Response Profile of the Face-Sensitive N170 Component: A Rapid Adaptation Study

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To study the response profile of the face-selective N170 component, an adaptation procedure was employed where adaptor and test stimuli were presented in rapid succession. Test stimuli came from 4 different face categories (upright, inverted, and eyeless faces and eyes-only images). The same face stimuli, as well as upright and inverted houses, served as adaptors. Strong N170 amplitude reductions indicative of adaptation were found for all types of face test stimuli preceded by face adaptors relative to house adaptors, demonstrating that at a generic level, the N170 reflects the activation of face-selective neurons by full faces and by face parts. The highly specific pattern of N170 adaptation effects for different combinations of adaptor and test stimulus categories suggests additional distinct contributions of eye-selective neurons and of face-sensitive neurons that are tuned to deviations from canonical stimulus orientations to the N170 component. Results demonstrate that the N170 is generated by multiple neural sources at both early and later stages of configural face processing and that rapid adaptation techniques provide a powerful tool to dissociate these sources.

Keywords: adaptation, event-related brain potentials, face perception, N170 component

Introduction

The existence of qualitative differences between the processing of faces and the processing of nonface objects is still a topic of intensive debate. One key difference between faces and objects is that the former are more difficult to perceive, identify, and remember when they are presented upside down. This "face inversion effect" (Yin 1969) is often explained by assuming that inversion specifically disrupts the processing of configural information and that this type of information is much more important for face perception than for the perception of other visual objects. Face perception and recognition are based on the analysis of the overall configuration of faces and the specific spatial relationships between face components, whereas object perception is guided by the feature-based analysis of individual elements (e.g., Diamond and Carey 1986; Tanaka and Farah 1993). This contrast between the configural or holistic processing of faces and the part-based or featural analysis of other objects is often regarded as the key qualitative difference between face and object perception (e.g., Maurer et al. 2002).

Recent research into the neural correlates of the face inversion effect and its links to face-specific configural processing has focused on the face-sensitive N170 component of the event-related brain potential and its magnetic counterpart, the M170. Both N170 and M170 components reflect a differential electromagnetic brain response to faces as compared with nonface objects that is elicited between 140 and 200 ms after stimulus onset over lateral occipitotemporal cortex and is typically more pronounced over the right hemisphere (Bentin et al. 1996; Eimer 2000; Halgren et al. 2000; Itier and Taylor 2004). The N170 is accompanied by a "vertex positive potential" (VPP) at midline electrodes (Jeffreys 1989) that is likely to reflect the same underlying face-sensitive brain processes (Joyce and Rossion 2005). Importantly, several studies have demonstrated that the N170 component is systematically affected by face inversion: It is delayed and its amplitude is increased in response to inverted as compared with upright faces (Bentin et al. 1996; Eimer 2000; Rossion et al. 2000; Sagiv and Bentin 2001; Itier et al. 2007).

The latency shift of the N170 component for inverted as compared with upright faces is commonly attributed to a delay in the onset of face-specific processing that results when inversion alters the prototypical spatial relationships between face parts (e.g., Rossion et al. 2000). The increase of N170 amplitudes for inverted faces is often regarded as puzzling, because studies using functional magnetic resonance imaging (fMRI, e.g., Yovel and Kanwisher 2005), intracranial recordings in humans (McCarthy et al. 1999), or single-cell recordings in nonhuman primates (e.g., Perrett et al. 1988) have observed either no difference or a small reduction of neural responses to inverted as compared with upright faces. For this reason, the effect of face inversion on N170 amplitudes is often attributed to factors that are only indirectly related to inversion, such as the increased difficulty of processing inverted faces, which may require additional attentional resources (e.g., George et al. 1996; Rossion et al. 1999) or the additional recruitment of eye-selective neurons (Itier et al. 2007; Itier and Batty 2009) or object-selective neurons (Rossion et al. 1999, 2000) by inverted faces. Based on evidence from single-cell recording (Perrett et al. 1985), Itier and Batty (2009) have suggested that eye-selective neurons in fusiform gyrus and the superior temporal sulcus (STS) do not respond when eyes are presented in their usual context of an upright face but are released from this context-dependent inhibition when face inversion disrupts this prototypical face configuration, resulting in larger N170 components for inverted faces. In line with this hypothesis, Itier et al. (2007) found that this face inversion effect was strongly reduced for faces without eyes. The suggestion that the N170 enhancement for inverted faces reflects an additional recruitment of object-selective neurons by inverted faces (e.g., Rossion et al. 2000; Itier and Taylor 2002) is based on results from an fMRI study (Haxby et al. 1999) where face inversion was found to produce an increased activation of a ventral extrastriate region that responded preferentially to nonface objects (houses).

Rather than attributing inversion-induced N170 amplitude enhancements to indirect factors such as the activation of eye- or object-selective neurons, an alternative hypothesis is that this effect is more directly linked to face orientation. Behavioral

studies (e.g., Rhodes et al. 2004) have demonstrated that following psychophysical adaptation to upright and inverted faces with opposite distortions (such as an expansion or contraction of internal face features), the direction of figural aftereffects in response to subsequent test faces is contingent on face orientation, suggesting that upright and inverted faces activate distinct face-selective neural populations. If such orientation-sensitive neurons contribute to the N170 component, one could postulate that a subset of these cells is activated most strongly when face stimuli deviate from their canonical upright orientation and that this additional activation contributes to the effect of face inversion on N170 amplitude.

The aim of the present study was to use neural adaptation procedures to gain new insights into the response profile of the N170 component, how this component is affected by face inversion, and the factors that may be responsible for N170 face inversion effects. Neural adaptation effects reflect the reduction in the activity of single neurons or neural populations in response to test stimuli when these are preceded by physically or categorically identical adaptor stimuli. Adaptation (or repetition suppression) paradigms have been successfully employed in fMRI research to study the response profile of domain-specific brain regions (Henson 2003). Here, differences in adaptation effects between test stimuli that vary only along one dimension are interpreted as evidence that the region in question is sensitive to this dimension. Adaptation procedures also offer a powerful tool to study the category-selectivity of brain activity that is reflected by N170/M170 components. Jacques and Rossion (2004, 2006) demonstrated that N170 components to faces presented to the left or right of fixation were reduced in amplitude when another face was already present at fixation, relative to trials where this central face was replaced by a nonface stimulus. Kovacs et al. (2006) reported category-specific N170 adaptation effects when upright faces were preceded by upright face adaptors, relative to nonface adaptor stimuli. It has also been shown that N170 amplitudes are reduced when the same face is presented twice in rapid succession, relative to trials where the second face image shows a different individual (Jemel et al. 2005). Such identity-dependent N170 adaptation effect can even be observed when the 2 successively presented faces differ in their viewpoint (Caharel et al. 2009), suggesting that the N170 is linked to the configural processing of individual faces. However, such links between the N170 component and configural face processing have been challenged in magnetoencephalography (MEG) experiments by Harris and Nakayama (2007, 2008), who measured the response profile of the M170 component to upright faces that were immediately preceded by different categories of adaptor stimuli. Although the M170 was strongly attenuated when a face was preceded by another face, and much less so when the adaptor was a nonface, M170 adaptation effects were equal in size regardless of whether upright faces, inverted faces, or isolated face parts were used as adaptors, suggesting that the M170 is primarily sensitive to face components and not to the overall configuration of a face.

In contrast to all of these previous experiments, which measured N170/M170 adaptation effects for only one test stimulus category (upright faces), the present study aimed to obtain a more comprehensive picture of the response profile of the N170 component by studying adaptation effects for different categories of face test stimuli. It is now generally acknowledged that the N170 is not a monolithic component

that is associated with only one specific face perception stage but instead reflects the joint activity of multiple neural sources that implement different aspects of face-selective processing (Rossion and Jacques 2008). Investigating the profile of N170 adaptation effects for different combinations of adaptor and test stimulus categories can therefore be used to dissociate the relative contribution of these sources to the N170 component. Importantly, this approach may also shed new light on the factors that are responsible for the effects of face inversion on N170 amplitudes. We used a rapid adaptation procedure where an adaptor stimulus (S1) and a subsequent face test stimulus (S2) were both presented for 200 ms and were separated by a 200-ms blank interval. Adaptation effects were measured for the N170 component in response to S2 for different combinations of adaptor and test stimulus categories. In Experiment 1, 5 different adaptor categories (upright faces, inverted faces, eyeless faces, eyes-only, and upright houses) were combined with 4 types of face test stimuli (upright faces, inverted faces, eyeless faces, and eyes-only stimuli). In Experiment 2, 4 different adaptor types (upright faces, inverted faces, upright houses, and inverted houses) and 2 different test stimulus categories (upright and inverted faces) were used (see Fig. 1).

We measured category-specific N170 adaptation effects to investigate different hypotheses with respect to the neural
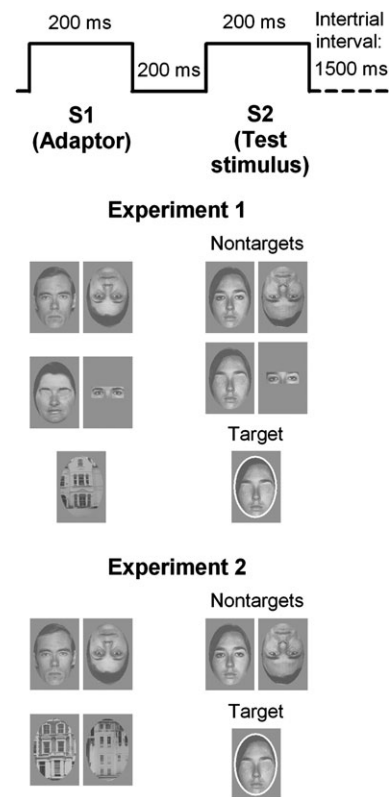

Figure 1. Trial structure and examples of the stimuli used in Experiments 1 and 2. In each trial, an adaptor stimulus (S1) was presented for 200 ms and was followed after a 200-ms interval by a test stimulus (S2, 200-ms duration). In Experiment 1, upright faces, eyeless faces, inverted faces, and eyes-only images were used as adaptors and test stimuli, whereas upright houses were only employed as adaptors. In Experiment 2, upright and inverted faces and houses served as adaptors and upright and inverted faces as test stimuli. Participants' task was to detect infrequent target events (a red oval outline shape surrounding one of the test stimuli, shown here in white).

processes that contribute to this component. At the most generic level, face-selective neurons that respond to the presence of a face or a face part in the visual field will be activated by upright, inverted, and eyeless faces as well as by eyes-only stimuli but not by houses. If the N170 component is associated with the activation of such neurons, N170 amplitudes in response to all face test stimuli should be attenuated whenever these test stimuli are preceded by a face or face part as adaptor relative to trials with house adaptors.

In addition to demonstrating this generic face-selectivity of the N170 component, we investigated the pattern of N170 adaptation effects for specific combinations of adaptor and test stimulus categories in order to test 3 different hypotheses that may account for the effects of face inversion on N170 amplitudes. If the activation of eye-selective neurons is inhibited in the context of upright faces (Itier et al. 2007), upright faces with and without eyes should be functionally equivalent in terms of N170 adaptation effects. When presented as adaptors, they should produce identical adaptation effects for all face test stimulus categories. When presented as test stimuli, they should show the same pattern of N170 adaptation across different adaptor categories. Furthermore, the pattern of N170 adaptation effects in response to eyes-only test stimuli can provide a critical test of the hypothesis that eye processing is inhibited for upright faces but not for inverted faces. Because eyes-only test stimuli will activate eye-selective neurons, N170 amplitudes to these stimuli should be attenuated whenever the same set of neurons has already been activated by the adaptor stimulus on the same trial. Therefore, N170 adaptation effects for eyes-only test stimuli should be stronger when they are preceded by eyes-only adaptors and inverted face adaptors, which are both assumed to activate eye-selective neurons, relative to eyeless face adaptors and upright face adaptors, which should not trigger an activation of these neurons. If inversion-induced N170 amplitude enhancements are linked to an additional activation of object-selective neurons by inverted faces (e.g., Rossion et al. 2000), N170 amplitudes in response to inverted face test stimuli should be reduced when they are preceded by inverted face adaptors relative to trials with other types of face adaptors, due to an attenuated response of object-selective neurons. Furthermore, because such object-selective neurons should also be activated by houses, the usual N170 face inversion effect (larger N170 components for inverted as compared with upright faces) should be strongly attenuated if not eliminated on trials where upright or inverted face test stimuli are preceded by house adaptors, reflecting the adaptation of object-selective neurons. These predictions were tested in Experiment 1.

If the N170 face inversion effect is linked to an increased activation of face-selective neurons that are tuned to deviations from the prototypical upright orientation of faces, strong N170 adaptation effects should be observed for inverted face test stimuli that are preceded by inverted face adaptors. However, and in contrast to the object-selective neuron account, this hypothesis does not predict any reduction of N170 face inversion effects on trials with upright house adaptors. It does however leave open the possibility that orientation-specific N170 adaptation effects might show some transfer across stimulus categories, that is, between inverted house adaptors and inverted face test stimuli. These predictions were tested in Experiment 2.

Experiment 1

Materials and Methods

Participants

Nineteen paid volunteers participated in this experiment. One was excluded due to an insufficient number of trials per condition after electroencephalography (EEG) artifact rejection (see below for rejection criteria), one because of excessive alpha activity at posterior electrodes, and a third participant due to the absence of N170 components in response to S2. The remaining 16 participants (8 males) were 19–39 years old (mean age 27.3 years) and had normal or corrected-to-normal vision. Fourteen were right handed, and 2 were left handed. Informed consent was obtained from all participants.

Stimuli and Procedure

Stimuli were presented on a cathode ray tube monitor at a viewing distance of 100 cm. E-Prime software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and behavioral response collection. Each stimulus category (upright faces, inverted faces, eyeless faces, eyes-only, and houses) included 12 individual images, resulting in a total of 60 different images. Upright and inverted faces were images of 12 different individuals (6 male and 6 female) that were selected from a standard set of faces (Ekman and Friesen 1976), all with neutral facial expression. Eyeless faces were created using Paint Shop Pro 7 by removing the eye region from all 12 upright faces and replacing it with skin tone from the same face. Eyes-only stimuli were generated by cropping the eye region (including the eyebrows) from each of the 12 upright faces. In addition, a set of 12 house images was cropped to generate the same oval outline shape as upright, inverted, and eyeless faces. The angular size of eyes-only images was $4.3° \times 1.6°$, and the angular size of all other images (upright, inverted, and eyeless faces, and houses) was $5.7° \times 8.1°$. Face and house stimuli were equated for luminance (20.5 cd/m^2) and were presented against an equiluminant gray background.

On each trial, 2 images (S1: adaptor stimulus; S2: test stimulus) were presented successively for 200 ms each, separated by a 200-ms interstimulus interval (see Fig. 1). Upright faces, inverted faces, eyeless faces, eyes-only, and houses were presented with equal probability as S1. Only the 4 face stimuli (but not houses) were presented equiprobably as S2. The intertrial interval was 1500 ms. The experiment included 8 experimental blocks that each contained 180 trials, with a break after 90 trials. In each block, 8 trials were presented for each of the 20 combinations of the 5 S1 categories and the 4 S2 categories, resulting in 160 trials per block. No response was required on these trials. In the remaining 20 target trials per block, S2 was presented together with a red oval outline shape that was positioned so that it was aligned with the outer contours of full-face images (see Fig. 1). Each block contained 1 target trial for each of the 20 possible combinations of S1 and S2 categories. Participants' task was to detect these target shapes and to respond with a left-hand or right-hand button press. Response hand was changed from left to right, or vice versa, after 4 successive experimental blocks. All combinations of S1 and S2 categories were presented in random order, with 2 constraints: S1 and S2 on the same trial were never images of the same individual, and S1 on any given trial was never an image of the same person as S2 on the preceding trial.

EEG Recording and Data Analysis

EEG was DC-recorded with a BrainAmps DC amplifier (upper cut-off frequency 40 Hz, 500-Hz sampling rating) and Ag–AgCl electrodes mounted on an elastic cap from 23 scalp sites (Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, and Oz, according to the extended international 10–20 system). Horizontal electro-oculogram (EOG) was recorded bipolarly from the outer canthi of both eyes. An electrode placed on the left earlobe served as reference for the online recording, and EEG was re-referenced off-line to the average of the left and right earlobes. Electrode impedances were kept below 5 kΩ.

EEG data were analyzed for nontarget trials only, to avoid contamination with brain activity associated with response execution. EEG was epoched off-line from 100 ms before to 700 ms after S1 onset, relative to a 100-ms pre-S1 baseline. Epochs with activity exceeding ±30 μV in the HEOG channel (reflecting horizontal eye movements) or ±60 μV at Fpz (indicating eye blinks or vertical eye movements) were excluded from analysis, as were epochs with voltages exceeding ±80 μV at any other electrode and trials where a manual response was recorded. Following artifact rejection, EEG waveforms were averaged separately for each of the 20 possible combinations of S1 category (upright faces, inverted faces, eyeless faces, eyes-only, or houses) and S2 category (upright faces, inverted faces, eyeless faces, or eyes-only). N170 components in response to S1 stimuli were quantified within a 150–190 ms time interval after S1 onset, relative to a 100-ms pre-S1 baseline, for lateral posterior electrodes P7 (left hemisphere) and P8 (right hemisphere) where the N170 is maximal. Repeated-measures analyses of variance (ANOVAs) were performed on N170 peak amplitudes and latencies for the factor S1 category and recording hemisphere. The N170 component in response to S2 was slightly delayed relative to the N170 triggered by S1 (see Fig. 2, bottom panel). N170 amplitudes to S2 were therefore measured for a 160–200 ms interval after S2 onset, relative to a 100-ms baseline from 50 ms before to 50 ms after S2 onset. Because category-specific N170 modulations in response to S1 were more pronounced over the right hemisphere, in line with previous observations (e.g., Bentin et al., 1996), analyses of category-specific N170 adaptation effects were focused on event-related potentials (ERPs) obtained at right posterior electrode P8. N170 peak and mean amplitudes were analyzed in repeated-measures ANOVAs. For all analyses, Greenhouse–Geisser corrections to the degrees of freedom or Bonferroni corrections for multiple comparisons were performed where appropriate.

Results

Behavioral Performance

Participants' accuracy in detecting targets (oval outline shapes) in S2 was very high, with errors (missed targets, or False Alarms on nontarget trials) occurring on less than 1% of all trials. Mean response time (RT) was 426 ms, and there was a small but reliable effect of S2 category on RTs ($F(3,45) = 4.1$; $P < 0.03$). RTs were fastest when target shapes were presented together with eyes-only stimuli (420 ms), intermediate for targets with eyeless faces (424 ms), and slowest when targets appeared together with inverted or upright faces (429 and 430 ms, respectively), but none of these differences reached Bonferroni-corrected significance levels.

ERPs to adaptors (S1)
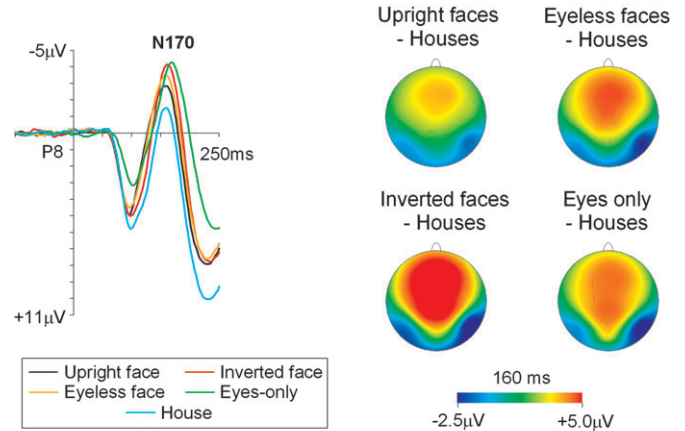
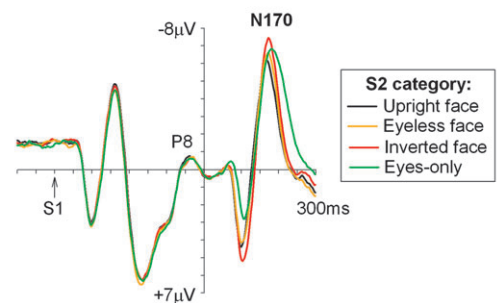**ERPs to adaptors (S1) and test stimuli (S2)**

Figure 2. Top left panel: Grand-averaged ERPs elicited in Experiment 1 in the 250-ms interval after S1 (adaptor) onset at right posterior electrode P8, shown separately for each of the 5 adaptor categories. Top right panel: Topographical distribution maps of difference potentials obtained by subtracting ERPs measured 160 ms after S1 onset in response to house adaptors from ERPs to each of the 4 different face adaptor types. Larger negative and positive amplitudes for face relative to house adaptors are shown in blue and red, respectively. Bottom panel: Grand-averaged ERPs elicited in Experiment 1 at lateral posterior electrode P8 from 100 ms prior to S1 onset to 300 ms after S2 onset. Waveforms are shown separately for each for the 4 S2 categories and are collapsed across different S1 categories. S1 onset is marked by an arrow, and the origin of the *y*-axis represents S2 onset.

N170

N170 triggered by S1 (adaptor stimuli). Figure 2 (top panel) shows ERPs elicited at right posterior electrode P8 in response to the 5 different S1 adaptor stimulus categories, together with topographic maps, which show the scalp distribution of ERP amplitude differences observed 160 ms after S1 onset between each of the 4 different types of face adaptors and houses. All 4 face adaptor categories triggered a right-hemisphere dominant N170 component as well as an enhanced positivity that was maximal at Cz (VPP).

An initial analysis conducted on ERP peak amplitudes at P7 and P8 in the 150–190 ms post-S1 time window revealed a main effect of S1 category ($F(4,60) = 8.63$; $P < 0.001$) as well as an interaction between S1 category and hemisphere ($F(4,60) = 4.04$; $P < 0.02$), demonstrating that N170 amplitudes were affected by S1 category and that this category-specific modulation was more pronounced over the right hemisphere (electrode P8). Follow-up analyses therefore focused on the N170 component at P8. As expected, N170 peak amplitudes

were reliably larger for face adaptors (collapsed across all 4 face adaptor categories) than for house adaptors ($F(1,15) = 17.0$; $P < 0.001$). When ERPs for the 4 face adaptor categories were analyzed together (excluding ERPs to house adaptors), a main effect of face adaptor category emerged ($F(3,45) = 4.94$; $P < 0.01$), and simple effect contrast analyses revealed that the N170 to inverted faces and eyes-only stimuli was reliably larger than the N170 to upright faces (both $P < 0.05$), whereas there were no reliable differences in N170 amplitudes between upright faces with and without eyes or between inverted faces and eyes-only stimuli. In addition, a main effect of face adaptor category was also present for N170 peak latency ($F(3,45) = 19.4$; $P < 0.001$), and simple effects contrast analyses confirmed that the N170 was delayed for eyes-only stimuli relative to all 3 other face categories and for inverted relative to upright faces (all $P < 0.05$).

N170 triggered by S2 (test stimuli): adaptation-unspecific effects of S2 category To illustrate the time course of ERP components triggered when S1 and S2 are presented in rapid succession, Figure 2 (bottom panel) shows ERPs to S1 and S2 at P8, separately for each of the 4 S2 categories, but collapsed across all 5 S1 categories. Waveforms are plotted relative to a baseline from 50 ms prior to 50 ms after S2 onset. As can be seen in this figure, the 200-ms S1–S2 interval was sufficiently long to obtain a clear N170 to S2 that was not contaminated by any residual sensory response elicited by S1. Importantly, the category-specific N170 amplitude modulations that were observed in response to S1 remained present for the N170 in response to S2. The N170 was again larger and slightly delayed for inverted faces and eyes-only stimuli relative to upright and eyeless faces. This was substantiated by main effects of S2 category on N170 peak amplitudes ($F(3,45) = 5.92$; $P < 0.002$), with simple effects analyses confirming that the N170 to inverted face and eyes-only test stimuli was larger than the N170 to upright faces (both $P < 0.05$), whereas there were no reliable N170 amplitude differences between upright faces with and without eyes or between inverted faces and eyes-only stimuli. A main effect of S2 category was also obtained for N170 peak latencies ($F(3,45) = 10.94$; $P < 0.001$), and simple effect contrasts demonstrated that N170 peak latency was reliably delayed for eyes-only stimuli relative to the other 3 face categories (all $P < 0.05$) and that the N170 latency delay for inverted relative to upright faces was almost significant ($P < 0.06$).

N170 triggered by S2 (test stimuli): category-specific adaptation effects To illustrate the overall pattern of N170 adaptation effects for the 5 S1 adaptor categories, as well as differences in N170 adaptation for different face test stimulus categories, Figure 3 (top panel) shows ERPs observed in response to S2 at right posterior electrode P8, separately for all combinations of adaptor (S1) and test stimulus (S2) category. It is immediately evident that for all 4 test stimulus categories, N170 amplitudes were largest on trials where these stimuli were preceded by house adaptors (blue lines in Fig. 3, top panel) relative to trials where they were preceded by 1 of the 4 types of face adaptors. To isolate this generic face-specific N170 adaptation effect, ERPs for trials where test stimuli were preceded by 1 of the 4 face adaptors (upright faces, inverted faces, eyeless faces, and eyes-only) were collapsed, separately

for each S2 category and were then compared with ERPs for trials where each of the 4 types of face test stimuli was preceded by house adaptors. A highly significant main effect of adaptor type (faces vs. houses) was obtained for N170 peak amplitudes ($F(1,15) = 18.8$; $P < 0.001$), reflecting the attenuation of the N170 on trials with face adaptors relative to trials with house adaptors. Notably, there was no interaction between adaptor type and S2 category ($F(3,45) = 1.9$; $P = 0.14$), indicating that this generic face-specific N170 adaptation effect was elicited in a similar fashion for upright faces, inverted faces, eyeless faces, and eyes-only stimuli. Essentially the same pattern of results was obtained for an analogous analysis of N170 mean amplitudes measured in the 160- to 200-ms interval after S2 onset. Again, there was a main effect of adaptor type ($F(1,15) = 18.2$; $P < 0.001$) but no interaction between adaptor type and S2 category ($F(3,45) = 1.4$; $P = 0.26$).

Subsequent analyses focused on N170 adaptation effects observed on trials with face adaptors (upright faces, inverted faces, eyeless faces, or eyes-only stimuli). Figure 3 (top panel) suggests differences in N170 adaptation between the 4 test stimulus categories and for specific combinations of face adaptor and test stimuli. There was little evidence that N170 amplitudes to upright face and eyeless face test stimuli were differentially affected by face adaptor category. In contrast, N170 components to inverted face and to eyes-only test stimuli appeared to be systematically modulated by the identity of the preceding face adaptor. To substantiate these observations, N170 peak amplitudes in response to S2 were quantified separately for each of the 4 face test stimulus categories, as a function of S1 face adaptor category (upright faces, inverted faces, eyeless faces, and eyes-only), leaving out trials where houses served as adaptor stimuli.

In an initial omnibus ANOVA, an interaction between S1 face adaptor category and S2 category was found ($F(9,135) = 6.45$; $P < 0.001$). To explore this interaction, N170 adaptation effects were analyzed separately for each of the 4 categories of face test stimuli. For upright face and eyeless face test stimuli, there were no effects of S1 face adaptor identity (both $F(3,45) < 1.8$; both $P > 0.15$), suggesting that for these 2 test stimulus categories, upright, inverted, and eyeless faces, as well as eyes-only adaptors resulted in equivalent levels of N170 adaptation. Importantly, a different pattern of results emerged for inverted face and eyes-only test stimuli. For eyes-only test stimuli, there was a significant effect of adaptor category ($F(3,45) = 4.36$; $P < 0.013$). To explicitly test the hypothesis that eye-sensitive neurons are activated by eyes-only adaptors and inverted face adaptors, but not by upright face and eyeless face adaptors, an ANOVA was conducted on N170 peak amplitudes that included the 2-level factors eye-specific adaptation (present: eyes-only and inverted face adaptors; absent: upright face and eyeless face adaptors) and adaptor category. A main effect of eye-specific adaptation ($F(1,15) = 9.26$; $P < 0.01$) that did not interact with adaptor category ($F(1,15) = 2.3$; $P = 0.15$) confirmed that adaptation of the N170 to eyes-only test stimuli was indeed more pronounced with eyes-only and inverted faces adaptors than with upright face or eyeless face adaptors. For inverted face test stimuli, a main effect of face adaptor category was observed ($F(3,45) = 10.6$; $P < 0.001$), and simple effects contrast analyses revealed that N170 adaptation was stronger when these stimuli were preceded by an inverted face adaptor relative to upright face, eyeless face, or eyes-only adaptors (all $P < 0.05$).
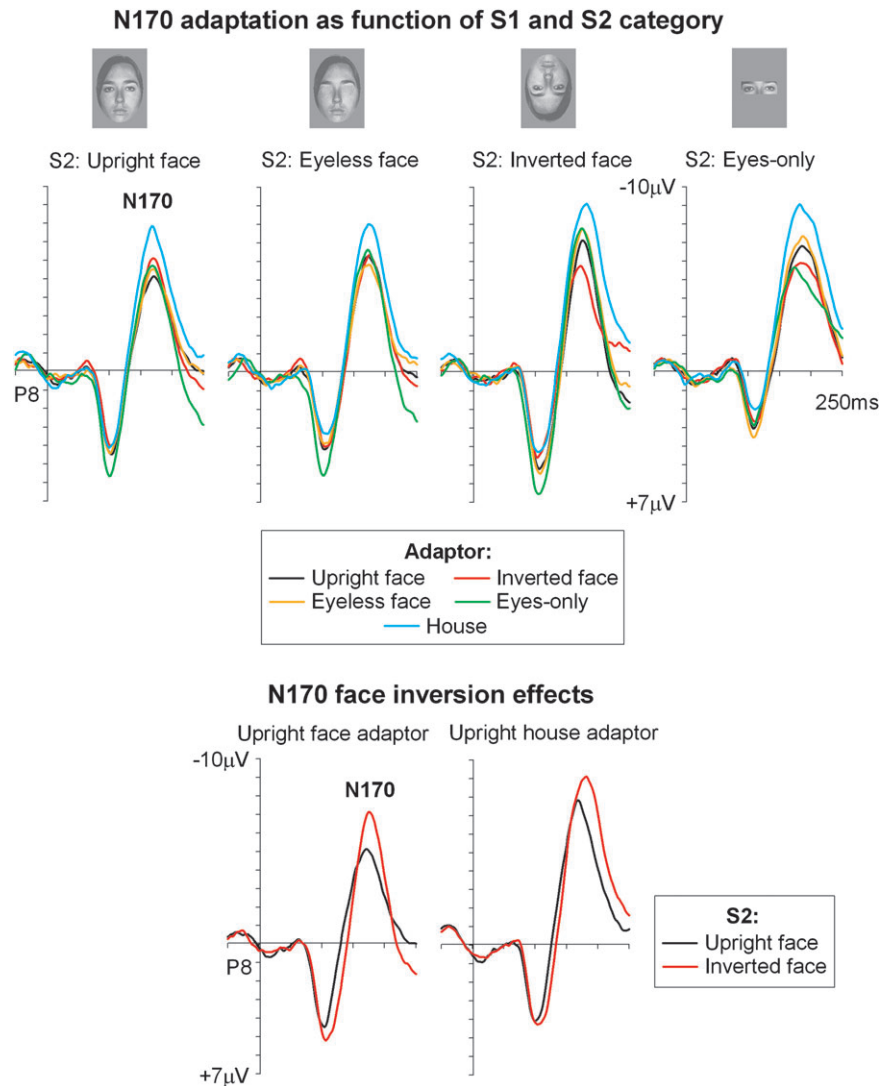
Figure 3. Grand-averaged ERPs elicited in Experiment 1 at P8 in the 250-ms interval after S2 onset. Top panel: ERP waveforms plotted separately for each of the 4 face test stimulus types as a function of adaptor category. Bottom panel: ERPs to upright and inverted test faces, plotted separately for trials where these faces were preceded by upright face adaptors and by house adaptors.

To further confirm the reliability of these category-specific N170 adaptation effects, additional analyses were performed on N170 mean amplitudes computed for the 160- to 200-ms time interval following S2 onset. Results were essentially the same as for the N170 peak analysis. S1 face adaptor identity and S2 category interacted in the omnibus ANOVA ($F(9,135) = 3.39$; $P < 0.014$), due to the fact that face adaptor category modulated N170 mean amplitudes in response to inverted face and eyes-only test stimuli ($F(3,45) = 5.38$ and 3.52; $P < 0.01$ and 0.03, respectively) but not for upright face and eyeless face test stimuli (both $F < 1$). For eyes-only test stimuli, a main effect of eye-specific adaptation ($F(1,15) = 8.01$; $P < 0.02$) did not interact with adaptor category ($F(1,15) < 1.5$). For inverted face test stimuli, N170 mean amplitudes were attenuated on trials with inverted face adaptors relative to trials with upright face, eyeless face, or eyes-only adaptors (all $P < 0.05$). Figure 4 summarizes the overall pattern of category-specific N170 adaptation effects. It shows mean N170 amplitudes for all 4 test stimulus categories as a function of adaptor category. The general face-specific adaptation effect, reflected by N170 reductions on trials with face adaptors relative to trials with house adaptors, was

clearly present for all 4 test stimulus categories. Although N170 adaptation effects for upright and eyeless face test stimuli did not differ systematically between the 4 face adaptor categories, category-specific adaptation effects are evident for inverted face and eyes-only test stimuli, with N170 amplitude reductions on trials where inverted faces were preceded by inverted face adaptors, and trials where eyes-only test stimuli were preceded by eyes-only and inverted face adaptors.

The observation that N170 adaptation effects for inverted face test stimuli were maximal when these stimuli were preceded by inverted face adaptors is in line not only with the hypothesis that the N170 reflects the activity of neurons that are sensitive to deviations from canonical stimulus orientations but also with the claim that inverted faces recruit object-selective neurons. To further investigate this second hypothesis, we tested whether the presence of a house adaptor attenuates or eliminates inversion-induced N170 amplitude enhancements in response to subsequent face test stimuli. N170 peak amplitudes to upright versus inverted face test stimuli were compared as a function of whether these faces
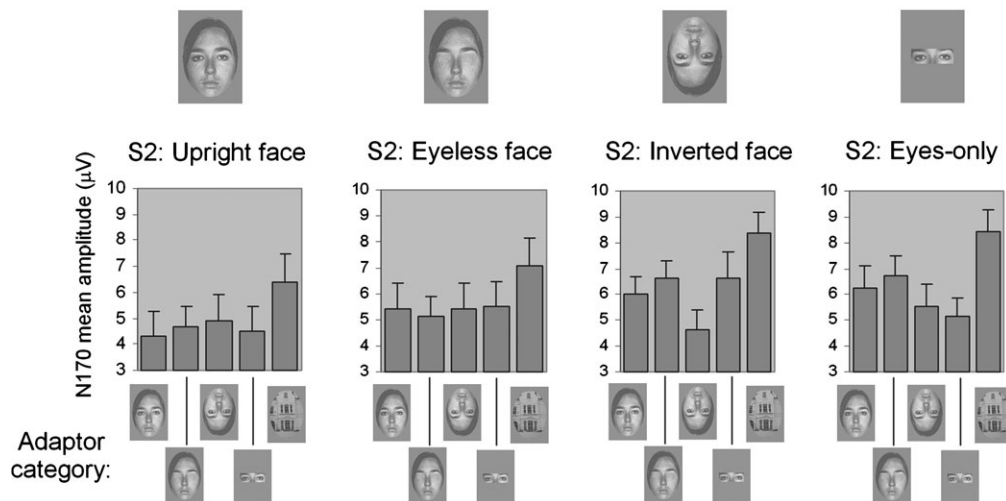
N170 mean amplitudes to S2 at P8

Figure 4. N170 mean amplitudes obtained in Experiment 1 at P8 in the 160- to 200-ms interval after test stimulus (S2) onset, shown separately for each of the 4 face test stimulus types as a function of adaptor category.

were preceded by upright face or house adaptors (see Fig. 3, bottom panel). There were main effects of adaptor category (upright face vs. house; $F(1,15) = 35.5$; $P < 0.001$) and test face orientation (upright vs. inverted; $F(1,15) = 10.6$; $P < 0.005$), reflecting the fact that N170 components were larger for faces preceded by houses and larger for inverted relative to upright test faces. Critically, there was no interaction between these 2 factors ($F < 1$), demonstrating that house adaptors did not modulate the usual face inversion effect on N170 amplitudes in response to face test stimuli. To further confirm this conclusion, the N170 to upright and inverted test faces preceded by house adaptors was compared with the N170 in response to upright and inverted adaptor (S1) faces. Again, there was no significant difference in the size of the inversion-induced N170 amplitude enhancement between these 2 face stimulus categories ($F(1,15) = 2.9$; $P = 0.10$).

Experiment 2

Materials and Methods

Participants

Twelve paid volunteers participated in this experiment. One was excluded due to a large number of eye movements and another because of excessive posterior alpha activity. The remaining 10 participants (5 males) were all right handed, 21–38 years old (mean age 26.4 years), and had normal or corrected-to-normal vision.

Stimuli, Procedure, EEG Recording, and Data Analysis

These were identical to Experiment 1, with the following exceptions: Upright faces, inverted faces, upright houses, and inverted houses served as S1 stimuli, and upright or inverted faces were shown as S2 (see Fig. 1, bottom panel). The experiment included 4 experimental blocks consisting of 176 trials per block, with a break after 88 trials. In each block, 20 trials were presented in random order for each of the 8 combinations of the 4 S1 categories and the 2 S2 categories, resulting in 160 trials per block. Each block also contained 16

target trials (2 trials for each of the 8 possible combinations of S1 and S2 categories).

Results

Behavioral Performance

Response errors occurred on less than 1% of all trials. Mean RT was 399 ms, and there was no effect of S2 category (upright vs. inverted face) on RTs ($t(9) < 1$).

N170

Figure 5 (top left panel) shows the N170 component elicited at electrode P8 in response to each of the 4 S1 (adaptor) stimulus categories, collapsed across trials with upright and inverted face test stimuli. As expected, the N170 was larger for faces than for houses and larger for inverted relative to upright faces. In contrast, no inversion-induced N170 amplitude enhancement was triggered in response to houses. An analysis of N170 peak amplitudes in the 150- to 190-ms time window after S1 onset revealed main effects of S1 category (face vs. house; $F(1,9) = 26.8$; $P < 0.01$) and S1 orientation (upright vs. inverted; $F(1,9) = 14.5$; $P < 0.01$), as well as an interaction between these 2 factors ($F(1,9) = 9.5$; $P < 0.02$), reflecting the fact that inversion-induced N170 amplitude enhancements were present for faces ($t(9) = 4.2$; $P < 0.01$), but not houses ($t(9) < 1$). Figure 5 (top right panel) shows the N170 at P8 in response to upright and inverted face test stimuli (collapsed across all 4 adaptor categories). Analyses of N170 peak amplitudes in the 160- to 200-ms time window after S2 onset confirmed that this component was larger for inverted as compared with upright faces ($t(9) = 2.9$; $P < 0.02$).

Figure 5 (bottom panel) illustrates the pattern of N170 adaptation effects observed in Experiment 2. ERPs obtained at electrode P8 in response to upright and inverted face test stimuli are shown separately for each of the 4 adaptor categories. For upright test face stimuli, the N170 was attenuated on trials with faces as adaptors relative to house-adaptor trials. In contrast, the orientation of these adaptor stimuli (upright vs. inverted) had no influence on the N170. This was confirmed in an ANOVA conducted on N170 peak
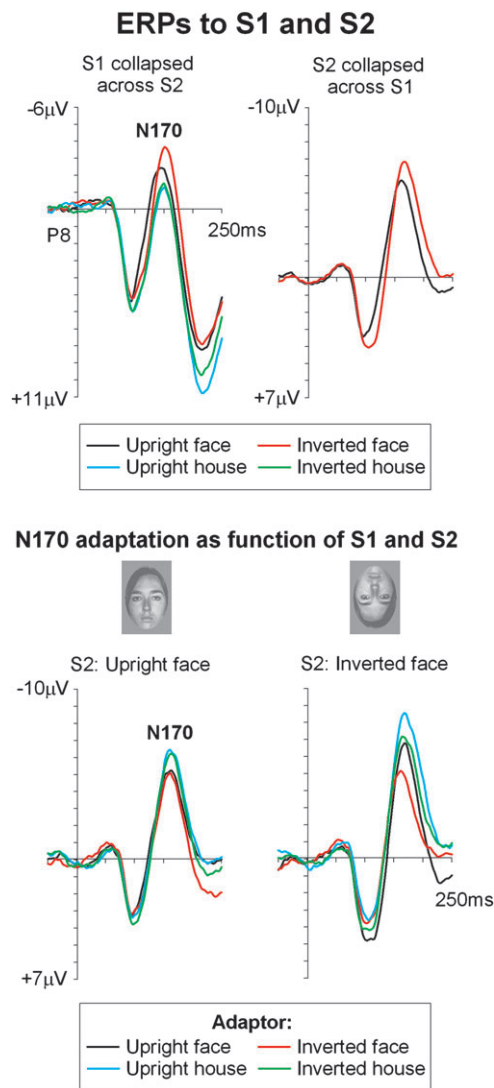
ERPs to S1 and S2

N170 adaptation as function of S1 and S2

Figure 5. Grand-averaged ERPs elicited in Experiment 2 at P8 in the 250-ms interval after S1/S2 onset. Top left panel: ERPs in response to each of the 4 adaptor categories (S1), collapsed across trials with upright and inverted test stimuli. Top right panel: ERPs to upright and inverted test stimuli (S2), collapsed across all 4 S1 categories. Bottom panel: ERPs to upright and inverted face test stimuli as a function of adaptor category.

amplitudes triggered in response to upright face test stimuli in the 160- to 200-ms time window after S2 onset for the factors S1 category (face vs. house) and S1 orientation (upright vs. inverted). There was a main effect of S1 category ($F(1,9) = 10.3$, $P < 0.02$), confirming the generic face-specific adaptation effect observed in Experiment 1, but no effect of S1 orientation ($F < 1$) and no interaction between these 2 factors ($F < 1$). Essentially the same results were obtained for N170 mean amplitudes. For inverted face test stimuli, a very different pattern of N170 adaptation effects was obtained, with both adaptor category and adaptor orientation now strongly affecting N170 amplitudes (Fig. 5, bottom right). An analysis of N170 peak amplitudes revealed a main effect of S1 category ($F(1,9) = 26.1$, $P < 0.01$), again due to an N170 attenuation on trials with face adaptors relative to trials with house adaptors. This effect was accompanied by a main effect of S1 orientation ($F(1,9) = 10.86$, $P < 0.01$), as N170 amplitudes to inverted faces

were reduced when they were preceded by an inverted adaptor stimulus. Importantly, there was no indication of any interaction between S1 category and S1 orientation ($F < 1$), demonstrating that this inversion-induced adaptation of N170 components triggered by inverted face test stimuli was not restricted to trials with face adaptors, but was equally strong when inverted faces were preceded by inverted as compared with upright houses. Corresponding analyses of N170 mean amplitudes obtained the same results.

To further investigate the possible impact of house adaptors on N170 face inversion effects, N170 amplitude differences in response to upright and inverted face test stimuli were also compared as a function of adaptor category (upright face vs. upright house). As in Experiment 1, there was no interaction between adaptor category and test face orientation ($F < 1$), thus confirming the observation from Experiment 1 that N170 amplitude differences in response to upright versus inverted face test stimuli are not attenuated or eliminated when these stimuli are preceded by house adaptors.

Discussion

The present study employed rapid adaptation procedures to study the processes that are reflected by the face-sensitive N170 component. In contrast to previous N170/M170 adaptation experiments (Jacques and Rossion 2004, 2006; Kovacs et al. 2006; Harris and Nakayama 2007, 2008), we studied the impact of different adaptor categories not just on the N170 in response to upright faces, but also for other face test stimulus categories (inverted faces, eyeless faces, and eyes-only stimuli). Results revealed a complex but systematic pattern of category-specific N170 adaptation effects that provides new insights into the neural processes that contribute to the N170 component.

The N170 results observed in response to adaptor stimuli (S1) confirmed previous findings. The N170 to face adaptors was larger than the N170 to house adaptors, and the N170 to inverted face adaptors was larger and delayed relative to the N170 to upright face adaptors, replicating the typical N170 face inversion effect observed in numerous previous studies (e.g., Bentin et al. 1996; Eimer 2000; Rossion et al. 2000; Sagiv and Bentin 2001; Itier et al. 2007). In Experiment 1, the N170 to eyes-only S1 stimuli was also larger and delayed relative to the N170 to upright face adaptors, again in line with earlier findings (Bentin et al. 1996; Itier et al. 2007). As can be seen in Figure 2 (bottom panel), N170 amplitudes were larger for test stimuli (S2) as compared with adaptors (S1), which contrasts with previous adaptation studies (e.g., Kovacs et al. 2006; Harris and Nakayama 2008) where the N170 was usually larger in response to S1. This is most likely due to the fact that target shapes could only appear together with S2 stimuli, which will have resulted in an attentional enhancement of visual ERP responses to these stimuli. Importantly, the pattern of category-specific N170 modulations observed for adaptor stimuli was also found in both experiments for S2 stimuli, thus demonstrating that the general sensitivity of the N170 component to differences between face categories can be observed not only for adaptors but also for subsequent test stimuli, even when they are presented in rapid succession. This makes it possible to interpret differential N170 amplitude modulations in response to test stimuli as indicators of category-specific adaptation.

In both experiments, N170 amplitudes triggered by face test stimuli were generally larger on trials with nonface adaptors (houses) relative to trials where face adaptors were presented.

In Experiment 1, the size of this general face-specific N170 adaptation effect did not differ significantly across the 4 face test stimulus types, suggesting that at a generic level, the N170 component reflects the activation of neurons that respond equally strongly to full faces and to face parts. The N170 is reduced in amplitude whenever 2 stimuli that activate these neurons are presented in rapid succession. Although previous studies have already shown similar N170/M170 adaptation for upright faces that were preceded by upright faces (Jacques and Rossion 2004, 2006; Kovacs et al. 2006; Harris and Nakayama 2007) or face parts (Harris and Nakayama 2008), the present study demonstrates for the first time that this generic face-specific adaptation effect is elicited across a range of face adaptor and test stimuli.

In addition to this generic face-specific N170 adaptation effect, a distinctive pattern of N170 amplitude modulations was found for different combinations of face adaptors and face test stimuli in Experiment 1. When upright faces were used as test stimuli, no reliable N170 amplitude differences emerged between face adaptor categories. In other words, upright faces, inverted faces, eyeless faces, and eyes-only stimuli were equally effective adaptors. This is in line with the observation of Harris and Nakayama (2008) that adaptation of the magnetoencephalographic M170 component to upright faces was equally strong when upright faces, inverted faces, or face parts were used as adaptors. These authors suggested that the M170 is exclusively sensitive to face parts, but not to facial configuration, and therefore likely to be generated at stages that precede face-specific configural processing. However, other aspects of the present results suggest that the N170 also reflects processes that are sensitive to the configuration of face stimuli.

On trials with eyes-only test stimuli, N170 amplitude was modulated by the category of a preceding face adaptor, with larger N170 adaptation effects for eyes-only and inverted face adaptors than for upright face and eyeless face adaptors (Fig. 3, top panel). This result provides support for the hypothesis that eye-sensitive neurons are inhibited in response to upright faces but not inverted faces (Itier et al. 2007; see also Itier and Batty 2009, for an in-depth review of neural correlates of eye and gaze processing). If such neurons are only activated by eyes-only and inverted face adaptors, they should be less responsive on trials where these adaptors are followed by eyes-only test stimuli, resulting in a stronger attenuation of N170 amplitudes relative to trials with upright or eyeless face adaptors. In addition, if eye-sensitive neurons are inhibited when eyes are presented in the context of an upright face, N170 adaptation effects for eyes-only test stimuli preceded by upright face adaptors should not differ from adaptation effects found with eyeless face adaptors. Both predictions were confirmed in Experiment 1. Furthermore, if eye-selective cells are not activated in response to upright faces, upright faces with and without eyes should be functionally equivalent in terms of their impact on the N170. In line with this prediction, there were no overall N170 amplitude differences between upright faces and eyeless faces (see also Eimer 1998; Itier et al. 2007). Regardless of whether they were presented as adaptors or as test stimuli, these 2 stimulus categories produced very similar N170 adaptation effects, thus further underlining that the presence or absence of eyes in upright faces has no systematic effect on the N170 component. Although all these observations support the idea that the activity of eye-sensitive neurons contributes to the N170 only when eyes are presented outside the context of an upright face, one aspect of the results

in Experiment 1 is not entirely in line with this hypothesis. If eye-sensitive neurons are activated by inverted faces, there should have been a measurable N170 adaptation effect on trials where inverted face test stimuli were preceded by eyes-only adaptors, relative to trials with upright or eyeless face adaptors. However, no such differential N170 modulation was observed. The reasons for the absence of this specific N170 adaptation effect are unclear, and will need to be investigated in future experiments.

A different pattern of category-specific N170 adaptation effects was observed for trials where inverted faces were used as test stimuli. In Experiment 1, the N170 was attenuated when inverted faces served as adaptor stimuli, relative to trials with upright face, eyeless face, or eyes-only adaptors. Experiment 2 confirmed the existence of a strong N170 adaptation effect when inverted faces are preceded by inverted as compared with upright faces. At first sight, this pattern of results seems to support the hypothesis that face inversion triggers the additional recruitment of object-sensitive neurons that contribute to N170 amplitude (e.g., Rossion et al. 2000). Adaptation of these neurons by inverted face adaptors should produce an N170 attenuation that is specific to trials with inverted face test stimuli. Furthermore, the fact that the decrease in N170 amplitude for inverted face test stimuli was found only with inverted face adaptors, and not for eyeless face or eyes-only adaptors suggests that this adaptation effect is not produced whenever face adaptors deviate in some way from the prototypical facial configuration of an upright face but is more specifically linked to the processing of inverted faces.

However, the hypothesis that the activity of object-sensitive neurons contributes to the N170 in response to inverted faces also predicts that effects of face inversion on N170 amplitudes should be strongly attenuated if not eliminated when upright or inverted face test stimuli are preceded by house adaptors. Because houses will also activate object-sensitive neurons, these neurons should be less responsive to subsequently presented inverted faces, thereby reducing N170 face inversion effects (i.e., amplitude differences in response to inverted vs. upright face test stimuli). In fact, inversion-induced N170 amplitude modulations were very similar in both experiments when upright or inverted faces were preceded by upright face adaptors and when they were preceded by upright house adaptors. This observation strongly suggests that the strong N170 amplitude reduction observed for inverted test faces preceded by inverted face adaptors is not primarily due to an adaptation of object-sensitive neurons and that other factors must be responsible for this effect.

Instead of attributing inversion-induced N170 amplitude modulations solely to indirect factors such as the additional recruitment of eye-selective or object-selective neurons, the possibility remains that these effects also reflect a more direct contribution of face-selective neurons that are tuned to stimulus orientation (e.g., Rhodes et al. 2004). Enhanced N170 amplitudes to inverted faces might result if some of these cells are activated maximally when faces deviate from their canonical upright orientation. The pattern of adaptation effects observed in Experiment 2 provides initial supportive evidence for this hypothesis. When upright faces were presented as test stimuli, N170 adaptation was exclusively determined by the category of the preceding adaptor (face vs. house) but was entirely unaffected by the orientation of these adaptors (upright vs. inverted). In marked contrast, N170

adaptation effects for inverted face test stimuli were driven not just by adaptor category but also by adaptor orientation. As in Experiment 1, strong N170 amplitude reductions were observed when inverted faces were preceded by inverted as compared with upright face adaptors. Remarkably, adaptation effects of similar size were also observed following inverted as compared with upright house adaptors (Fig. 5, bottom panel). This pattern of results, which was highly consistent across all participants, suggests that the effects of face inversion on N170 amplitudes could at least in part reflect the activity of orientation-sensitive neurons that are activated maximally by stimuli that deviate from their canonical upright orientation.

The observation that orientation-induced N170 adaptation effects were of similar size in Experiment 2 regardless of whether inverted face test stimuli were preceded by inverted face adaptors or by inverted house adaptors might suggests that these effects and the underlying neural mechanisms are essentially face unspecific. However, the effects of stimulus inversion observed for the N170 in response to S1 stimuli (face and house adaptors) points in a different direction. Previous studies (e.g., Rossion et al. 2000; Itier et al. 2006) have found that the inversion on nonface stimuli such as houses does not affect N170 amplitudes (but see Eimer 2000, for a small but reliable effect of house inversion on the size of the N170), and this was also observed in Experiment 2. The usual N170 amplitude increase was observed for inverted as compared with upright face adaptors, but no analogous inversion-induced ERP effect was found in the same time window for inverted versus upright house adaptors (Fig. 5, top left panel). In other words, the difference between upright and inverted house adaptors had no measurable impact on the N170 to these stimuli themselves but produced strong and consistent N170 adaptation in response to subsequently presented inverted faces. This dissociation between temporally proximal and distal effects of house orientation on N170 amplitudes is remarkable and requires careful examination in future research. A scenario that may account for these findings is that the orientation-sensitive neurons responsible for the attenuated N170 to inverted faces preceded by inverted face or house adaptors are predominantly face-selective and are therefore maximally activated in response to faces that deviate from their standard upright position. However, they are connected to other visual areas that process the orientation of nonface objects, such as houses, and receive input from these areas whenever objects in a noncanonical orientation are encountered. Due to this orientation-specific priming of face-sensitive visual areas by nonface objects, the N170 to inverted face is attenuated when it is immediately preceded by an inverted house. This account is obviously speculative at present and needs to be examined in future experiments.

Although the scalp topography of face-sensitive N170/VPP components, as shown in Figure 2, strongly suggests that they are generated in bilateral posterior temporal regions, the exact location of the cortical generators of N170 and M170 components still remains somewhat controversial. Source analyses have identified the posterior fusiform gyrus as the main locus of the M170 (e.g., Halgren et al. 2000). For the N170, some localization studies have identified similar generator regions in posterior fusiform gyrus and the lateral inferior occipital cortex (e.g., Rossion et al. 2003), whereas others (e.g., Itier and Taylor 2004) have suggested the posterior STS as the primary cortical origin of the N170. This difference may in part reflect the differential sensitivity of MEG and EEG measures to tangential versus radial sources, which implies that the M170 and N170 do not necessarily reflect identical underlying cortical processes (see Itier and Batty 2009, for more details). For this reason, it is also not guaranteed that future experiments using rapid adaptation procedures to study the response profiles of M170 or N170 components will always produce convergent results.

Another possible reason why previous source localization studies of the N170 have obtained partially inconsistent findings is that the N170 is not a monolithic component that is tightly linked to one distinct aspect of face processing but instead reflects the activity of multiple simultaneously active face-sensitive brain processes. The results observed in the present study support this view, as the pattern of N170 adaptation effects strongly suggested that this component is associated with the activity of distinct neuronal populations that are associated with different aspects of face processing. At the most basic level, the N170 is associated with the activation of face-selective neurons that is triggered whenever a face or part of a face is present in the visual field and reflects a relatively early stage in the structural encoding of face parts. However, this does not imply that the N170 is insensitive to more global aspects of configural face processing and its disruption through face inversion. The pattern of N170 adaptation effects observed in this study provides new evidence that face inversion is associated with a disinhibition of eye-selective neurons and may also trigger an activation of face-sensitive neurons that are tuned to deviations from canonical upright orientations. The current findings demonstrate that the rapid adaptation procedure can be a powerful tool to identify and dissociate the impact of different aspects of face processing on face-selective brain responses.

Notes

References

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

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

Diamond R, Carey S. 1986. Why faces are and are not special: an effect of expertise. J Exp Psychol Gen. 115:107–117.

Eimer M. 1998. Does the face-specific N170 component reflect the activity of a specialized eye processor? Neuroreport. 9:2945–2948.

Eimer M. 2000. Effects of face inversion on the structural encoding and recognition of faces—evidence from event-related brain potentials. Cogn Brain Res. 10:145–158.

Ekman P, Friesen W. 1976. Pictures of facial affect. Palo Alto (CA): Consulting Psychologists Press.

George N, Evans J, Fiori N, Davidoff J, Renault B. 1996. Brain events related to normal and moderately scrambled faces. Cogn Brain Res. 4:65-76.

Halgren E, Raij T, Marinkovic K, Jousmaki V, Hari R. 2000. Cognitive response profile of the human fusiform face area as determined by MEG. Cereb Cortex. 10:69-81.

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

Harris AM, Nakayama K. 2008. Rapid adaptation of the M170 response: importance of face parts. Cereb Cortex. 18:467-476.

Haxby JV, Ungerleider LG, Clark VP, Schouten JL, Hoffman EA, Martin A. 1999. The effect of face inversion on activity in human neural systems for face and object perception. Neuron. 22:189-199.

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

Itier RJ, Alain C, Sedore K, McIntosh AR. 2007. Early face processing specificity: it's in the eyes!. J Cogn Neurosci. 19:1815-1826.

Itier RJ, Batty M. 2009. Neural bases of eye and gaze processing: the core of social cognition. Neurosci Biobehav Rev. 33:843-863.

Itier RJ, Latinus M, Taylor MJ. 2006. Face, eye and object early processing: what is the face specificity? Neuroimage. 29:667-676.

Itier RJ, Taylor MJ. 2002. Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. Neuroimage. 15:353-372.

Itier RJ, Taylor MJ. 2004. N170 or N1? Spatiotemporal differences between object and face processing using ERPs. Cereb Cortex. 14:132-142.

Jacques C, Rossion B. 2004. Concurrent processing reveals competition between visual representations of faces. Neuroreport. 15:2417-2421.

Jacques C, Rossion B. 2006. The speed of individual face categorization. Psychol Sci. 17:485-492.

Jeffreys DA. 1989. A face-responsive potential recorded from the human scalp. Exp Brain Res. 78:193-202.

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. 43:2024-2040.

Joyce C, Rossion B. 2005. The face-sensitive N170 and VPP components manifest the same brain processes: the effect of reference electrode site. Clin Neurophysiol. 116:2613-2631.

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

Maurer D, Le Grand R, Mondloch CJ. 2002. The many faces of configural processing. Trends Cogn Sci. 6:255-260.

McCarthy G, Puce A, Belger A, Allison T. 1999. Electrophysiological studies of human face perception. II: response properties of face-specific potentials generated in occipitotemporal cortex. Cereb Cortex. 9:431-444.

Perrett DI, Mistlin AJ, Chitty AJ, Smith PAJ, Potter DD, Broennimann R, Harries M. 1988. Specialized face processing and hemispheric-asymmetry in man and monkey: evidence from single unit and reaction-time studies. Behav Brain Res. 29:245-258.

Perrett DI, Smith PAJ, Potter DD, Mistlin AJ, Head AS, Milner AD, Jeeves MA. 1985. Visual cells in the temporal cortex sensitive to face view and gaze direction. Proc R Soc Lond B. 223:293-317.

Rhodes G, Jefferey L, Watson TL, Jaquet E, Winkler C, Crawford CWG. 2004. Orientation-contingent face aftereffects and implications for face-coding mechanisms. Curr Biol. 14:2119-2123.

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

Rossion B, Gauthier I, Tarr MJ, Despland P, Bruyer R, Linotte S, Crommelinck M. 2000. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. Neuroreport. 11:69-74.

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.

Rossion B, Joyce CA, Cottrell GW, Tarr MJ. 2003. Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. Neuroimage. 20:1609-1624.

Sagiv N, Bentin S. 2001. Structural encoding of human and schematic faces: holistic and part-based processes. J Cogn Neurosci. 13:937-951.

Tanaka JW, Farah MJ. 1993. Parts and wholes in face recognition. Q J Exp Psychol. 46A:225-245.

Yin RK. 1969. Looking at upside-down faces. J Exp Psychol. 81:141-145.

Yovel G, Kanwisher N. 2005. The neural basis of the behavioral face-inversion effect. Curr Biol. 15:2256-2262.