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Research report

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 the 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.

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1. 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.

2. 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.

2.1. Materials and methods

2.1.1. 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.

2.1.2. 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 × 704 pixels. Faces were presented with PsychToolbox 3.0.8 (Brainard, 1997) in MATLAB 7.6 (MathWorks Inc.) at visual angles of 7.2 × 5.2° or 9.0 × 6.5° on an liquid crystal display (LCD) monitor (mean luminance¹: 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).

2.1.3. 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

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.

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: $7.2 \times 5.2^\circ$, 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 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.

2.1.4. Behavioural data analysis

We performed analyses of variance (ANOVAs) 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.

2.2. 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: $F(2,38) = 6.85$, $p = .007$, $\epsilon_{HF} = .74$, $\eta_p^2 = .27$; see Fig. 2A]. This effect was the most pronounced at ambiguous S2 morph levels and was reversed to PR direction at unambiguous S2 morph levels [corresponding to the ends of the morph-continuums; interaction of S1 condition and S2 morph level: $F(20,380) = 10.56$, $p < .001$, $\eta_p^2 = .36$]. PR means that participants were more likely to classify S2 as identity A following presentation of S1_A and as identity B

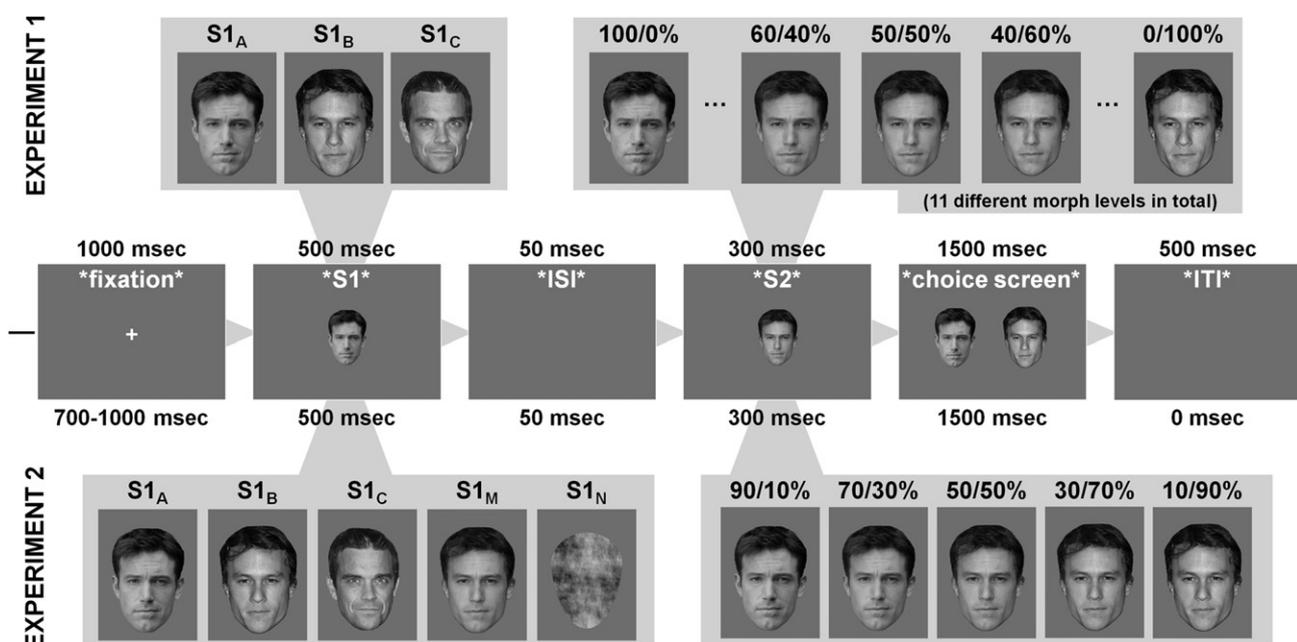


Fig. 1 – Trial structure of Experiments 1 (upper half) and 2 (lower half). Note that the expressions in asterisks are for illustration only and were not presented on the screen.

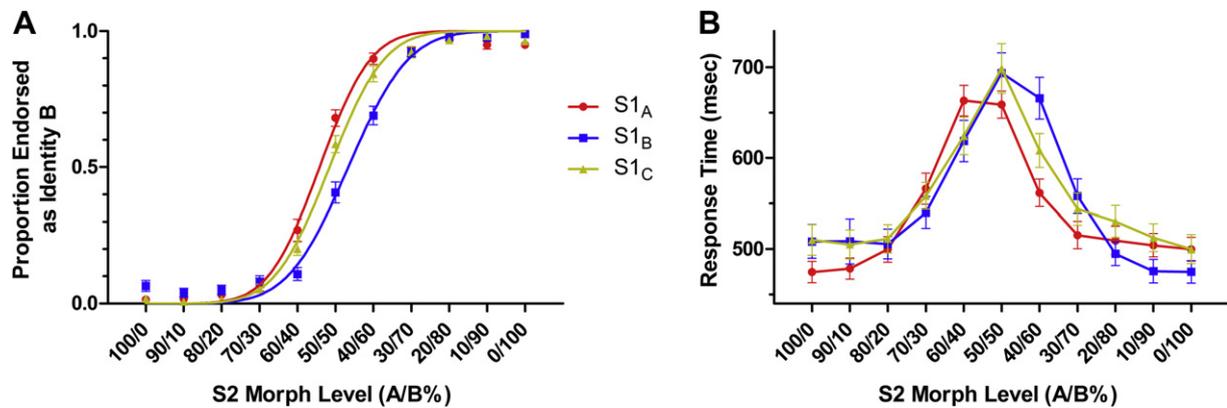


Fig. 2 – A: Accuracy data (in proportion endorsed as identity B) and B: response times (in msec) at each S2 morph level following S1_A, S1_B, and S1_C. Error bars show ± 1 standard error of the mean (SEM).

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 p s < .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).

RTs revealed an interaction of S1 condition and S2 morph level, $F(20,380) = 5.55$, $p < .001$, $\eta_p^2 = .23$ (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: $F(10,190) = 140.66$, $p < .001$, $\epsilon_{HF} = .59$, $\eta_p^2 = .88$], 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.

2.3. 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.

3. 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.

3.1. Materials and methods

3.1.1. 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.

3.1.2. 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).

3.1.3. 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 (randomized 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 \times 5 S2 morph levels) with 42 trials per condition (14 identity triplets \times 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.

3.1.4. 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 μ V 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).

3.1.5. 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%.

3.1.6. 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 cluster³ 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.

3.2. Results

3.2.1. 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: $F(4,84) = 4.63$, $p = .011$, $\epsilon_{HF} = .58$, $\eta_p^2 = .18$; see Fig. 3A]. The effect was again the 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: $F(16,336) = 16.10$, $p < .001$, $\epsilon_{HF} = .48$, $\eta_p^2 = .43$]. 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.

RTs exhibited slower responses to more ambiguous stimuli [main effect of S2 morph level: $F(4,84) = 137.73$, $p < .001$, $\epsilon_{HF} = .34$, $\eta_p^2 = .87$], and a prominent peak shift in RT curves depending on S1 condition [interaction of S1 condition and S2 morph level: $F(16,336) = 7.10$, $p < .001$, $\epsilon_{HF} = .71$, $\eta_p^2 = .25$; 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).

3.2.2. ERP data

Fig. 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, $F(16,336) = 3.17$, $p < .001$, $\epsilon_{HF} = .95$, $\eta_p^2 = .13$. Post-hoc t-tests showed reduced P1

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.

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.

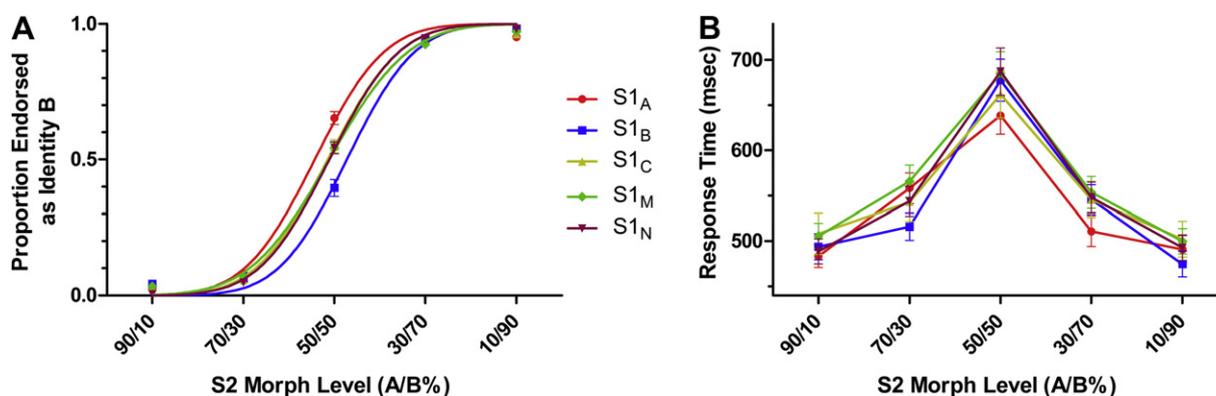


Fig. 3 – A: Accuracy data (in proportion endorsed as identity B) and B: response times (in msec) at each S2 morph level following S1_A, S1_B, S1_C, S1_M, and S1_N. Error bars show ±1 standard error of the mean (SEM).

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, $F(4,84) = 12.51, p < .001, \epsilon_{HF} = .49, \eta_p^2 = .43$. 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 $ps > .20$.

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: $F(4,84) = 36.63, p < .001, \epsilon_{HF} = .46, \eta_p^2 = .64$]. This effect was further qualified by an interaction of electrode, S1 condition, and S2 morph level, $F(48,1008) = 2.96, p < .001, \eta_p^2 = .12$, 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: $F(16,336) = 5.18, p < .001, \epsilon_{HF} = .69, \eta_p^2 = .20$], further qualified by interactions with the factors row and electrode [interaction of row, S1 condition, and S2 morph level: $F(16,336) = 4.79, p < .001, \eta_p^2 = .19$, and interaction of electrode, S1 condition, and S2 morph level, $F(32,672) = 3.06, p < .001, \eta_p^2 = .13$]. 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: $F(4,84) = 25.51, p = .001, \epsilon_{HF} = .71, \eta_p^2 = .55$].⁵

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

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.

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, $t(21) = -2.49, p = .021, d = -.24$], 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.

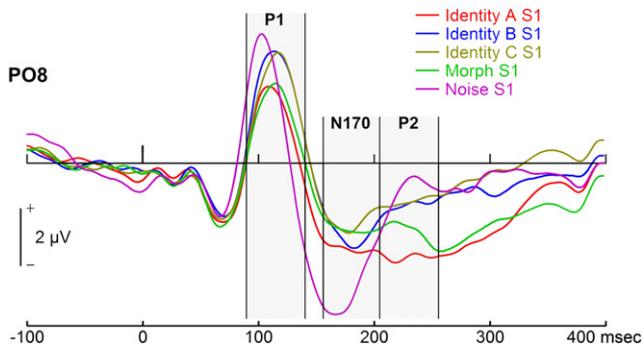


Fig. 4 – Sample ERPs for a 90/10% S2 following identity A, B, C, and morph, as well as noise S1s at PO8. The light grey areas show the analysed time windows.

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, $F(32,672) = 1.39$, $p = .077$, $\eta_p^2 = .06$, 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 AEs. 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

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.

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.

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

3.3. 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

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, $r(20) = .470$, $p = .027$.

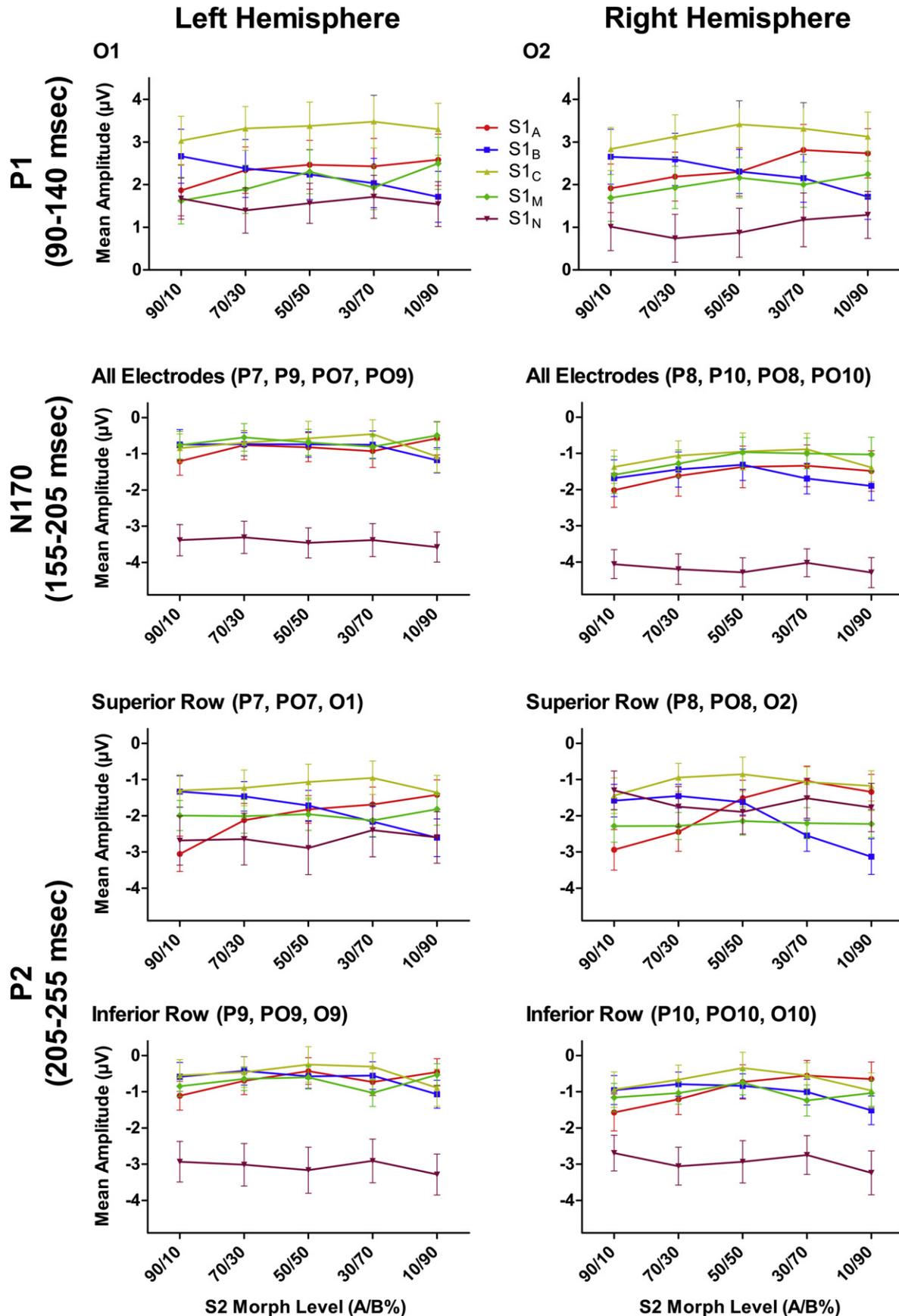


Fig. 5 – P1, N170, and P2 mean amplitudes at each S2 morph level following identity A, B, C, and morph, as well as noise S1s for representative left- and right-hemispheric electrode clusters. Error bars show ± 1 standard error of the mean (SEM).

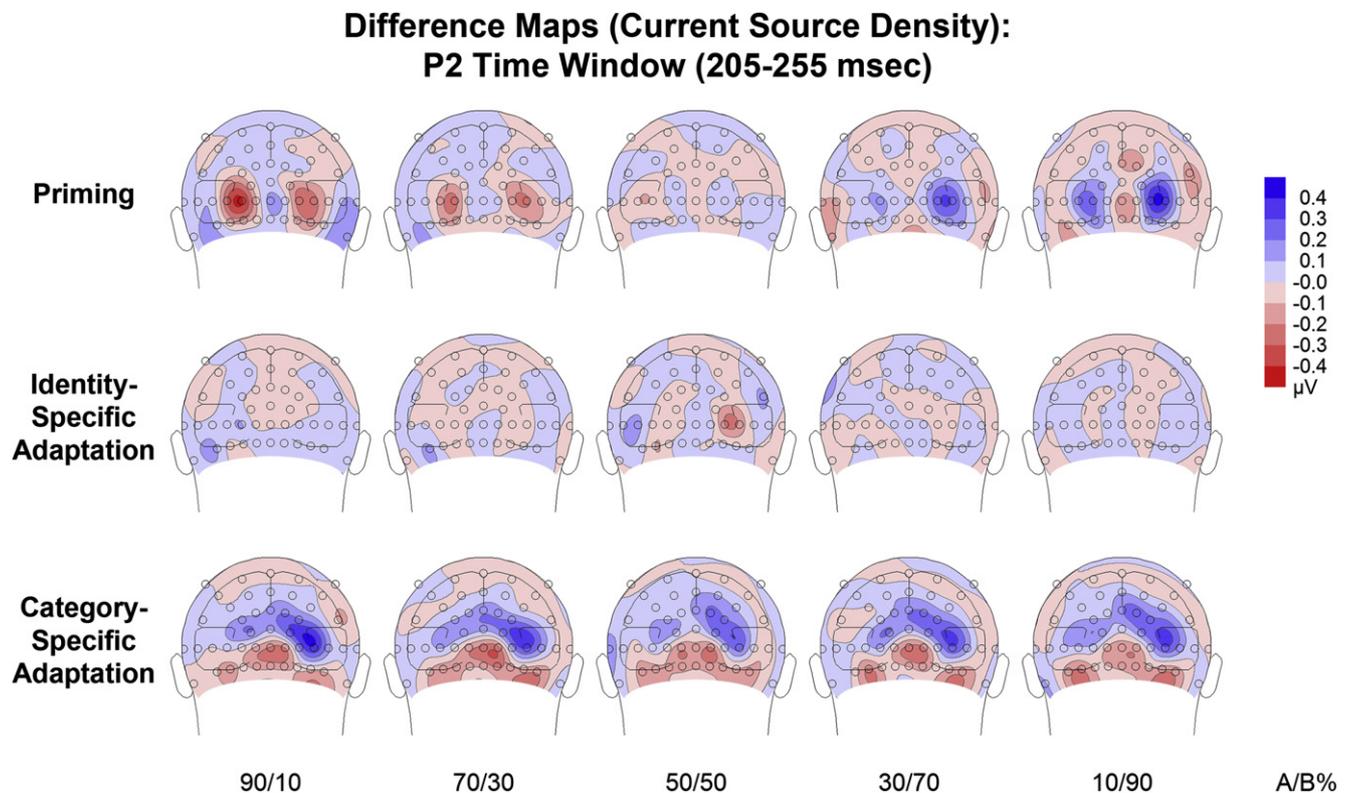


Fig. 6 – Topographical CSD maps for PR (difference between $S1_A$ and $S1_B$ conditions), identity-specific adaptation (difference between $S1_M$ and the mean of $S1_A$ and $S1_B$ conditions), and category-specific adaptation (difference between $S1_N$ and the mean of all other $S1$ conditions) at each $S2$ morph level for the P2 time window (205–255 msec). All maps were created using spherical spline interpolation and show a 110° equidistant projection from a back view perspective (including electrode positions).

these identities lead to higher behavioural aftereffects. However, further research will be necessary to clarify this issue.

4. 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, 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 AEs induced by relatively short adaptation periods are more transient in nature (Rhodes et al., 2007). Since our paradigm did not test whether the AEs induced by an S1 would survive for longer than the presentation of the following S2, both perceptual and representational explanations of the present AEs 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 AE 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 and 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 and 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 AEs 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.

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