Study I, we found a possible reflection of identity-specific adaptation in the P2 time window, where mean amplitudes for ambiguous S2 faces were more negative following identity A or B as compared to the 50/50% morph. Furthermore this effect was correlated to the behavioural AE. However, ERP modulations specific to S1 identity did not start before 300 ms post S2 onset in Study II. In Study III, we did not find gender-specific fMRI adaptation effects in any brain region, perhaps due to limitations in the spatial resolution of the fMRI recordings used here (see Study III Discussion). Therefore, it is not possible to draw direct conclusions regarding the brain sources of specific adaptation, possibly related to the identity-specific ERP effects of the previous studies, on the basis of our fMRI data. However, Study III revealed a dissociation of gender-specific adaptation and image-specific PR between left and right FFA, in that the signal of left FFA was additionally reduced for PR as compared to specific adaptation while there was no difference between both in right FFA. Together with the finding that specific neural adaptation and PR effects were never observed for the same stimulation in ERPs, and although both effects were partly observed in similar ERP time windows, this suggests that different underlying mechanisms might be involved. Furthermore, the adaptation and PR effects which were observed for gender perception in fMRI might partly reflect different processes than the ERP effects measured for identity perception, as already discussed for the behavioural data.

Some fMRI studies (e.g., Cziraki et al., 2010; Furl et al., 2007) recently introduced a different way to assess specific adaptation effects. For example, Cziraki et al. (2010) assigned trials to conditions depending on the response that was given in a particular trial. This method allowed to compare trials when prior adaptation biased the perception of an ambiguous test stimulus away from the adaptor with trials when it did not, and therefore revealed the neural correlates of "successful" adaptation. In our Study II, we observed response-specific ERP effects starting at around 125 - 175 ms, which were most pronounced for the P2 and N250 components. In trials when adaptation biased the perception of identity ambiguous test faces, the P2 amplitudes were less positive/more negative as compared to trials when adaptation did not lead to a contrastive bias. This is in line with the idea that N250(r) (Bindemann et al., 2008; Schweinberger et al., 2004; Schweinberger, Pickering, Jentzsch, et al., 2002), as well as P2 (see above) could be involved in individual recognition. Furthermore, the P2 was suggested to reflect task difficulty (Philiastides, Ratcliff, & Sajda, 2006), or, more recently, increased perceptual processing demands (Banko, Gal, Kortvelyes, Kovács, & Vidnyanszky,

2011). However, a different line of research (Kaufmann & Schweinberger, 2012; Schulz, Kaufmann, Kurt, & Schweinberger, 2012; Schulz, Kaufmann, Walther, & Schweinberger, 2012) proposed that P2 amplitude might as well be related to the typicality or distinctiveness of test faces in reference to a face space (Valentine, 1991). In face learning paradigms, reduced P2 amplitudes were observed for naturally distinctive and caricatured as compared to non-distinctive test faces (Schulz, Kaufmann, Kurt, et al., 2012), or different levels of caricaturing as compared to veridical faces (Kaufmann & Schweinberger, 2012). Congruently, it was also found that in comparison to veridical test faces, the P2 amplitude was increased for anti-caricatures, whereas it was decreased for caricatures (Schulz, Kaufmann, Walther, et al., 2012). Moreover, reduced typicality also lead to reduced P2 amplitudes in the context of other race or age biases (Stahl, Wiese, & Schweinberger, 2008, 2010; Wiese, Schweinberger, & Hansen, 2008). The response-specific P2 amplitude reduction in our Study II can be interpreted in analogy to these findings, in that test faces might have become less typical in trials when adaptation led to contrastive biases as compared to trials when it did not have this contrastive effect, perhaps due to a transient shift of the centre of face space towards the adaptor (Webster & MacLin, 1999). This is also well in line with recent findings of Burkhardt et al. (2010) on the face distortion AE, showing that the amplitude of a P250 component for test faces decreased if the perceived distortion was increased by adaptation. Although the idea that P2 might reflect face typicality is already around for some time (see, e.g., Halit, de Haan, & Johnson, 2000), evidence for this interpretation is growing stronger recently, and future research will help to further evaluate it in the context of face processing. We also did response-specific analyses for the fMRI data, but the results were less systematic (see Study III Results and Discussion) and will not be discussed in detail here. However, these analyses showed some dissociation of AE and PR in the gender paradigm, and therefore provided some support for the idea that both phenomena might involve different mechanisms and perhaps recruit different neuron populations.

In conclusion, our studies showed that category-specific adaptation effects could be observed together with adaptation effects specific to the adapted dimension in a single paradigm, and our data suggested that these effects might run in parallel in time. The observed differences between categorical and specific adaptation effects, in neural timing as well as in proposed anatomical substrates, points to an relative independence of both effects, and again stresses the importance of their separation as already suggested by Kloth et al. (2010). Our data also included hints for an anatomical separation of both categorical and specific effects.

In line with the idea that exclusive mechanisms might underlie AEs and PR we also found hints for a dissociation of the respective specific effects.

Besides looking at the behavioural and neural correlates of AE and PR individually, another aim of this thesis was to find possible ways to relate both kinds of effects. The following section will address this point.

4.3 The relation between behavioural and neural effects

In the preceding sections, the behavioural and neural correlates of AEs and PR, as well as how AEs and PR might be related to each other, were discussed in the context of the present studies. Additionally, it was pointed out that factors of the stimulation, i.e., similarity and/or ambiguity, might have determined which of both phenomena could be observed in our studies, and that different mechanisms might underlie both AEs and PR. As the neural reflections of repetition-related effects are still heavily discussed (see, e.g., Gotts et al., 2012; Grill-Spector et al., 2006), the following section will show how neural and behavioural effects could be related regarding the present results. Nevertheless, the specification of a neural implementation of these effects (Gotts et al., 2012; Grill-Spector et al., 2006) is beyond the scope of this thesis.

The major relation between behavioural and neural data was first of all given by the design of our studies. Similar to the behavioural PR effects, the specific ERP modulations were observed for unambiguous S2s following identity congruent S1s in Study I. This is in line with findings of other studies on PR using veridical face stimuli (e.g., Bindemann et al., 2008; Schweinberger, Pickering, Jentzsch, et al., 2002) as well. On the contrary, identity-specific adaptation was observed for the most unambiguous S2 morph level in Studies I and II, for which behavioural AEs (e.g., Hills et al., 2010; Hole, 2011; Kloth et al., 2010; Kovács et al., 2006) were also observed. Although Study III did not show a clear BOLD reflection of gender-specific AEs for androgynous test faces (see the Discussion section of Study III for details), our results suggested an independence of both AE and PR, as they were never observed for the same S2 stimuli, behaviourally and neurally. However, this also showed that the picture was not completely clear over all aspects of our data.

Study II, that investigated the S1 dependence of AEs, revealed that the behavioural findings were only partly mirrored by the ERP data. Only later time windows around 300 - 400 ms showed a symmetrical modulation of ERPs by S1 condition (with reference to the 50/50% S1) in our analyses. Although this effect suggested some role of ambiguity similar to the behavioural data (see Study II for a detailed discussion), the influence of (physical)

similarity that was found in behaviour was not reflected by the ERPs. It might be that our stimulus preparation resulted in too subtle physical differences between the S1 stimuli, so that no ERP effects of S1 condition were induced on components such as P1 and N170, which are thought to process lower level image characteristics (for a review, see Schweinberger, 2011). Furthermore, effects similar to the identity-specific effects in the late time windows were not described in the literature yet, so further studies are necessary to evaluate the relation between behaviour and ERPs in this context.

Correlation analyses offer another, more direct way to assess the relatedness of behavioural and neural effects. In Study I, we calculated behavioural as well as neural effect measures (see the respective studies for details) and correlated both. Interestingly, the observed identity-specific adaptation effect was positively correlated with behavioural AEs, suggesting that higher neural effects went with higher behavioural effects. As such an identity-specific ERP adaptation was not described in previous studies, replications of this effect would be useful to validate its interpretation as a potential neural reflection of behavioural AEs. Interestingly, our correlation analyses also yielded a significant relation between behavioural AE and ERP PR. Our speculative interpretation was that behavioural AEs might be higher when ERPs are particularly specific to the repetition of the original identities. However, some high brain-behaviour correlations were questioned recently (Vul, Harris, Winkielman, & Pashler, 2009), and other measures were recommended to determine correlations of ERP effects and behaviour (Rousselet & Pernet, 2012), so these effects should be treated cautiously in the first place. In Studies II and III, no correlation measures were calculated.

In Studies II and III, we were able to analyse neural data depending on the response given, a method that was recently used in fMRI research on face perception as well (Cziraki et al., 2010; Furl et al., 2007). Thereby, we found ERP modulations in trials when responses were biased away from the S1 as compared to trials when they were not in Study II which were discussed in detail in a previous section. Furthermore, Study III showed a contrast between brain regions modulated by the specific response of the participants (related to AE) and such regions modulated by participants' RTs (related to PR). The latter analyses was actually more complicated than the response-related analyses that directly depended on the participants' responses, as we did a median split of the trials by RT and compared slow with fast trials in the following. In consequence, different trials were used for both response and RT-specific analyses, and the latter also relied on additional assumptions regarding the RT reflection of PR effects, for example that neural PR and RTs are highly correlated (see, e.g.,

Henson, 2003). In fact, recent studies have questioned a correlation of behavioural PR and RS (Sayres & Grill-Spector, 2006), and pointed to the general difficulty of relating behavioural and neural data (Buracas et al., 2005). Therefore, as long as the neural mechanisms behind PR are not completely understood (Gotts et al., 2012), the interpretation of the observed region-wise dissociation of AE-related and PR-related neural activity must remain speculative, and future studies will have to show if RT-specific analyses similar to these used in Study III help our understanding of the mechanisms underlying PR and AE.

Finally, the robust categorical adaptation effects in ERPs and fMRI were discussed intensely in the previous sections. However, it is unclear from our studies whether there is any behavioural reflection of these effects. First of all, the results of Experiment 2 of Study I suggested no special effect of noise versus face adaptation for classifications and RTs, as the noise condition was not different from the two face control conditions here. Similar results were obtained in a study on the neural correlates of face distortion AEs (Zimmer & Kovács, 2011a), where no difference in distortion ratings was observed for S2s following noise and veridical face adaptors. The picture in Study III was very similar; there was no difference in gender classification scores between noise and androgynous adaptors, as well as no RT differences between noise and all other face conditions, except for the repetition of the same androgynous face showing image-specific PR. The only behavioural effect that might point towards category-specific processing was found in the comparison of the noise S1 condition with the 50/50% morphed face S1 in Study II. However, there was just a trend for a noise deficit in RTs here, so an over-interpretation of this result should be avoided, especially because studies looking at categorical adaptation typically did not find or could not analyse potential behavioural reflections of these effects (e.g., Amihai et al., 2011; Kloth et al., 2010; Kovács et al., 2008; Kovács et al., 2006; Zimmer & Kovács, 2011a). However, the lack of a behavioural reflection of categorical adaptation in our studies seems rather unproblematic, because our paradigms first of all aimed at determining the relationship of specific AEs and PR, both in behaviour and neurally. Thus, it is not necessarily straightforward to assume that there is a behavioural reflection for each ERP effect observed here, as the experimental design and the measurement of the effects can both play a role as well. For example, while ERPs and BOLD signal obviously were sensitive to the comparison of face and noise S1s in the present studies, the behavioural measures might have simply been not sensitive to this categorical effect. Further studies using paradigms that specifically aim at investigating the behavioural reflections of categorical adaptation might be informative in this context.

In conclusion, the results of the current studies propose that behavioural AE and PR might be related to the specific neural effects observed, and both sources suggest that AE and PR might be different phenomena with exclusive underlying mechanisms. This is also in line with the ideas of Huber (2008), who assumed two different processes, which work on different time scales, in a recent model on immediate repetition-related phenomena in word recognition. Although there were behavioural reflections for most of the neural effects observed (or vice versa) in the present studies, it was suggested that possible relationships should be interpreted rather cautiously (Buracas et al., 2005; Sayres & Grill-Spector, 2006), in line with the ongoing debate on the neural correlates of repetition-related phenomena (e.g., Gotts et al., 2012; Grill-Spector et al., 2006). This is especially important as different paradigms can be more or less sensitive to measure certain behavioural or neural effects, which might have been the reason for the non-existent behavioural reflection of categorical adaptation in the present studies. However, if interpreted cautiously and under consideration of the restrictions of the methods used, the relationships between behavioural and neural data can provide a better understanding of the processes involved, and are therefore worth further investigation.

4.4 The importance of the paradigm

In some of the previous sections it was mentioned that, besides the factors already described, certain other aspects of the paradigms might have contributed to the findings as well and might also be involved in determining whether AEs or PR were observed. The following section will address some of these points, but starts with a "historical" view on the development of the original paradigm.

In the beginning of this work, the designs of many studies on AEs and PR were examined. These studies obviously differed in a multitude of parameters, first and foremost the timing and the stimulation itself. Although the role of timing for PR was not as easily accessible as it was for AEs (Leopold et al., 2005; Rhodes et al., 2007), the decision to look for a timing that might appeal to both AEs and PR was made. After an inspiring conversation with Vicky Bruce at a local workshop, we decided to probe face repetition-related effects within two dimensions, face identity and gender. As PR effects on gender decisions were rarely observed (e.g., Ganel & Goshen-Gottstein, 2002; Goshen-Gottstein & Ganel, 2000), especially the investigation of effects on face identity perception was promising. Therefore, the original paradigm focused on the perception of facial identity and rigorously implemented our preliminary considerations on timing. We chose a pretty short S1 duration (500 ms) and

an even shorter S2 duration (300 ms), because studies of PR typically used short S1s, and there were also reports of face AEs with such a short adaptation period (Kovács et al., 2008). To avoid any effects of apparent motion between S1 and S2, a 50 ms inter-stimulus interval (ISI) was introduced. Indeed, ISI was suggested as a possible factor to determine whether AEs or PR were induced in a recent study on object recognition (Daelli et al., 2010), but we decided to keep it constant here to investigate the role of stimulation in isolation. The presentation of S2 was chosen with respect to the data of Leopold et al. (2005), who showed that AEs increased with decreasing S2 duration. In direct succession, a choice screen (e.g., Daelli et al., 2010; Fox et al., 2008; Rieth & Huber, 2010) was used to allow participants to solve the task. As AEs were typically observed for ambiguous morphed test faces and PR was found with veridical test faces, we decided to use S2 stimuli of different morph levels from several identity continua, while the S1 was either one of the two original faces of a continuum, a face of an unrelated identity, a 50/50% morph, or a Fourier phase randomized face (for further details, see Methods section of Study I). Altogether, the only manipulation in this paradigm was the stimulation, but all other factors such as timing and task were kept constant. In the following, this paradigm was adapted to the research questions and the respective methodological needs in Studies II and III.

Certain parameters of the paradigms had to be set based on the results of a variety of pilot studies, which were not mentioned in the "The Present Studies" section explicitly. First of all, we tested our original paradigm (the one used in Study I) with a complete randomization of S1 and S2 conditions. As AEs were hardly observable in this pilot experiment, we decided to use blocking of S1 conditions in Study I, because this turned out as the best way to induce both robust AEs and PR. Nevertheless, we had to randomly vary identity continua within blocks, as a pilot study using only one identity continuum per block (but randomized S1 presentations within these blocks) showed bottom effects for RTs, probably due to a high activation of all identities within a block, so that identity congruence of S1 and S2 within a trial did not play any additional role. While the paradigm used in Study I was closely related to the insights from these pilot studies, Studies II and III introduced specific changes to this paradigm. In Study II, a completely randomized account was chosen, but S1 duration was increased to feed AEs, and Study III again used a blocking of S1 conditions combined with increased S1 presentation time. In consequence, some of the differences in the effects of these three studies might be related to blocking. For example, the categorical adaptation effects on N250 in Study I and Study II were opposite in direction, and a look at the general morphology of the ERPs of both studies suggested that component

latencies of the noise condition relative to the other conditions might differ as well. Although categorical adaptation is thought of as a general phenomenon (Cziraki et al., 2010; Kloth et al., 2010; Kovács et al., 2008; Kovács et al., 2006; Zimmer & Kovács, 2011a), these results implicate that such effects can be modulated by the order and/or blocking of trials. However, the N170 and P2 reductions for face as compared to noise stimuli at (inferior) occipito-temporal electrodes seems to be a commonality of such effects, at least in our studies.

Some identity-specific effects were also modulated by the paradigm here. Reliable PR was found in Experiment 1 of Study I, but Experiment 2 showed weaker effects, which were not significant in the overall analyses of RT data. For now it remains possible that this was due to the paradigm changes that were introduced in comparison to Experiment 1, in that there were more S1 conditions, less S2 conditions, and an increased repetition number of each condition. Nevertheless, this is quite speculative, as our pilot studies and previous findings were not informative regarding this particular point. Additionally, image PR effects for the repetition of the same ambiguous 50/50% morph were only found in Study III, but not in Studies I or II. However, a trend for a small category-specific PR effect was found in the comparison of the noise control and 50/50% S1 morph of Study II, suggesting at least some benefit of image repetition, although this could not be observed in comparison to the other face S1s. The benefit of adaptation (Oruc & Barton, 2011; Rhodes et al., 2010; Theodoni et al., 2011) for the RTs could have simply been stronger than that of image repetition in Study II and therefore possibly masked RT effects of image repetition. Additionally, image repetitions only occurred in relatively few trials over the experiment, reducing the relevance of S1 for responses. An increased probability of image repetitions over the experiment might actually lead to an increased magnitude of PR, as it was suggested for masked priming studies in word recognition (e.g., Bodner & Masson, 2001). Additionally, in a pilot study to Study II that used a similar design with the original faces of each continuum as additional S2s, we also found only weak identity-specific PR as a trend in one of the conditions. As a possible explanation, the long S1 duration (3000 ms) together with the randomized trial order and the low proportion of image repetitions could have reduced image-specific as well as identity-specific PR here. Quite contrary to the other studies, all ambiguous S1s were presented within one block in Study III, and, as S2s were only ambiguous 50/50% morphs as well, S1 and S2 were either identical ambiguous faces, or different ambiguous faces. Consequently, the relevance of the S1 for the response to the S2 was high over this block, as participants were able to use information from S1 for their response to S2 in half of the trials. As there was no similar relevance of S1 for participants' responses in Studies I and II, this might explain why

image PR was especially strong in Study III. Note that, altogether, this might also pose a problem for the interpretation of PR effects over the three studies, and that it might not be straightforward to assume that the underlying mechanisms are necessarily the same, as already mentioned before.

Altogether, the paradigm used seems of a high importance for the investigation of face repetition-related phenomena. While previous studies generally set parameters differently depending on whether AE or PR was investigated, or suggested a role of timing parameters in determining which effect emerged (Daelli et al., 2010; Huber, 2008), our studies used constant timing and task to induce both effects. This suggests that stimulus-related factors, i.e., ambiguity and similarity, might have determined whether AE or PR were observed. However, other aspects of the paradigm seem relevant as well, as also proposed by our pilot studies and differences in the results of the current studies. In particular, the factors related to the format of stimulus presentation could be interesting for future studies, as our results suggested some differences between blocked and randomized accounts in the investigation of face repetition-related effects.

5.   Outlook

Our studies showed that face AEs and PR can be induced within the same paradigm, and therefore presented a novel way to investigate the relation between both phenomena. Our results suggested that ambiguity and/or similarity might affect both AEs and PR and might determine which effect emerges if other factors are kept constant. Together with our electrophysiological and brain-imaging data, this proposed that the underlying neural mechanisms of AEs and PR might be, at least partially, exclusive, and might possibly involve distinct neural circuitries. Additionally, face-specific processing could be separated from the processing of object category per se, and both might run in parallel over the first few hundred milliseconds following the test stimulus.

Based on the present and prior results, a complete account of face-repetition-related phenomena cannot be provided. Still, the present studies can be considered a further step to improve our understanding of these processes. Although our studies presented a quite coherent picture overall, the results should be substantiated, and there are also questions left open. First of all, further studies will have to disentangle the roles of ambiguity and similarity from each other regarding AEs and PR. Although the results of Study II suggested that both stimulus characteristics play a role for AEs, a clear separation of both was not possible with the design used. In a recent study (Walther et al., in preperation), we assessed the influence of ambiguity with similarity kept constant and demonstrated that an identical stimulation can or cannot lead to repetition-related effects depending on the task context. However, a clear dissociation of both factors is still missing, and future studies should address this point. Furthermore, replications of our results would be desirable, and could as well take care of important other aspects of the paradigm which might play an important role in the context of face repetition-related effects. Several studies suggested that presentation timing affects repetition-related phenomena, for example AEs (Leopold et al., 2005; Rhodes et al., 2007), or AEs and PR (Daelli et al., 2010), so considering these factors in paradigms similar to the one used here might shed some light on the underlying mechanisms of both phenomena and their relatedness. Several differences between our studies might be attributed to whether stimulus presentation was blocked or random, so this factor should be assessed in upcoming studies as well. To learn more about the neural basis of the involved processes, future studies could use response-specific data analyses (Cziraki et al., 2010; Furl et al., 2007) or other more direct ways of relating behavioural and neural data. Moreover, a combined EEG and fMRI study might be helpful to relate the neural correlates of AEs and PR observed with each method

(especially in the identity paradigm), while it could make use of the superior temporal resolution of EEG and the excellent spatial resolution of up-to-date fMRI.

Another interesting point for future studies is the generalisability of the identity and gender effects described here. Although different kinds of AEs might be considered as similar to some degree (see, e.g., Webster & MacLeod, 2011), a recent study (Storrs & Arnold, 2012) suggested that AEs of colour, face distortion, and face gender and their underlying mechanisms might differ qualitatively. Furthermore, in models of face processing (Bruce & Young, 1986; Burton et al., 1990), identity PR, and probably identity AEs (Hills et al., 2010) are thought to tap into different and higher-level processing stages than other stimulus features such as gender, and might therefore involve different brain areas (Haxby et al., 2000). As discussed before, it also seems genuine to assume some differences between gender and identity AEs/PR and their neural correlates in our studies, but direct evidence for this could not be provided. A combined EEG/fMRI study might further elucidate that point.

Once further additional data have been obtained, AEs and PR might be integrated into an account of face perception, perhaps on the basis of existing models of face perception (e.g., Bruce & Young, 1986; Burton et al., 1990). Such a model should also try to account for the neural correlates of both AEs and PR in a conclusive way. In this context in particular and in future research on this topic in general, special care should be taken in the distinction of specific and categorical processes, and in relating the behavioural and neural correlates of AEs and PR.

Summary

This thesis investigated how the perception of social information within a given face is influenced by prior visual experiences, focusing on adaptation-related aftereffects (AEs) and immediate repetition priming (PR) of face identity and gender. According to the literature, both AEs and PR typically show quite different behavioural consequences: While AEs were observed as contrastive biases in the perception of ambiguous faces, PR was reflected by response facilitations for repeated faces. However, a variety of studies suggested similarities between AEs and PR, regarding some of their functional properties and neural correlates. As most of the previous studies focused on either one or the other phenomenon, little is known about the relationship between AEs and PR. The present studies attempted to fill this gap.

Specifically, Study I investigated face identity AEs and PR within the same stimulus repetition paradigm, keeping timing and task constant. Following face or Fourier phase randomized (noise) stimuli, participants had to classify test faces varying on a morph continuum between two famous identities. Study I revealed that AEs and PR can be observed within the same paradigm and subjects, behaviourally and in event-related potentials (ERPs). As the same test stimuli never showed both AEs and PR simultaneously, the results of Study I suggested a role of similarity or ambiguity in determining which effect emerged. Together with the different ERP reflections of identity-specific AEs and PR in the P2 and N250 time windows, this also suggested that both phenomena are based on different, exclusive mechanisms. Additionally, identity-specific effects could be separated from category-specific ERP modulations, i.e., modulations by whether the first stimulus was a face or noise, suggesting that processing of face identity and object category might run in parallel here. Study II further investigated the factors underlying face identity AEs in a similar paradigm, and suggested that AEs depend on both similarity and ambiguity. The results confirmed and extended the findings of Study I, as there were again different ERP modulations by stimulus category and face identity, and as the identity-specific ERP modulations were most strikingly revealed by response-specific analyses of the ERP data in the P2 and N250 time windows. In Study III, AEs and image-specific PR were investigated in the perception of face gender using functional magnetic resonance imaging (fMRI). In line with the previous findings, Study III suggested dissociations between (1) gender-specific AEs and image-specific PR in behaviour, (2) brain areas associated with AEs and PR, and (3) brain areas associated with gender-specific and categorical processes, and proposed the fusiform face area (FFA) as a candidate region for gender-specific processing.

In conclusion, the present studies showed that similarity between adaptor and test faces, and ambiguity of the test face both determine whether AE or PR is observed, and suggested that exclusive mechanisms might underlie both phenomena. Furthermore, the results also revealed that the processing of face identity or gender run in parallel to object-category processing during the earlier processing stages.

Zusammenfassung

Diese Arbeit untersuchte, wie die Wahrnehmung sozialer Informationen in Gesichtern durch vorangegangene visuelle Erfahrungen beeinflusst wird, und fokussierte dabei auf Adaptations-bezogene Nacheffekte ("adaptation-related aftereffects", AEs) und kurzfristiges Wiederholungs-Priming (PR) von Identität und Geschlecht in Gesichtern. Bezugnehmend auf die Literatur, zeigen AEs und PR typischerweise recht unterschiedliche Auswirkungen in Verhaltensmessungen: Während AEs in Form von kontrastiven Verschiebungen in der Wahrnehmung nicht eindeutiger Gesichter beobachtet wurden, zeigte sich bei PR eine Steigerung der Reaktionsgeschwindigkeit für wiederholte Gesichter. Eine Reihe von Studien deutete jedoch auf eine Ähnlichkeit zwischen AEs und PR in Hinblick auf einige ihrer funktionalen Eigenschaften und neuronalen Korrelate hin. Weil sich ein Großteil der vorangegangenen Studien entweder auf das eine oder das andere Phänomen konzentrierte, ist nur wenig über die Beziehung zwischen AEs und PR bekannt. Die vorliegenden Studien sollten diese Lücke schließen.

Im Speziellen untersuchte Studie I AEs und PR für Gesichtsidentität innerhalb desselben Stimulus-Wiederholungs-Paradigmas unter Konstanthaltung der zeitlichen Parameter und der Aufgabe. Auf Gesichts- oder Fourier-Phasen randomisierte ("Noise") Stimuli folgend mussten Probanden Gesichter klassifizieren, die auf einem Kontinuum zwischen zwei berühmten Identitäten variierten. Studie I zeigte auf, dass AEs und PR im selben Paradigma und für die selben Probanden auf Verhaltensebene und in Ereignis-korrelierten Potentialen ("event-related potentials", ERPs) beobachtet werden können. Da die selben Test-Stimuli niemals AEs und PR zugleich zeigten, lassen die Ergebnisse von Studie I vermuten, dass Ähnlichkeit und Ambiguität der Stimuli eine Rolle dafür spielten, welcher Effekt auftrat. Dies legte zusammen mit den unterschiedlichen ERP Reflektionen von identitätsspezifischen AEs und PR in den P2 und N250 Zeitfenstern auch nahe, dass beide Phänomene auf unterschiedlichen, exklusiven Mechanismen beruhen. Zusätzlich konnten identitätsspezifische Effekte von kategoriespezifischen ERP Modulationen (d.h. Modulationen dadurch, ob der erste Stimulus ein Gesicht oder Noise war) getrennt werden, was darauf hindeutet, dass Prozesse der Gesichtsidentifikation und der Objektkategorisierung hier parallel ablaufen. In einem ähnlichen Paradigma untersuchte Studie II weiterhin die Faktoren, die Einfluss auf Gesichtsidentitäts-AEs nehmen, und ließ vermuten, dass AEs sowohl von Ähnlichkeit als auch von Ambiguität abhängen. Die Ergebnisse bestätigten und erweiterten die Befunde von Studie I, da es wieder unterschiedliche ERP Modulationen durch Stimulus-Kategorie und Gesichtsidentität gab, und da die identitätsspezifischen ERP Modulationen am deutlichsten in

antwortspezifischen Analysen der ERP-Daten in den P2 und N250 Zeitfenstern zu erkennen waren. In Studie III wurden AEs und bildspezifisches PR für die Wahrnehmung des Geschlechts von Gesichtern mittels funktionaler Magnetresonanztomographie untersucht. Ähnlich vorangegangener Befunde deutet Studie III hin auf Dissoziationen zwischen (1) geschlechtsspezifischen AEs und bildspezifischem PR in Verhaltensmessungen, (2) Gehirnregionen, die mit AEs und PR assoziiert sind, und (3) Gehirnregionen, die mit geschlechtsspezifischen und kategorialen Prozessen in Verbindung stehen. Zudem legt Studie III die fusiform face area (FFA) als mögliche Region für geschlechtsspezifische Verarbeitung nahe.

Schlussfolgernd zeigten die vorliegenden Studien, dass Ähnlichkeit zwischen Adaptor- und Test-Gesichtern und Ambiguität des Test-Gesichts bestimmen, ob AE oder PR beobachtet wird. Sie deuteten zudem darauf hin, dass beiden Phänomenen exklusive Mechanismen zugrunde liegen. Außerdem legten die Ergebnisse nahe, dass die Verarbeitung von Gesichtsidentität oder -Geschlecht in frühen Verarbeitungsstufen parallel zur Verarbeitung der Objektkategorie ablaufen.

References

Amihai, I., Deouell, L. Y., & Bentin, S. (2011). Neural adaptation is related to face repetition irrespective of identity: A reappraisal of the N170 effect. *Experimental Brain Research, 209*(2), 193-204.

Andrews, T. J., & Ewbank, M. P. (2004). Distinct representations for facial identity and changeable aspects of faces in the human temporal lobe. *Neuroimage, 23*(3), 905-913.

Anstis, S., Verstraten, F. A. J., & Mather, G. (1998). The motion aftereffect. *Trends in Cognitive Sciences, 2*(3), 111-117.

Banko, E. M., Gal, V., Kortvelyes, J., Kovács, G., & Vidnyanszky, Z. (2011). Dissociating the effect of noise on sensory processing and overall decision difficulty. *Journal of Neuroscience, 31*(7), 2663-2674.

Beale, J. M., & Keil, F. C. (1995). Categorical effects in the perception of faces. *Cognition, 57*(3), 217-239.

Benson, P. J., & Perrett, D. I. (1991). Synthesizing continuous-tone caricatures. *Image and Vision Computing, 9*(2), 123-129.

Bindemann, M., Burton, A. M., Leuthold, H., & Schweinberger, S. R. (2008). Brain potential correlates of face recognition: Geometric distortions and the N250r brain response to stimulus repetitions. *Psychophysiology, 45*(4), 535-544.

Bodner, G. E., & Masson, M. E. J. (2001). Prime validity affects masked repetition priming: Evidence for an episodic resource account of priming. *Journal of Memory and Language, 45*(4), 616-647.

Brooks, B. E., Rosielle, L. J., & Cooper, E. E. (2002). The priming of face recognition after metric transformations. *Perception, 31*(3), 297-313.

Bruce, V., & Valentine, T. (1985). Identity priming in the recognition of familiar faces. *British Journal of Psychology, 76*, 373-383.

Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology, 77*, 305-327.

Buracas, G. T., Fine, I., & Boynton, G. M. (2005). The relationship between task performance and functional magnetic resonance imaging response. *Journal of Neuroscience, 25*(12), 3023-3031.

Burkhardt, A., Blaha, L. M., Jurs, B. S., Rhodes, G., Jeffery, L., Wyatte, D., . . . Busey, T. (2010). Adaptation modulates the electrophysiological substrates of perceived facial distortion: Support for opponent coding. *Neuropsychologia, 48*(13), 3743-3756.

Burton, A. M., Bruce, V., & Johnston, R. A. (1990). Understanding face recognition with an interactive activation model. *British Journal of Psychology, 81*, 361-380.

Caharel, S., Jacques, C., d'Arripe, O., Ramon, M., & Rossion, B. (2011). Early electrophysiological correlates of adaptation to personally familiar and unfamiliar faces across viewpoint changes. *Brain Research, 1387*, 85-98.

Caharel, S., Jiang, F., Blanz, V., & Rossion, B. (2009). Recognizing an individual face: 3D shape contributes earlier than 2D surface reflectance information. *Neuroimage, 47*(4), 1809-1818.

Calder, A. J., & Young, A. W. (1996). Self priming: A short-term benefit of repetition. *Quarterly Journal of Experimental Psychology, 49*(4), 845-861.

Campanella, S., Hanoteau, C., Depy, D., Rossion, B., Bruyer, R., Crommelinck, M., & Guerit, J. M. (2000). Right N170 modulation in a face discrimination task: An account for categorical perception of familiar faces. *Psychophysiology, 37*(6), 796-806.

Carbon, C. C., & Ditye, T. (2011). Sustained effects of adaptation on the perception of familiar faces. *Journal of Experimental Psychology-Human Perception and Performance, 37*(3), 615-625.

Carbon, C. C., & Ditye, T. (2012). Face adaptation effects show strong and long-lasting transfer from lab to more ecological contexts. *Frontiers in Perception Science, 3*.

Carbon, C. C., Strobach, T., Langton, S. R. H., Harsanyi, G., Leder, H., & Kovács, G. (2007). Adaptation effects of highly familiar faces: Immediate and long lasting. *Memory & Cognition, 35*(8), 1966-1976.

Cave, C. B. (1997). Very long-lasting priming in picture naming. *Psychological Science, 8*(4), 322-325.

Clifford, C. W. G. (2002). Perceptual adaptation: Motion parallels orientation. *Trends in Cognitive Sciences, 6*(3), 136-143.

Clifford, C. W. G., Wenderoth, P., & Spehar, B. (2000). A functional angle on some after-effects in cortical vision. *Proceedings of the Royal Society B-Biological Sciences, 267*(1454), 1705-1710.

Cziraki, C., Greenlee, M. W., & Kovács, G. (2010). Neural correlates of high-level adaptation-related aftereffects. *Journal of Neurophysiology, 103*(3), 1410-1417.

Daelli, V., van Rijsbergen, N. J., & Treves, A. (2010). How recent experience affects the perception of ambiguous objects. *Brain Research, 1322*, 81-91.

Davies-Thompson, J., Gouws, A., & Andrews, T. J. (2009). An image-dependent representation of familiar and unfamiliar faces in the human ventral stream. *Neuropsychologia, 47*(6), 1627-1635.

Desimone, R. (1996). Neural mechanisms for visual memory and their role in attention. *Proceedings of the National Academy of Sciences of the United States of America, 93*(24), 13494-13499.

Downing, P. E., Jiang, Y. H., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science, 293*(5539), 2470-2473.

Durgin, F. H., & Proffitt, D. R. (1996). Visual learning in the perception of texture: Simple and contingent aftereffects of texture density. *Spatial Vision, 9*(4), 423-474.

Eimer, M. (2000). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology, 111*(4), 694-705.

Eimer, M. (2011). The face-sensitive N170 component of the event-related brain potential. In A. J. Calder, G. Rhodes, M. H. Johnson & J. V. Haxby (Eds.), *The Oxford Handbook of Face Perception* (pp. 345-366). Oxford: University Press.

Eimer, M., Kiss, M., & Nicholas, S. (2010). Response profile of the face-sensitive N170 component: A rapid adaptation study. *Cerebral Cortex, 20*(10), 2442-2452.

Ellis, A. W., Flude, B. M., Young, A., & Burton, A. M. (1996). Two loci of repetition priming in the recognition of familiar faces. *Journal of Experimental Psychology-Learning Memory and Cognition, 22*(2), 295-308.

Ellis, A. W., Young, A. W., & Flude, B. M. (1990). Repetition priming and face processing - Priming occurs within the system that responds to the identity of a face. *Quarterly Journal of Experimental Psychology, 42*(3), 495-512.

Ellis, A. W., Young, A. W., Flude, B. M., & Hay, D. C. (1987). Repetition priming of face recognition. *Quarterly Journal of Experimental Psychology, 39*(2), 193-210.

Fox, C. J., & Barton, J. J. S. (2007). What is adapted in face adaptation? The neural representations of expression in the human visual system. *Brain Research, 1127*(1), 80-89.

Fox, C. J., Oruc, I., & Barton, J. J. (2008). It doesn't matter how you feel. The facial identity aftereffect is invariant to changes in facial expression. *Journal of Vision, 8*(3), 11-13.

Frisby, J. (1979). *Seeing: Illusion, Brain and Mind.* Oxford: University Press.

Furl, N., van Rijsbergen, N. J., Treves, A., & Dolan, R. J. (2007). Face adaptation aftereffects reveal anterior medial temporal cortex role in high level category representation. *Neuroimage, 37*(1), 300-310.

Ganel, T., Gonzalez, C. L. R., Valyear, K. F., Culham, J. C., Goodale, M. A., & Kohler, S. (2006). The relationship between fMRI adaptation and repetition priming. *Neuroimage, 32*(3), 1432-1440.

Ganel, T., & Goshen-Gottstein, Y. (2002). Perceptual integrality of sex and identity of faces: Further evidence for the single-route hypothesis. *Journal of Experimental Psychology-Human Perception and Performance, 28*(4), 854-867.

Ganis, G., Smith, D., & Schendan, H. E. (2012). The N170, not the P1, indexes the earliest time for categorical perception of faces, regardless of interstimulus variance. *Neuroimage, 62*(3), 1563-1574.

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform "face area" is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience, 12*(3), 495-504.

Goshen-Gottstein, Y., & Ganel, T. (2000). Repetition priming for familiar and unfamiliar faces in a sex-judgment task: Evidence for a common route for the processing of sex and identity. *Journal of Experimental Psychology-Learning Memory and Cognition, 26*(5), 1198-1214.

Gosling, A., & Eimer, M. (2011). An event-related brain potential study of explicit face recognition. *Neuropsychologia, 49*(9), 2736-2745.

Gotts, S. J., Chow, C. C., & Martin, A. (2012). Repetition priming and repetition suppression: A case for enhanced efficiency through neural synchronization. *Cognitive Neuroscience, 3*(3-4), 227-237.

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences, 10*(1), 14-23.

Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica, 107*(1-3), 293-321.

Halit, H., de Haan, M., & Johnson, M. H. (2000). Modulation of event-related potentials by prototypical and atypical faces. *Neuroreport, 11*(9), 1871-1875.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*(6), 223-233.

Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in Neurobiology, 70*(1), 53-81.

Henson, R. N. A., Shallice, T., Gorno-Tempini, M. L., & Dolan, R. J. (2002). Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cerebral Cortex, 12*(2), 178-186.

Hills, P. J., Elward, R. L., & Lewis, M. B. (2010). Cross-modal face identity aftereffects and their relation to priming. *Journal of Experimental Psychology-Human Perception and Performance, 36*(4), 876-891.

Hole, G. (2011). Identity-specific face adaptation effects: Evidence for abstractive face representations. *Cognition, 119*(2), 216-228.

Huber, D. E. (2008). Immediate priming and cognitive aftereffects. *Journal of Experimental Psychology-General, 137*(2), 324-347.

Huber, D. E., & O'Reilly, R. C. (2003). Persistence and accommodation in short-term priming and other perceptual paradigms: Temporal segregation through synaptic depression. *Cognitive Science, 27*(3), 403-430.

Jaquet, E., & Rhodes, G. (2008). Face aftereffects indicate dissociable, but not distinct, coding of male and female faces. *Journal of Experimental Psychology-Human Perception and Performance, 34*(1), 101-112.

Jeffery, L., Rhodes, G., & Busey, T. (2007). Broadly tuned, view-specific coding of face shape: Opposing figural aftereffects can be induced in different views. *Vision Research, 47*(24), 3070-3077.

Jemel, B., Pisani, M., Rousselle, L., Crommelinck, M., & Bruyer, R. (2005). Exploring the functional architecture of person recognition system with event-related potentials in a within- and cross-domain self-priming of faces. *Neuropsychologia, 43*(14), 2024-2040.

Jenkins, R., Beaver, J. D., & Calder, A. J. (2006). I thought you were looking at me - Direction-specific aftereffects in gaze perception. *Psychological Science, 17*(6), 506-513.

Jiang, F., Blanz, V., & O'Toole, A. J. (2006). Probing the visual representation of faces with adaptation - A view from the other side of the mean. *Psychological Science, 17*(6), 493-500.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17*(11), 4302-4311.

Kanwisher, N., Tong, F., & Nakayama, K. (1998). The effect of face inversion on the human fusiform face area. *Cognition, 68*(1), B1-B11.

Kaufmann, J. M., & Schweinberger, S. R. (2012). The faces you remember: Caricaturing shape facilitates brain processes reflecting the acquisition of new face representations. *Biological Psychology, 89*(1), 21-33.

Kloth, N., & Schweinberger, S. R. (2008). The temporal decay of eye gaze adaptation effects. *Journal of Vision, 8*(11):4, 1-11.

Kloth, N., Schweinberger, S. R., & Kovács, G. (2010). Neural correlates of generic versus gender-specific face adaptation. *Journal of Cognitive Neuroscience, 22*(10), 2345-2356.

Kovács, G., Cziraki, C., Vidnyanszky, Z., Schweinberger, S. R., & Greenlee, M. W. (2008). Position-specific and position-invariant face aftereffects reflect the adaptation of different cortical areas. *Neuroimage, 43*(1), 156-164.

Kovács, G., Zimmer, M., Banko, E., Harza, I., Antal, A., & Vidnyanszky, Z. (2006). Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cerebral Cortex, 16*(5), 742-753.

Kovács, G., Zimmer, M., Harza, I., & Vidnyanszky, Z. (2007). Adaptation duration affects the spatial selectivity of facial aftereffects. *Vision Research, 47*(25), 3141-3149.

Laurence, S., & Hole, G. (2011). The effect of familiarity on face adaptation. *Perception, 40*(4), 450-463.

Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level after effects. *Nature Neuroscience, 4*(1), 89-94.

Leopold, D. A., Rhodes, G., Muller, K. M., & Jeffery, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society B-Biological Sciences, 272*(1566), 897-904.

Little, A. C., DeBruine, L. M., & Jones, B. C. (2005). Sex-contingent face after-effects suggest distinct neural populations code male and female faces. *Proceedings of the Royal Society B-Biological Sciences, 272*(1578), 2283-2287.

Liu, H. S., Agam, Y., Madsen, J. R., & Kreiman, G. (2009). Timing, timing, timing: Fast decoding of object information from intracranial field potentials in human visual cortex. *Neuron, 62*(2), 281-290.

Maccotta, L., & Buckner, R. L. (2004). Evidence for neural effects of repetition that directly correlate with behavioral priming. *Journal of Cognitive Neuroscience, 16*(9), 1625-1632.

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., . . . Tootell, R. B. H. (1995). Object-related activity revealed by functional magnetic-resonance-imaging in human occipital cortex. *Proceedings of the National Academy of Sciences of the United States of America, 92*(18), 8135-8139.

McNeill, A., Burton, A. M., & Ellis, A. (2003). When sex isn't special: Priming onto a sex decision. *Visual Cognition, 10*(6), 641-650.

Megreya, A. M., & Burton, A. M. (2006). Unfamiliar faces are not faces: Evidence from a matching task. *Memory & Cognition, 34*(4), 865-876.

Nemrodov, D., & Itier, R. J. (2012). Is the rapid adaptation paradigm too rapid? Implications for face and object processing. *Neuroimage, 61*(4), 812-822.

Oruc, I., & Barton, J. J. S. (2011). Adaptation improves discrimination of face identity. *Proceedings of the Royal Society B-Biological Sciences, 278*(1718), 2591-2597.

Philiastides, M. G., Ratcliff, R., & Sajda, P. (2006). Neural representation of task difficulty and decision making during perceptual categorization: A timing diagram. *Journal of Neuroscience, 26*(35), 8965-8975.

Rhodes, G., Evangelista, E., & Jeffery, L. (2009). Orientation-sensitivity of face identity aftereffects. *Vision Research, 49*(19), 2379-2385.

Rhodes, G., Jaquet, E., Jeffery, L., Evangelista, E., Keane, J., & Calder, A. J. (2011). Sex-specific norms code face identity. *Journal of Vision, 11*(1).

Rhodes, G., & Jeffery, L. (2006). Adaptive norm-based coding of facial identity. *Vision Research, 46*(18), 2977-2987.

Rhodes, G., Jeffery, L., Clifford, C. W. G., & Leopold, D. A. (2007). The timecourse of higher-level face aftereffects. *Vision Research, 47*(17), 2291-2296.

Rhodes, G., Jeffery, L., Watson, T. L., Jaquet, E., Winkler, C., & Clifford, C. W. G. (2004). Orientation-contingent face aftereffects and implications for face-coding mechanisms. *Current Biology, 14*(23), 2119-2123.

Rhodes, G., Watson, T. L., Jeffery, L., & Clifford, C. W. G. (2010). Perceptual adaptation helps us identify faces. *Vision Research, 50*(10), 963-968.

Rieth, C. A., & Huber, D. E. (2010). Priming and habituation for faces: Individual differences and inversion effects. *Journal of Experimental Psychology-Human Perception and Performance, 36*(3), 596-618.

Rossion, B., & Caharel, S. (2011). ERP evidence for the speed of face categorization in the human brain: Disentangling the contribution of low-level visual cues from face perception. *Vision Research, 51*(12), 1297-1311.

Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage, 39*(4), 1959-1979.

Rotshtein, P., Henson, R. N. A., Treves, A., Driver, J., & Dolan, R. J. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience, 8*(1), 107-113.

Rousselet, G. A., & Pernet, C. R. (2012). Improving standards in brain-behavior correlation analyses. *Frontiers in Human Neuroscience, 6*, 1-11.

Sagiv, N., & Bentin, S. (2001). Structural encoding of human and schematic faces: Holistic and part-based processes. *Journal of Cognitive Neuroscience, 13*(7), 937-951.

Sayres, R., & Grill-Spector, K. (2006). Object-selective cortex exhibits performance-independent repetition suppression. *Journal of Neurophysiology, 95*(2), 995-1007.

Schulz, C., Kaufmann, J. M., Kurt, A., & Schweinberger, S. R. (2012). Faces forming traces: Neurophysiological correlates of learning naturally distinctive and caricatured faces. *Neuroimage, 63*(1), 491-500.

Schulz, C., Kaufmann, J. M., Walther, L., & Schweinberger, S. R. (2012). Effects of anticaricaturing vs. caricaturing and their neural correlates elucidate a role of shape for face learning. *Neuropsychologia, 50*(10), 2426-2434.

Schweinberger, S. R. (2011). Neurophysiological correlates of face recognition. In A. J. Calder, G. Rhodes, M. H. Johnson & J. V. Haxby (Eds.), *The Oxford Handbook of Face Perception* (pp. 345-366). Oxford: University Press.

Schweinberger, S. R., Huddy, V., & Burton, A. M. (2004). N250r: A face-selective brain response to stimulus repetitions. *Neuroreport, 15*(9), 1501-1505.

Schweinberger, S. R., Pickering, E. C., Burton, A. M., & Kaufmann, J. M. (2002). Human brain potential correlates of repetition priming in face and name recognition. *Neuropsychologia, 40*(12), 2057-2073.

Schweinberger, S. R., Pickering, E. C., Jentzsch, I., Burton, A. M., & Kaufmann, J. M. (2002). Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. *Cognitive Brain Research, 14*(3), 398-409.

Schweinberger, S. R., Zäske, R., Walther, C., Golle, J., Kovács, G., & Wiese, H. (2010). Young without plastic surgery: Perceptual adaptation to the age of female and male faces. *Vision Research, 50*(23), 2570-2576.

Stahl, J., Wiese, H., & Schweinberger, S. R. (2008). Expertise and own-race bias in face processing: An event-related potential study. *Neuroreport, 19*(5), 583-587.

Stahl, J., Wiese, H., & Schweinberger, S. R. (2010). Learning task affects ERP-correlates of the own-race bias, but not recognition memory performance. *Neuropsychologia, 48*(7), 2027-2040.

Storrs, K. R., & Arnold, D. H. (2012). Not all face aftereffects are equal. *Vision Research, 64*, 7-16.

Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M. M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience, 11*(9), 1004-1006.

Theodoni, P., Kovács, G., Greenlee, M. W., & Deco, G. (2011). Neuronal adaptation effects in decision making. *Journal of Neuroscience, 31*(1), 234-246.

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature, 381*(6582), 520-522.

Tiddeman, B., Burt, M., & Perrett, D. (2001). Prototyping and transforming facial textures for perception research. *IEEE Computer Graphics and Applications, 21*(5), 42-50.

Tranel, D., Damasio, A. R., & Damasio, H. (1988). Intact recognition of facial expression, gender, and age in patients with imparied recognition of face identity. *Neurology, 38*(5), 690-696.

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science, 247*(4940), 301-306.

Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion, and race in face recognition. *Quarterly Journal of Experimental Psychology, 43*(2), 161-204.

van Turennout, M., Ellmore, T., & Martin, A. (2000). Long-lasting cortical plasticity in the object naming system. *Nature Neuroscience, 3*(12), 1329-1334.

VanRullen, R., & Thorpe, S. J. (2001). The time course of visual processing: From early perception to decision-making. *Journal of Cognitive Neuroscience, 13*(4), 454-461.

Vul, E., Harris, C., Winkielman, P., & Pashler, H. (2009). Puzzlingly high correlations in fMRI studies of emotion, personality, and social cognition. *Perspectives on Psychological Science, 4*(3), 274-290.

Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature, 428*(6982), 557-561.

Webster, M. A., & MacLeod, D. I. A. (2011). Visual adaptation and face perception. *Philosophical Transactions of the Royal Society B-Biological Sciences, 366*(1571), 1702-1725.

Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomical Bulletin and Review, 6*(4), 647-653.

Wiese, H., Schweinberger, S. R., & Hansen, K. (2008). The age of the beholder: ERP evidence of an own-age bias in face memory. *Neuropsychologia, 46*(12), 2973-2985.

Wiese, H., Schweinberger, S. R., & Neumann, M. F. (2008). Perceiving age and gender in unfamiliar faces: Brain potential evidence for implicit and explicit person categorization. *Psychophysiology, 45*(6), 957-969.

Wig, G. S., Grafton, S. T., Demos, K. E., & Kelley, W. M. (2005). Reductions in neural activity underlie behavioral components of repetition priming. *Nature Neuroscience, 8*(9), 1228-1233.

Yamashita, J. A., Hardy, J. L., De Valois, K. K., & Webster, M. A. (2005). Stimulus selectivity of figural aftereffects for faces. *Journal of Experimental Psychology-Human Perception and Performance, 31*(3), 420-437.

Zäske, R., Schweinberger, S. R., Kaufmann, J. M., & Kawahara, H. (2009). In the ear of the beholder: Neural correlates of adaptation to voice gender. *European Journal of Neuroscience, 30*(3), 527-534.

Zhao, L., & Chubb, C. (2001). The size-tuning of the face-distortion after-effect. *Vision Research, 41*(23), 2979-2994.

Zimmer, M., & Kovács, G. (2011a). Electrophysiological correlates of face distortion after-effects. *Quarterly Journal of Experimental Psychology, 64*(3), 533-544.

Zimmer, M., & Kovács, G. (2011b). Position specificity of adaptation-related face aftereffects. *Philosophical Transactions of the Royal Society B-Biological Sciences, 366*(1564), 586-595.

List of Abbreviations

AE(s)	adaptation-related aftereffect(s)
BOLD	blood oxygen level dependent
EEG	electroencephalography
ERP	event-related potential
FFA	fusiform face area
fMRI	functional magnetic resonance imaging
fMRIa	functional magnetic resonance imaging adaptation
FRU	face recognition unit
IAC	interactive activation and competition
ISI	inter-stimulus interval
LO	lateral occipital cortex
OFA	occipital face area
PIN	person identity node
PR	priming
RS	repetition suppression
RT	reaction time
S1	first stimulus
S2	second stimulus

Ehrenwörtliche Erklärung

Ich erkläre hiermit, dass mir die geltende Promotionsordnung der Fakultät für Sozial- und Verhaltenswissenschaften der Friedrich-Schiller-Universität Jena bekannt ist.

Ferner erkläre ich, dass ich die vorliegende Dissertation selbstständig angefertigt habe, keine Textabschnitte eines Dritten oder eigener Prüfungsarbeiten ohne Kennzeichnung übernommen habe und alle benutzten Quellen und Hilfsmittel in der Arbeit angegeben habe. Insbesondere habe ich nicht die Hilfe eines Promotionsberaters in Anspruch genommen.

Bei der Auswahl und Auswertung des Materials sowie der Herstellung der Einzelmanuskripte haben mich die angegebenen Koautoren unentgeltlich unterstützt. Eine Darstellung der Anteile aller Autoren befindet sich in der Anlage zu dieser Erklärung. Darüber hinaus hat kein Dritter unmittelbar oder mittelbar geldwerte Leistungen von mir für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

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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Ort, Datum   Unterschrift

Beiträge der Autoren

Studie I ist einem Teil des DFG-geförderten Projekts "The Temporal Context of Face Recognition" von Prof. Dr. Gyula Kovács angegliedert, in dem Adaptations- und Priming-Effekte für Gesichter separiert werden sollten. Zusammen mit Herrn Kovács und Herrn Daniel Kaiser erarbeitete ich das Design der Studie. Die Stimuluserstellung, Programmierung und Datenerhebung oblag meiner Verantwortung. Danach analysierte und interpretierte ich die Daten, unterstützt von Herrn Kovács. Ich führte eine Literaturrecherche durch und schrieb ein Manuskript, welches schließlich von Herrn Kovács, Herrn Prof. Dr. Stefan R. Schweinberger, Herrn Kaiser und mir gemeinsam diskutiert und überarbeitet wurde.

Studie II wurde im Rahmen desselben DFG-Projekts durchgeführt. Meine Idee zu dieser Studie entstand in Anknüpfung an Studie I. Das allgemeine Design plante ich gemeinsam mit Herrn Kovács und Herrn Schweinberger. Im Rahmen eines Studentenprojekts (Empirisches Praktikum) betreute ich gemeinsam mit Herrn Schweinberger eine Gruppe von Bachelor-Studentinnen in der Umsetzung des Experimentes. Dies umfasste das spezielle Design, die Stimulusauswahl und -bearbeitung, Programmierung und Datenerhebung, und geschah teils in Absprache mit Herrn Kovács. Ich analysierte und interpretierte die Daten, recherchierte relevante Literatur und schrieb ein Manuskript, welches im Anschluss gemeinsam mit Herrn Kovács und Herrn Schweinberger überarbeitet wurde.

Studie III war wiederum Teil des DFG-geförderten Projekts "The Temporal Context of Face Recognition". Das Design dieser Studie erarbeitete ich gemeinsam mit Herrn Kovács und Herrn Kaiser. Die Stimuli wurden von Herrn Kaiser und mir erstellt. Datenerhebung und -analyse wurden von Herrn Kovács und Herrn Kaiser durchgeführt und beide schrieben zusammen das Manuskript, das dann in Zusammenarbeit mit Herrn Schweinberger und mir mehrfach diskutiert und überarbeitet wurde.

_____   _____

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Publications

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Walther, C., Schweinberger, S. R., Kaiser, D., & Kovács, G. (2012). Neural correlates of priming and adaptation in familiar face perception. *Cortex.* http://dx.doi.org/10.1016/j.cortex.2012.08.012

Schweinberger, S. R., **Walther, C.**, Zäske, R., Kovács, G. (2011). Neural correlates of adaptation to voice identity. *British Journal of Psychology*, 102(SI), 748-764.

Schweinberger, S. R., Zäske, R., **Walther, C.**, Golle, J., Kovács, G., & Wiese, H. (2010). Young without plastic surgery: Perceptual adaptation to the age of female and male faces. *Vision Research*, 50(23), 2570-2576.