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RESEARCH****Research Report****The N170 component and its links to configural face processing: A rapid neural adaptation study****Martin Eimer***, Angela Gosling, Susan Nicholas, Monika Kiss

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ABSTRACT

A neural adaptation paradigm where adaptor and test stimuli were presented in rapid succession was employed to investigate links between the face-sensitive N170 component and configural face processing. In Experiment 1, schematic adaptor stimuli preceded naturalistic images of upright faces, inverted faces, or isolated eyes. Relative to a baseline condition with schematic house adaptors, upright and inverted schematic faces adapted the N170 to subsequent naturalistic faces, demonstrating that this component is associated with neural processes involved in the analysis of first-order relational face configuration. In Experiment 2, two-tone Mooney faces adapted the N170 to naturalistic faces relative to a baseline condition with Mooney houses, suggesting links between the N170 and holistic face processing. Results demonstrate that the N170 component does not exclusively reflect the detection and analysis of individual face parts, but also the processing of first-order configural and global gestalt features of faces. They also show that neural adaptation procedures can be used to identify the neural mechanisms that are responsible for category-specific ERP components such as the N170.

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1. Introduction

Humans are highly skilled in face recognition, and this ability has been attributed to the configural processing of faces. Configural processing is based on relations between component parts of faces, and is often contrasted with featural or part-based processing, which focuses on local information such as individual facial features and their properties (e.g., Maurer et al., 2002; McKone and Yovel, 2009). It has been suggested that configural face perception includes several levels of processing (Maurer et al., 2002; see also Diamond and Carey, 1986; Tanaka and Farah, 1993; Rossion and Gauthier, 2002): Initially, generic first-order relational information (two eyes above nose, nose above mouth) is retrieved, which is then

combined into a holistic gestalt-like representation. Finally, second-order relational information (i.e., spatial distances between facial features) is processed, which distinguishes individual faces and forms the basis of face recognition.

Evidence for face-specificity in visual processing comes from event-related potential (ERP) and magnetoencephalographic (MEG) studies. The N170 component and its MEG counterpart (M170) reflect face-selective electromagnetic responses in occipitotemporal areas that are triggered 150–190 ms after stimulus onset (e.g., Bentin et al., 1996; Eimer, 2000a; Halgren et al., 2000). Because of their face-sensitivity, these components are regarded as early manifestations of face-selective cortical processing. Several studies have shown that the N170 is not affected by the familiarity of faces (e.g., Bentin and Deouell,

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2000; Eimer, 2000a), indicating that this component is associated with perceptual face processing stages that precede the identification of individual faces. The question to what degree N170/M170 components are linked to configural (as opposed to part-based) face processing is still a matter of debate. For example, the fact that the N170 is larger in response to eyes presented in isolation than to full faces has led to the suggestion that this component is primarily linked to the processing of individual face components, and in particular the eyes (e.g., Bentin et al., 1996). However, subsequent studies have provided substantial evidence that the N170 is also sensitive to configural face processing. It has been repeatedly demonstrated that N170 amplitudes and latencies are strongly modulated by face inversion, with enhanced and delayed N170 components to inverted as compared to upright faces (e.g., Eimer, 2000b; Rossion et al., 2000; Itier et al., 2007). Adverse effects of stimulus inversion on face perception (e.g., Yin, 1969) are generally regarded as a hallmark of configural face processing. The fact that the N170 is highly sensitive to face inversion therefore strongly suggests that the underlying neural processes are not just involved in the part-based processing of face components, but also in the analysis of configural face properties.

Further positive evidence for a link between the N170 component and configural face processing comes from ERP studies that have measured the N170 in response to schematic face stimuli and two-tone Mooney faces. Schematic face stimuli (such as Smiley faces) retain the overall spatial configuration of faces, but no parts that could be individually recognized as face components. Therefore, schematic faces are assumed to primarily engage configural processing. With respect to the classification proposed by Maurer et al. (2002), schematic faces allow the retrieval of first-order relational information, and may also be processed at the subsequent holistic level (see also Latinus and Taylor, 2006). Mooney faces (Mooney, 1957) usually contain no individually recognizable facial features and, unlike schematic faces, no prototypical first-order configural arrangement of their component parts. To be recognized as faces, their global structure that is provided by shape-from-shading information needs to be processed. It has therefore been argued that the first face-specific processing stage activated by Mooney faces is holistic (Latinus and Taylor, 2005, 2006). If the N170 component is sensitive to configural face processing, it should not just be triggered by naturalistic face images, but also in response to schematic faces, or even by two-tone Mooney images of faces. This has indeed been demonstrated in previous ERP studies. Schematic faces were found to trigger an N170 that did not differ from the N170 in response to naturalistic faces, in line with the hypothesis that this component is associated with the processing of configural face information (Sagiv and Bentin, 2001; Latinus and Taylor, 2006). Inversion resulted in a delayed N170 for schematic faces, and either in a reduction (Sagiv and Bentin, 2001) or no effect (Latinus and Taylor, 2006) for N170 amplitude. There is also some evidence that Mooney faces elicit face-specific N170 components, suggesting that in the absence of first-order relational information, the N170 is sensitive to holistic face processing. Latinus and Taylor (2005, 2006) observed larger N170 components for Mooney faces as compared to scrambled non-face Mooney control stimuli. Inversion did not affect the latency of the N170 to Mooney

faces, and an attenuation of N170 amplitude for inverted Mooney faces was only found in one of these two studies (Latinus and Taylor, 2005). Furthermore, George et al. (2005) demonstrated that N170 amplitudes to inverted Mooney faces were larger on trials where these stimuli were identified as faces.

In summary, these previous ERP studies have obtained initial evidence that the face-sensitive N170 component does not just reflect a neural response to individual face parts, but is also associated with configural face processing. However, this conclusion has recently been called into question by the results of an MEG study by Harris and Nakayama (2008), where a rapid neural adaptation procedure (first developed by Jeffreys, 1996) was used to investigate links between the M170 component and configural versus part-based face processing. Neural adaptation (or repetition suppression) paradigms provide a new and potentially powerful technique to determine the functional properties of ERP components and their links to underlying neural processing modules. Neural adaptation effects are observed when the activity level of single neurons or neural populations in response to test stimuli is reduced because these stimuli were preceded by physically identical or categorically equivalent adaptor stimuli. Adaptation paradigms have been widely used in fMRI research to study the response profile of domain-specific brain regions (e.g., Henson, 2003), and were more recently also employed in EEG and MEG investigations of the N170/M170 component. N170 adaptation was demonstrated by Jacques and Rossion (2004, 2006) by showing that N170 amplitudes to laterally presented faces were reduced when another face was already present at fixation, relative to trials where a central non-face control stimulus was present (see also Kovacs et al., 2006, for similar observations). Whereas these studies used N170 adaptation to demonstrate the general face-selectivity of this component, a more recent study from our group (Eimer et al., 2010) has shown that N170 adaptation effects reflect the activation of face-selective neurons by full faces as well as by individual face parts, such as the eyes.

Harris and Nakayama (2008) measured the M170 component to test faces that were preceded by full faces, scrambled faces, or isolated face parts as adaptors, and observed equally strong M170 adaptation effects for all three adaptor categories. Critically, they found no M170 adaptation effects at all on trials where adaptors were schematic line drawings of face configurations. This pattern of adaptation effects suggests that the M170 is linked to the detection of individual face parts, but does not reflect the processing of face-specific first-order relational properties. According to Harris and Nakayama (2008), the M170 reflects the activity of a structural encoding mechanism that is responsible for the part-based analysis of face components, and should therefore not be interpreted as a marker of configural face processing.

The aim of the present study was to use rapid neural adaptation procedures to study the links between the N170 and configural face processing by measuring N170 adaptation effects produced by schematic face adaptors (Experiment 1) or Mooney face adaptors (Experiment 2) on the N170 elicited by photographic images of faces. In both experiments, adaptor stimuli (S1) and test stimuli (S2) were presented for

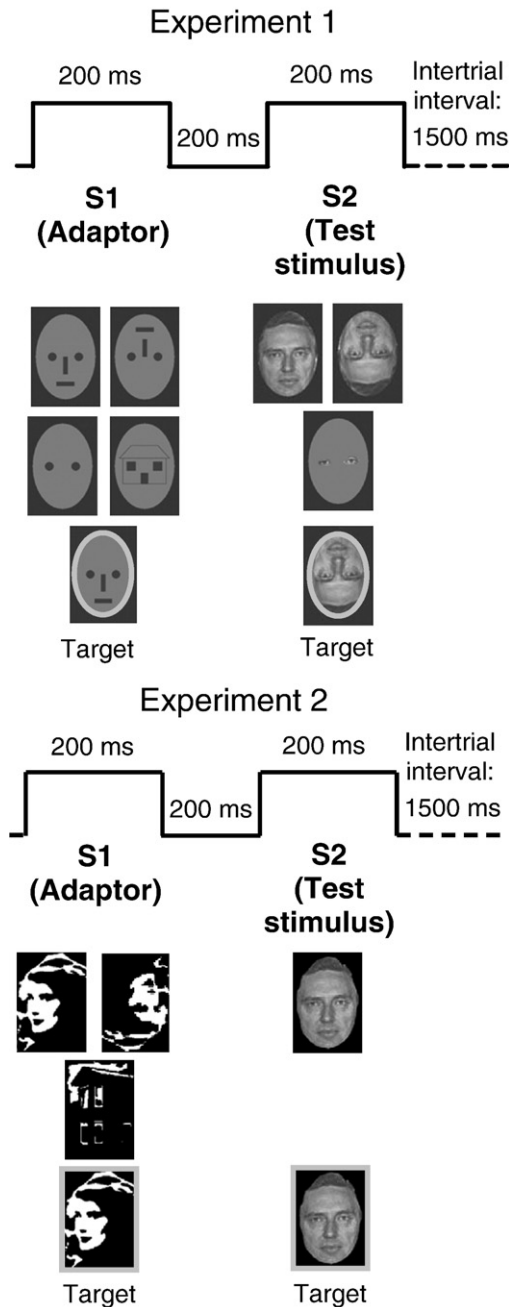


Fig. 1 – Schematic illustration of the trial structure and of the adaptor and test stimuli used in Experiment 1 (top) and Experiment 2 (bottom). Target-defining red outline shapes are shown in grey.

200 ms, and were separated by a 200 ms interstimulus interval (Fig. 1). Participants monitored these stimulus sequences in order to detect and respond to infrequent target stimuli defined by the presence of a red outline shape that was aligned with the outer contours of an adaptor or test stimulus. Analogous to the MEG study by Harris and Nakayama (2008), Experiment 1 investigated whether schematic line drawings of face configurations produce N170 adaptation effects in response to naturalistic test face stimuli. Naturalistic face stimuli were preceded by different

types of schematic adaptors (Fig. 1, top). Upright schematic faces showed the prototypical face configuration. Schematic houses, albeit visually similar, did not. The presence of N170 adaptation effects (i.e., reduced N170 amplitudes) for upright naturalistic face stimuli preceded by upright schematic faces, relative to trials with schematic house adaptors, would demonstrate links between the N170 and configural face processing. As naturalistic inverted faces and isolated eyes also trigger robust N170 components (Bentin et al., 1996), which are subject to adaptation when preceded by naturalistic face stimuli (Eimer et al., 2010), these two types of test stimuli were included in addition to naturalistic upright faces. Furthermore, schematic inverted faces and schematic eyes were included as adaptors in Experiment 1. This was done to investigate whether these non-canonical stimuli would still elicit some first-order relational configural processing (as suggested by Latinus and Taylor, 2006, for inverted schematic faces), resulting in N170 adaptation effects for naturalistic test face stimuli.

In Experiment 2, two-tone Mooney stimuli were presented as adaptors, and upright naturalistic faces served as test stimuli. As discussed above, Mooney faces are assumed to engage holistic stages of configural face processing, but not the first-order relational stage (Latinus and Taylor, 2006). Adaptors were upright and inverted Mooney faces as well as Mooney houses (Fig. 1, bottom). The presence of N170 adaptation effects in response to upright naturalistic test faces preceded by upright Mooney faces, as compared to trials with Mooney house adaptors would provide additional evidence for an association between the N170 component and configural (holistic) face processing, and against the hypothesis that this component is exclusively linked to a part-based analysis of faces. Inverted Mooney faces were included as adaptor stimuli in order to test whether and to what degree these stimuli would also activate configural-holistic face processing, and therefore produce an adaptation of the N170 to subsequent naturalistic test faces.

2. Results

2.1. Experiment 1

2.1.1. Behaviour

Participants missed targets on less than 1% of all target trials. False Alarms occurred on less than 0.1% of all nontarget trials. Response times (RTs) to targets were faster when they were presented as S2 relative to S1 targets (404 versus 425 ms; $t(15) = 2.5$, $p < 0.03$). S2 category did not affect RTs ($F(2,30) = 1.3$, $p = 0.29$). There was an effect of S1 category ($F(3,45) = 4.49$, $p < 0.01$), as target RTs were slower on trials with schematic eyes (435 ms) relative to trials with schematic upright faces, inverted faces or houses (426, 416 and 422 ms, respectively; all $t(15) > 2.2$, all $p < 0.05$).

2.1.2. N170 to schematic adaptor stimuli (S1)

Fig. 2 (top panel) shows ERPs elicited at right posterior electrode P8 in response to each of the four different schematic adaptor stimulus categories. N170 amplitudes were larger for face-like configurations (upright and inverted

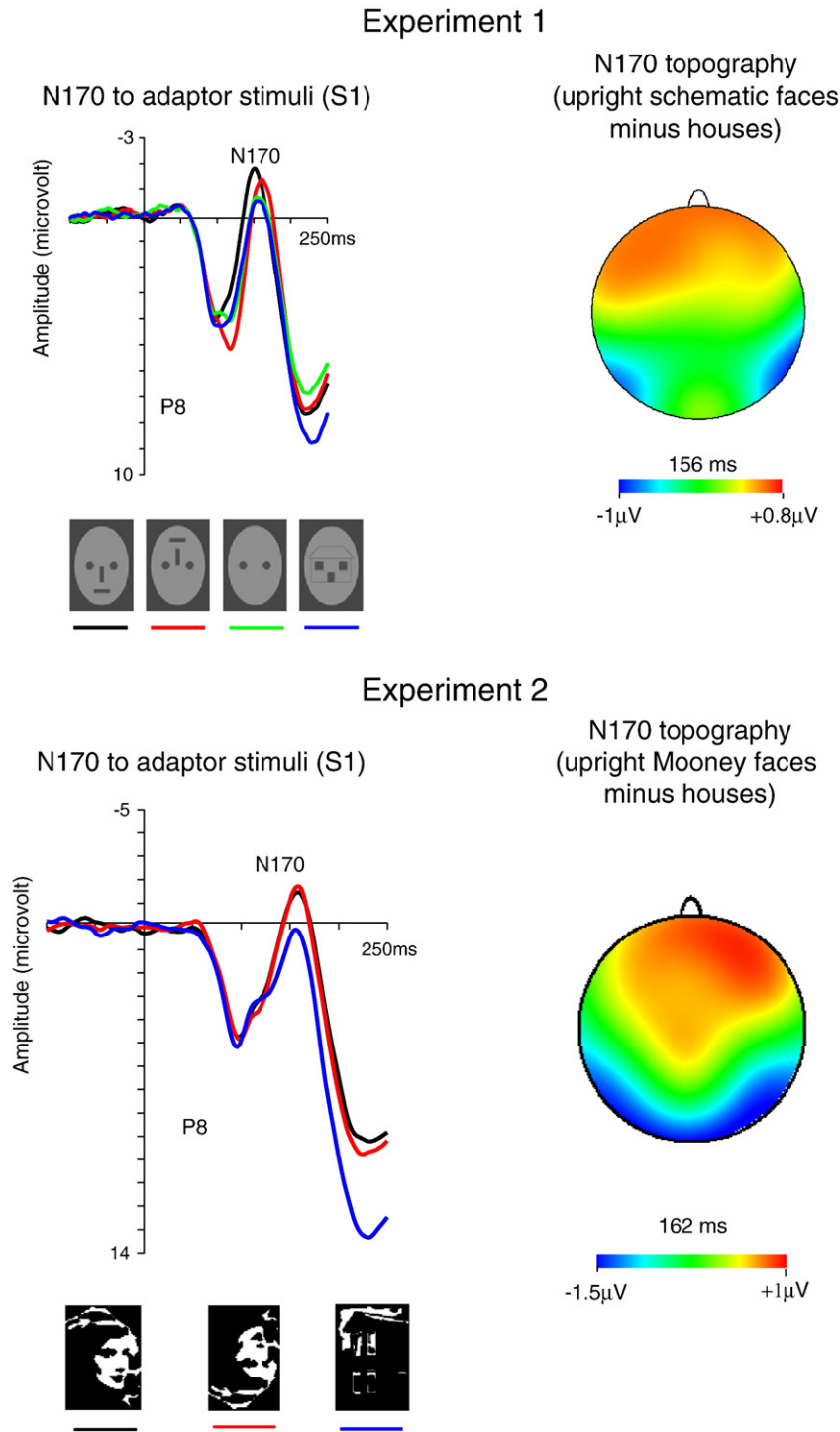


Fig. 2 – Grand-averaged ERPs elicited in Experiment 1 (top) and Experiment 2 (bottom) in response to S1 stimuli (adaptors) in the 250 ms interval after stimulus onset at right posterior electrode P8, shown separately for each adaptor category. Topographic maps show difference potentials obtained at the latency of the N170 peak (156 ms in Experiment 1; 162 ms in Experiment 2) by subtracting ERPs to schematic houses from ERPs to schematic upright faces. Larger negative amplitudes for faces are shown in blue.

schematic faces) than for schematic eyes and houses. The topographic map in Fig. 2 (top panel) shows the scalp distribution of ERP amplitude differences observed at N170 peak latency (156 ms after S1 onset) between upright schematic faces and houses. Relative to schematic houses, upright schematic faces triggered a posterior N170 component that

was larger over the right hemisphere. The presence of an enhanced N170 to upright and inverted schematic faces as compared to schematic eyes and houses was confirmed by a repeated-measures ANOVA conducted for N170 peak amplitudes measured at P8 in the 140–190 ms post-S1 time window, for the factor face configuration (present: upright/inverted

faces, absent: eyes/houses). A main effect of face configuration was obtained ($F(1,15)=10.76, p<0.005$), and simple effects contrast analyses revealed significant N170 amplitude differences between upright or inverted faces on the one hand and eyes or houses on the other (all $p<0.05$), whereas N170 amplitudes did not differ reliably between upright and inverted faces, or between eyes and houses. Fig. 2 (top panel) also shows an N170 delay for inverted relative to upright

schematic faces. A planned comparison of N170 peak latencies (obtained within the 140–190 ms time window after S1 onset) confirmed that this inversion-induced latency shift was reliable ($t(15)=2.86, p<0.02$).

2.1.3. N170 to naturalistic test stimuli (S2)

Fig. 3A shows the time course of visual ERP components to S1 and S2 at P8, separately for upright face, inverted face, and

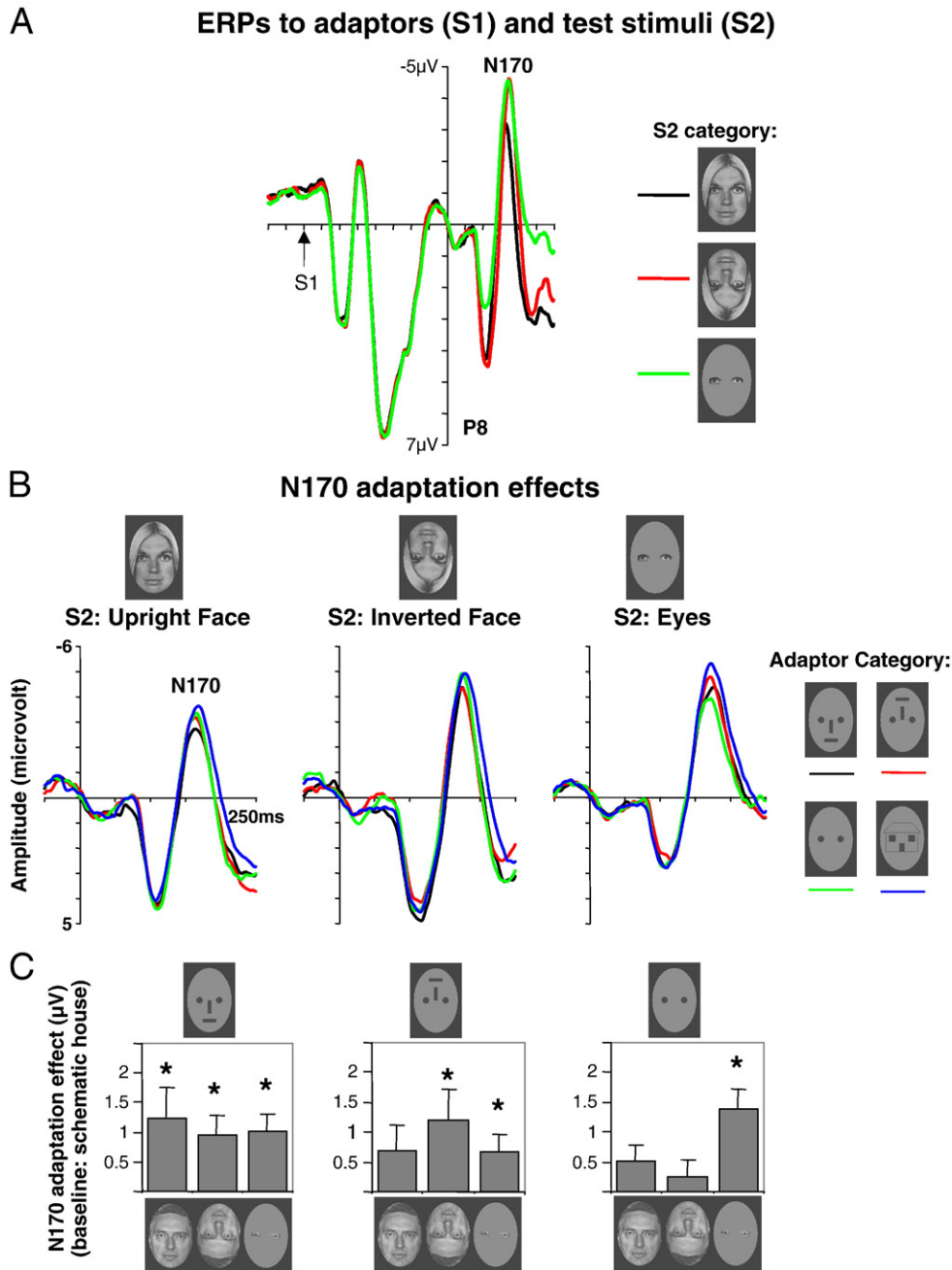


Fig. 3 – Experiment 1: (A) ERPs elicited at lateral posterior electrode P8 between 100 ms prior to S1 onset and 300 ms after S2 onset by naturalistic upright faces, inverted faces, and eyes (collapsed across S1 categories). The arrow marks S1 onset, the origin of the y-axis marks S2 onset. (B) ERPs elicited at P8 in the 250 ms interval after S2 onset by the three face test stimulus types as a function of adaptor category. (C) N170 adaptation effects (reduction of N170 amplitudes relative to trials with schematic house adaptors) produced by schematic upright face adaptors, inverted face adaptors, and eyes adaptors, plotted separately for all three face test stimulus types ($*p < 0.05$).

isolated eyes test stimuli, collapsed across all four schematic adaptor categories. The 200 ms S1–S2 interval was sufficiently long to allow the emergence of a pronounced N170 to naturalistic test stimuli that did not overlap with residual sensory responses to preceding adaptors. Importantly, the N170 to face test stimuli was modulated in the expected category-specific fashion: It was larger in amplitude and delayed for inverted relative to upright faces (the typical N170 face inversion effect), and larger for isolated eyes relative to full upright faces. A repeated-measures ANOVA of N170 peak amplitudes elicited at P8 in the 140–190 ms post-S2 time window revealed that the factor S2 category was significant ($F(2,30)=4.37$, $p<0.03$), and simple effects contrast analyses confirmed that the N170 to inverted faces and to eyes was significantly larger than the N170 to upright faces (both $p<0.05$), while N170 amplitudes did not differ between inverted faces and eyes. S2 category also affected N170 peak latency ($F(2,30)=8.16$, $p<0.001$), and simple effects contrasts demonstrated that the N170 peaked later for inverted faces and isolated eyes relative to upright faces (both $p<0.05$), while there was no N170 latency difference between isolated eyes and inverted faces.

2.1.4. N170 adaptation effects

Fig. 3B shows ERPs at P8 to upright face, inverted face, and isolated eyes test stimuli, separately for all four types of schematic adaptors. N170 amplitudes were larger when naturalistic face test stimuli were preceded by schematic house adaptors (blue lines in Fig. 3B) than when they were preceded by upright schematic faces (black lines) or by inverted schematic faces (red lines). Schematic eye adaptors (green lines) produced N170 attenuation for isolated eyes test stimuli, but not for upright and inverted faces. This pattern of N170 adaptation effects is further illustrated in Fig. 3C, which shows N170 amplitude reductions observed for the three face test stimulus types on trials where schematic upright faces, inverted faces, or eyes were presented as adaptors, relative to trials with schematic house adaptors.

An initial omnibus ANOVA of N170 peak amplitudes measured at P8 in the 140–190 ms post-S2 interval was conducted for the factors adaptor category (upright face, inverted face, eyes, house) and test stimulus category (upright face, inverted face, eyes). An effect of test stimulus category ($F(2,30)=4.37$, $p<0.03$) was accompanied by an effect of adaptor category ($F(3,45)=4.50$, $p<0.01$), and an interaction between both factors ($F(6,90)=2.73$, $p<0.02$), demonstrating that schematic adaptors produced category-specific N170 adaptation effects. To investigate the pattern of N170 adaptation in more detail, three separate analyses compared N170 amplitudes for naturalistic stimuli preceded by schematic house adaptors (baseline condition) and N170 amplitudes on trials with schematic upright face, inverted face, or eye adaptors, respectively. When the effects of schematic upright face and house adaptors were compared, a highly significant effect of adaptor category ($F(1,15)=12.75$, $p<0.003$) confirmed the attenuation of N170 amplitudes to naturalistic face stimuli that were preceded by schematic upright face adaptors (Fig. 3C, left). This effect did not interact with test stimulus category, and subsequent simple effects analyses confirmed reliable N170 adaptation effects for all three test

stimulus categories (all $p<0.05$). The analysis of N170 adaptation effects for schematic inverted faces relative to schematic house adaptors (Fig. 3C, middle) obtained a significant effect of adaptor category ($F(1,15)=5.21$, $p<0.04$) that did not interact with test stimulus category. Subsequent simple effects analyses revealed reliable N170 adaptation effects for naturalistic inverted faces and naturalistic eyes preceded by schematic inverted faces (both $p<0.05$). This effect approached significance for naturalistic upright faces ($p=0.07$). Finally, the analysis of N170 adaptation effects produced by schematic eyes relative to house adaptors obtained an effect of adaptor category ($F(1,15)=7.80$, $p<0.02$) that interacted with test stimulus category ($F(2,30)=4.03$, $p<0.03$). Simple effects analyses found no reliable N170 adaptation by schematic eyes for naturalistic upright and inverted faces, but a strong attenuation of N170 amplitudes for isolated eyes test stimuli ($p<0.001$; Fig. 3C, right).

2.2. Experiment 2

2.2.1. Behaviour

Participants missed targets on less than 2% of all target trials. False Alarms occurred on less than 0.1% of all nontarget trials. Target RTs did not differ between trials where targets were presented as S1 or S2 (392 ms and 393 ms, respectively), or between trials with upright Mooney face, inverted Mooney face, or Mooney house adaptors (effect of S1 category: $F<1$).

2.2.2. N170 to Mooney adaptors (S1)

Fig. 2 (bottom panel) shows ERPs elicited at right posterior electrode P8 in response to upright Mooney face, inverted Mooney face, and Mooney house adaptors. N170 amplitudes were larger for upright and inverted Mooney faces relative to Mooney houses. The topographic map in Fig. 2 (bottom) shows the scalp distribution of ERP amplitude differences observed at N170 peak latency (162 ms after S1 onset) between upright Mooney faces and Mooney houses. Relative to Mooney houses, upright Mooney faces triggered a posterior N170 component that was larger over the right hemisphere. A repeated-measures ANOVA conducted for N170 peak amplitudes measured at P8 in the 140–190 ms post-S1 time window revealed a main effect of S1 category (upright Mooney faces, inverted Mooney faces, Mooney houses; $F(2,22)=7.9$, $p<0.02$). Simple effects contrast analyses revealed that the N170 to Mooney houses was reliably reduced relative to upright as well as inverted Mooney faces (both $p<0.05$), but there was no N170 amplitude difference between upright and inverted Mooney faces. There were no reliable N170 latency differences between the three adaptor categories.

2.2.3. N170 adaptation effects

Fig. 4A shows ERPs triggered at P8 by naturalistic upright face test stimuli, separately for trials where they were preceded by upright Mooney faces, inverted Mooney faces, or Mooney houses. N170 amplitudes were largest when naturalistic faces were preceded by Mooney house adaptors, and smallest for trials with upright Mooney faces. An ANOVA of N170 peak amplitudes measured at P8 in the 140–190 ms post-S2 interval

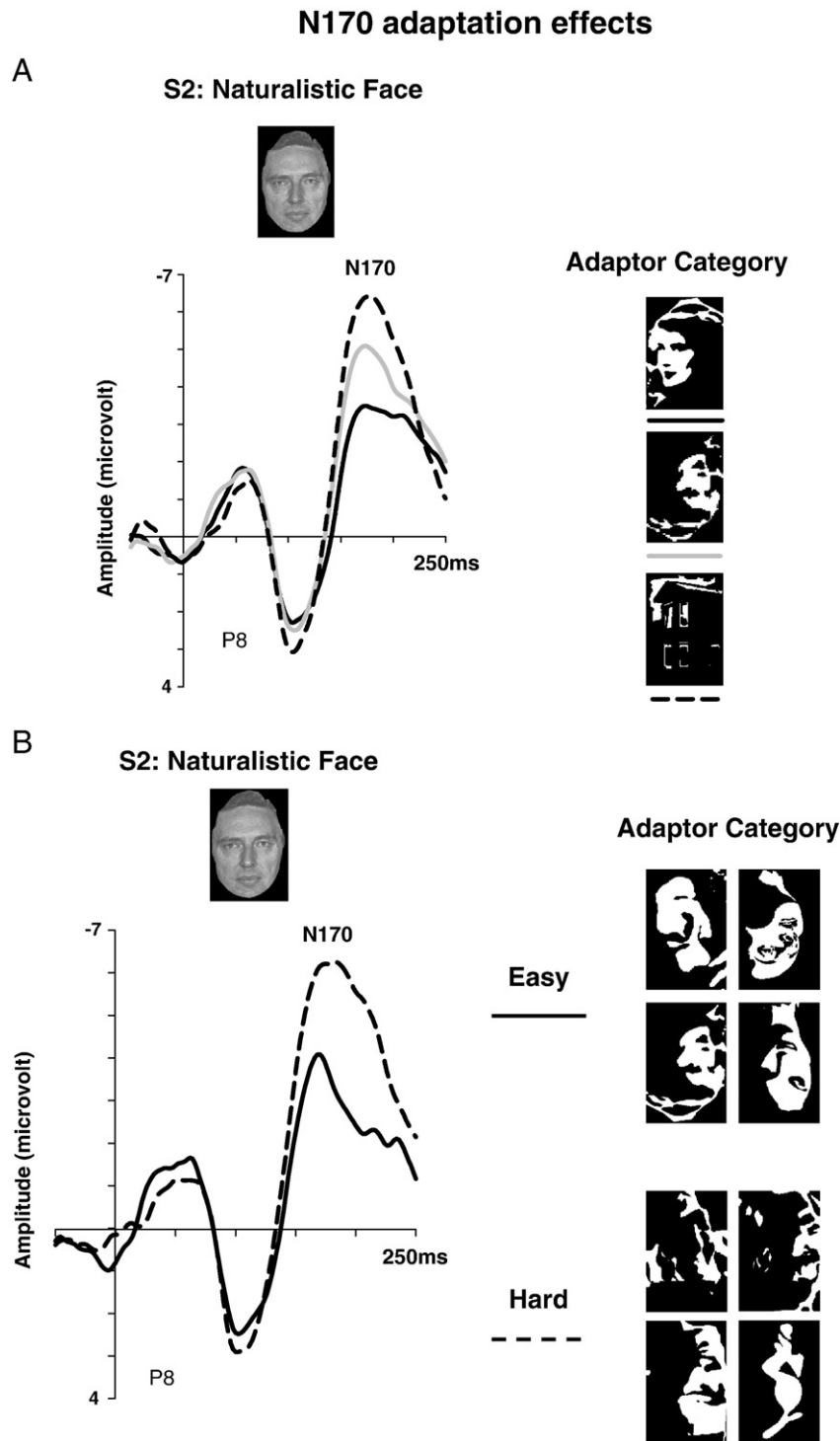


Fig. 4 – Experiment 2: (A) ERPs elicited at lateral posterior electrode P8 in the 250 ms interval after S2 onset by upright naturalistic face test stimuli, separately for the three adaptor categories (upright Mooney faces, inverted Mooney faces, Mooney houses). **(B)** ERPs elicited at P8 to upright naturalistic test faces preceded by inverted Mooney face adaptors that were easy or hard to recognize as faces. The adaptor stimuli included in these two sets are shown on the right.

demonstrated a main effect of adaptor category ($F(2,22)=12.63$, $p<0.005$). Follow-up contrasts confirmed that the N170 to naturalistic test faces preceded by upright and inverted Mooney faces was significantly attenuated relative to trials with Mooney house adaptors (both $p<0.05$). In addition, N170 amplitude was reduced on trials with upright Mooney face

adaptors relative to trials with inverted Mooney face adaptors ($p<0.05$).

To investigate whether N170 adaptation effects produced by inverted Mooney faces differed when these adaptor stimuli were either easy or difficult to recognize as faces, N170 amplitudes to test faces were quantified separately for trials

where these faces were preceded by “easy” or “hard” inverted Mooney face adaptors.¹ Fig. 4B shows these two sets of Mooney faces, together with ERPs at P8 for trials where naturalistic test faces were preceded by easy or hard inverted Mooney faces. N170 amplitude was reduced for trials with inverted Mooney face adaptors that were still recognizable as faces. This was confirmed by a paired t-test, which revealed significant N170 peak amplitude differences between these two types of trials for the 140–190 ms post-S2 latency window ($t(11)=2.24, p<0.05$).²

3. Discussion

We used rapid neural adaptation procedures to investigate links between the face-sensitive N170 component and configural face processing. Experiment 1 tested whether the N170 to naturalistic face stimuli was attenuated by schematic face adaptors, as compared to schematic house adaptors, as would be predicted if the N170 reflects face-selective neural populations that are sensitive to first-order relational configuration (Maurer et al., 2002), even when individually recognizable face components are absent. Experiment 2 investigated whether the N170 to naturalistic faces would adapt when these are preceded by Mooney faces, as compared to Mooney houses, as would be expected if neural processes that generate this component are linked to the holistic processing of face-like stimuli when no recognizable face features and no first-order relational information is available. The pattern of N170 adaptation effects observed in these two experiments provides new and conclusive evidence that the N170 is indeed associated with the configural processing of faces, and does not just reflect the part-based analysis of individual face parts by a structural encoder (Harris and Nakayama, 2008).

In Experiment 1, N170 adaptation was measured for naturalistic upright faces, inverted faces, and isolated eyes that were preceded by schematic adaptor stimuli. The critical comparison was between trials where these test stimuli were preceded by adaptors that matched the prototypical face template (upright schematic faces), and trials with schematic house adaptors. Schematic houses were visually very similar to schematic faces, except for the lack of a face-like configuration. N170 amplitudes were attenuated for naturalistic test stimuli that were preceded by upright schematic face adaptors, relative to trials with schematic house adaptors. This N170 adaptation effect was reliably present for all three types of face test stimuli, demonstrating that cortical processes involved in the detection and analysis of configural facial information do indeed contrib-

ute to the face-sensitive N170 component. Activation of these processes by schematic faces reduces their responsiveness to subsequently presented naturalistic face stimuli, resulting in attenuated N170 amplitudes. N170 adaptation effects were also found for inverted schematic face adaptors. These effects were reliable for inverted face and isolated eyes test stimuli, and there was a trend in the same direction for naturalistic upright faces. This suggests that first-order relational information conveyed by schematic faces was not completely disrupted after face inversion, although the absence of statistically significant N170 adaptation effects for upright face test stimuli indicates some impairment of this prototypical spatial configuration produced by inversion.

Further evidence that the N170 component is sensitive to configural face processing comes from the N170 to the schematic adaptor stimuli themselves (Fig. 2, top panel): Upright and inverted schematic faces elicited larger N170 amplitudes than schematic houses, and the N170 was delayed for inverted as compared to upright schematic faces, similar to the inversion-induced latency delay found for naturalistic test faces (Fig. 3A; see also Sagiv and Bentin, 2001; Latinus and Taylor, 2006, for analogous N170 latency delays for inverted schematic faces). These observations further underline that the N170 component to schematic adaptors is sensitive to face-like configural information. Notably, face inversion effects on N170 amplitudes differed across stimulus formats: Inversion increased the size of the N170 for naturalistic faces, but not for schematic faces, similar to previous observations by Latinus and Taylor (2006). It should be noted that Sagiv and Bentin (2001) even observed a reliable N170 reduction for inverted as compared to upright schematic faces.

In contrast to schematic upright and inverted face adaptors, there was no enhanced N170 for schematic eye adaptors relative to schematic houses (Fig. 2, top panel), suggesting that schematic eyes were not processed in a face-specific fashion, although they were shown in the context of full schematic and naturalistic faces (see Bentin et al., 2002, for contextual priming effects on the N170). Schematic eyes also did not produce reliable N170 adaptation effects for naturalistic upright or inverted test faces (Fig. 3C), which indicates that these adaptor stimuli did not provide sufficient configural information for first-order relational processing. However, the N170 to naturalistic isolated eyes was strongly attenuated when these were preceded by schematic eyes. As all adaptors contained an item pair along the horizontal meridian, this differential effect cannot be due simply to local sensory refractoriness. One possibility is that even though schematic eye adaptors did not elicit a measurable N170, they may still have primed eye-selective neurons, resulting in an attenuated response of these neurons to subsequent naturalistic eyes (see Itier and Batty, 2009, for links between the N170 and eye processing). The question whether this effect is indeed linked to eye-specific adaptation or to other factors (e.g., the global configural similarity of schematic and naturalistic eye stimuli) requires further investigation.

In Experiment 2, the N170 to upright naturalistic test faces was measured on trials where they were preceded by upright Mooney faces, inverted Mooney faces, or Mooney houses. The critical comparison was between trials with upright Mooney face and Mooney house adaptors. A strong attenuation of

¹ Out of the 12 inverted Mooney faces used in Experiment 2, 4 were consistently easy to be perceived as a face, whereas 4 others were consistently hard (see Fig. 4B). Easy and hard inverted Mooney faces were identified in a pilot study where observers had to make a speeded face/nonface discrimination in response to each of the inverted Mooney faces and Mooney houses used in the main study.

² A comparison of N170 amplitudes computed separately for the four easy and the four hard inverted S1 Mooney face adaptors revealed an amplitude reduction of 1.2 μ V for hard as compared to easy inverted Mooney faces, but this difference failed to reach overall statistical significance.

N170 amplitudes was observed for naturalistic faces preceded by upright Mooney faces. This is an important observation, as the perception of Mooney faces cannot proceed in an exclusively part-based fashion, and is assumed to primarily involve holistic processing. The fact that upright Mooney faces adapt the N170 to subsequent naturalistic faces thus provides additional evidence for the hypothesis that this component is associated with a configural-holistic level of face processing, and reflects the activity of neural processes that are sensitive to the global gestalt-like features of faces.

Reliable N170 adaptation effects were also found for inverted Mooney faces relative to Mooney house adaptors, and these effects were more pronounced for inverted Mooney faces that were more easily recognizable as faces (Fig. 4B). This suggests that at least some inverted Mooney faces also engaged configural face processing, and that this was determined by the specific features of individual images (see also George et al., 2005, for links between the N170 to Mooney stimuli and their recognizability as faces). Since the same Mooney stimuli were shown both upright and inverted (in order to exclude low-level visual differences between these two categories), priming from upright to inverted faces may also have contributed to the N170 adaptation effects found for inverted Mooney faces. The fact that N170 adaptation was generally less pronounced for inverted as compared to upright Mooney face adaptors indicates that inversion impaired the configural processing of Mooney faces, thereby reducing N170 adaptation effects. The N170 to both upright and inverted Mooney face adaptors was reliably larger than the N170 to Mooney houses (Fig. 2, bottom panel), which confirms and extends previous reports of enhanced N170 amplitudes to Mooney faces relative to scrambled Mooney control stimuli that did not resemble any object (Latinus and Taylor, 2005, 2006). The observation that there was no N170 amplitude difference between upright and inverted Mooney face adaptors is in line with results by Latinus and Taylor (2006), but contrasts with other studies that observed an N170 amplitude reduction for inverted Mooney faces (e.g., Latinus and Taylor, 2005; George et al., 2005). The presence of inversion effects on N170 amplitudes in response to Mooney faces will need to be clarified in future investigations.

Overall, the pattern of N170 adaptation effects obtained in this study is not in line with the hypothesis that N170/M170 components exclusively reflect the response of face-selective brain regions to individual face parts (Harris and Nakayama, 2008). In Experiment 1, schematic stimuli adapted the N170 to naturalistic test faces, even though they contained no recognizable face-like component parts, presumably because the spatial arrangement of their parts provided face-relevant first-order relational information (Maurer et al., 2002). In Experiment 2, two-tone Mooney faces adapted the N170 to naturalistic test faces, even though these stimuli did not include individually recognizable face parts, and did not afford first-order relational processing, but could only be recognized as faces on the basis of their global gestalt features. The general conclusion from both experiments that the N170 is linked to configural face processing is not in line with previous findings by Harris and Nakayama (2008), who used similar rapid adaptation procedures and found no adaptation of the M170 component by schematic faces. In their study, the absence of M170 adaptation effects was inferred from a direct

comparison between trials with naturalistic adaptors (photographs of houses) and trials with schematic face adaptors, whereas all adaptors were schematic in the present Experiment 1. It is possible that comparisons of neural adaptation effects produced within and across different image formats (schematic versus naturalistic stimuli) will yield different results. It is also important to note that due to differences in the relative sensitivity of EEG and MEG measures to tangential versus radial and medial versus lateral cortical sources, N170 and M170 components are not necessarily associated with identical underlying neural generator processes. If these components reflect contributions from anatomically distinct part-based and holistic-configural face processing systems (see below), and if the N170 and M170 components differ in their relative sensitivity to these neural sources, different patterns of N170 and M170 adaptation effects might emerge.

Another difference to the study of Harris and Nakayama (2008) was that faces were presented in front of a grey oval outline shape in the present Experiment 1. It is possible that this outline shape may have been processed as an external face contour, and may thus have encouraged the face-selective processing of schematic faces. This may have produced N170 adaptation in response to naturalistic test faces that was not observed by Harris and Nakayama (2008) who used rectangular adaptor and test stimuli. While this might conceivably have contributed to the adaptation effects by schematic face adaptors in Experiment 1, this explanation cannot account for the fact that strong N170 adaptation effects were also observed in Experiment 2 for Mooney face adaptors that were not presented against an oval background.

The conclusion from Experiment 2 that the N170 is linked to configural-holistic face processing is not just in line with the results of previous N170 studies with Mooney faces (e.g., Latinus and Taylor, 2005; George et al., 2005), but also with a recent investigation of the composite face illusion (CFI) that used N170 adaptation procedures (Jacques and Rossion, 2009). Composite faces consisting of two spatially aligned halves were presented in succession, and observers performed a matching task for the top parts of these faces. Relative to trials with identical adaptor and test faces, enhanced N170 amplitudes to test faces were found on trials where only their bottom half differed from the adaptor face, and a behavioural CFI was observed, suggesting that the N170 is associated with a holistic representation of individual composite faces.

The main conclusion from the present study that the N170 is sensitive to configural face processing (to first-order relational information provided by schematic faces as well as to the global-holistic processing afforded by Mooney faces) must not be taken to imply that this component is completely unrelated to the part-based processing of individual face features. It is now generally accepted that N170 is not a monolithic component that is uniquely associated with a single neural generator implementing one specific aspect of face perception, but instead reflects multiple neural sources (see also Rossion and Jacques, 2008). Even though the current results emphasize its links to configural face processing, there is substantial evidence that the N170 is also sensitive to individual face parts. N170 amplitudes are typically larger in response to isolated eyes than for full upright faces (Bentin et al., 1996; Itier et al., 2007), which was confirmed in Experiment 1 for naturalistic test stimuli (Fig. 3A).

In addition, face parts such as isolated eyes have been shown to adapt the N170 to subsequent full faces (Eimer et al., 2010). The assumption that the N170 reflects the activity of several distinct neural systems involved in the perceptual analysis of faces may also explain why N170 source localization studies have produced inconsistent results. While most studies suggest bilateral occipito-temporal cortex and posterior fusiform gyrus as main sources for the N170 (e.g., Bötzel et al., 1995; Rossion et al., 2003), others have localised the N170 in posterior superior temporal sulcus (e.g., Itier and Taylor, 2004). It has been suggested that the N170 reflects the joint activity of a part-based system in the posterior occipitotemporal sulcus and middle temporal gyrus that is associated with the detection and processing of individual face components (e.g., Pitcher et al., 2007), and a configural system in middle fusiform gyrus that is responsible for the analysis of spatial relations between face parts and the holistic perception of face configurations (Bentin et al., 1996; McCarthy et al., 1999; Sagiv and Bentin, 2001). In this framework, the N170 adaptation effects triggered by schematic faces and Mooney faces described here would reflect the modulation of configural-holistic face processing in fusiform gyrus, whereas N170 adaptation produced by face parts, as demonstrated in previous studies, would be generated independently in anatomically distinct lateral occipitotemporal areas.

There may be another reason why the N170 component is linked both to part-based and to configural face processing. In a recent review paper, McKone and Yovel (2009) have argued against the view that feature-based and configural-holistic face processing represent distinct and functionally separate stages. Based on evidence that effects of inversion on the perception of feature changes are often just as large as inversion effects on the perception of the spatial-relational changes, they claim that the representation of local features and configural properties of upright faces is not as independent as is often assumed. If face perception involves holistic representations that integrate both configural and feature-based information, as suggested by McKone and Yovel (2009), and if the N170 component was linked to such integrated representations, N170 adaptation effects should be produced by face parts as well as by naturalistic, schematic, and Mooney faces, as is indeed the case.

In summary, the N170 adaptation effects observed in this study provide new evidence that the N170 component is associated with face-selective neural processes that are sensitive to the spatial configuration of faces, as well as to their holistic gestalt features. They demonstrate that this component does not exclusively reflect the part-based analysis of face components, but can also be used to investigate brain mechanisms that are specifically involved in configural face processing.

4. Experimental procedures

4.1. Experiment 1

4.1.1. Participants

Eighteen paid volunteers were tested. One was excluded because of an insufficient number of trials after EEG artefact rejection, another due to the absence of N170 components in

response to S2. The remaining 16 participants (10 males) were 19–39 years old (mean age 28.1 years), right-handed, and had normal or corrected-to-normal vision.

4.1.2. Stimuli and procedure

Stimuli were presented on a CRT monitor at a viewing distance of 100 cm. E-Prime software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and response collection. Four schematic stimulus categories (upright faces, inverted faces, eyes, houses) and three naturalistic face stimulus categories (upright faces, inverted faces, eyes) were used, each including 12 individual images, resulting in a total of 84 different images (Fig. 1, top). Naturalistic faces were images of 12 different individuals (6 male, 6 female) from a standard set of faces (Ekman and Friesen, 1976), all with neutral expression. Isolated eyes stimuli were created using Paint Shop Pro 7 to extract the left and right eyes (excluding eyebrows and the central region between the eyes) from all 12 upright faces, and inserting these at the spatially corresponding locations of grey oval outline shapes. Schematic stimuli were created by arranging circles, bars, and rectangular shapes on top of grey oval outline shapes. To generate individual tokens of these stimuli, the size, spatial arrangement, or greyscale value of stimulus elements were varied. For all naturalistic and schematic stimuli, the central pair of eyes or 'windows' (for schematic houses) was always located on the horizontal midline of the oval background shapes. The angular size of all images was $5.7^\circ \times 8.1^\circ$, and their average luminance was 21 cd/m^2 . All stimuli were presented against a dark grey background (5 cd/m^2).

On each trial, two images (S1: adaptor stimulus; S2: test stimulus) were presented successively for 200 ms each, separated by a 200 ms interstimulus interval. Schematic upright faces, inverted faces, eyes, and houses were presented with equal probability as S1. Naturalistic upright faces, inverted faces, and eyes were presented equiprobably as S2. Intertrial interval was 1500 ms. The experiment included 4 experimental blocks that each contained 240 trials, with a break after every 80 trials. In each block, 18 trials were presented in random order for each of the 12 combinations of the 4 S1 categories and 3 S2 categories (216 trials per block). No response was required on these trials. The remaining 24 trials per block were target trials, where a red outline shape aligned with the outer contours of the oval stimulus shape was presented with equal probability together with S1 or S2. Each block contained 2 target trials for each of the 12 possible combinations of S1 and S2 category (with targets presented as S1 or S2, respectively). Participants had to press a response button when they detected a target. Response hand was alternated after two successive experimental blocks.

4.1.3. EEG recording and data analysis

EEG was DC-recorded with a BrainAmps DC amplifier (upper cut-off frequency 40 Hz, 500 Hz sampling rate) 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 electrooculogram (HEOG) was recorded bipolarly from the outer canthi of both eyes. An electrode placed on the left earlobe served as reference for online recording, and EEG was re-referenced off-line to the

average of the left and right earlobe. Electrode impedances were kept below 5 k Ω .

EEG data were analysed for nontarget trials only, to avoid contamination with response-related brain activity. EEG was epoched offline from 100 ms before to 700 ms after S1 onset. Epochs with activity exceeding $\pm 30 \mu\text{V}$ in the HEOG channel (reflecting horizontal eye movements) or $\pm 60 \mu\text{V}$ at Fpz (indicating eye blinks or vertical eye movements) were excluded from analysis, as were epochs with voltages exceeding $\pm 80 \mu\text{V}$ at any other electrode, and trials with manual responses. Following artefact rejection, EEG waveforms were averaged separately for all 12 combinations of S1 and S2 category. N170 components in response to S1 and S2 stimuli were measured at right lateral posterior electrode P8 where this component is maximal. N170 peak amplitudes and latencies were quantified within a 140–190 ms time interval after stimulus onset, relative to a 100 ms prestimulus baseline (for S1), and relative to a 100 ms baseline from 50 ms before to 50 ms after S2 onset (for S2). Repeated-measures analyses of variance (ANOVAs) were performed on N170 peak amplitude and latency measures.

4.2. Experiment 2

4.2.1. Participants

Twelve paid volunteers (7 males), aged 20–34 years (mean age 27.3 years) took part in the experiment. All were right-handed and had normal or corrected-to-normal vision.

4.2.2. Stimuli and procedure

Trial structure and general procedures were identical to Experiment 1, with the following exceptions. All adaptors were two-tone Mooney stimuli, and there were three different adaptor categories (upright faces, inverted faces, houses). Test stimuli were always upright naturalistic faces. Each of these four stimulus sets included 12 individual images. Naturalistic faces were identical to those used in Experiment 1. Upright and inverted Mooney faces were taken from the standard set of Mooney face stimuli (Mooney, 1957). Mooney houses were created from naturalistic images of houses by using Adobe Photoshop CS3 to generate two-tone images that were equivalent in terms of low-level visual properties to the Mooney faces. Angular size was $2.68^\circ \times 4.75^\circ$ for all Mooney stimuli and $2.68^\circ \times 4.57^\circ$ for naturalistic faces. Average foreground luminance was 68 cd/m² for Mooney stimuli and 21 cd/m² for naturalistic faces.

On each trial, two images (S1: adaptor stimulus; S2: test stimulus) were presented successively for 200 ms each, separated by a 200 ms interstimulus interval. Upright Mooney faces, inverted Mooney faces and houses were presented with equal probability as S1. Naturalistic upright faces were presented as S2 (Fig. 1, bottom). Intertrial interval was 1500 ms. The experiment included 4 experimental blocks that each contained 108 trials. In each block, 36 trials were presented in random order for each of the three S1 categories. Target trials were defined by the presence of a red rectangular outline shape aligned with the outer contours of the S1 or S2 stimuli, which was presented with equal probability together with S1 or S2. Each block contained 12 target trials (4 trials for each of the three S1 categories).

4.2.3. EEG recording and data analysis

All procedures were identical to Experiment 1.

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REFERENCES

- Bentin, S., Deouell, L.Y., 2000. Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cogn. Neuropsychol.* 17, 35–54.
- Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. *J. Cogn. Neurosci.* 8, 551–565.
- Bentin, S., Sagiv, N., Mecklinger, A., Friederici, A., von Cramon, Y.D., 2002. Priming visual face-processing mechanisms: electrophysiological evidence. *Psychol. Sci.* 13, 190–193.
- Bötzel, K., Schulze, S., Stodieck, S.R.G., 1995. Scalp topography and analysis of intracranial sources of face-evoked potentials. *Exp. Brain Res.* 104, 135–143.
- 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., 2000a. Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clin. Neurophysiol.* 111, 694–705.
- Eimer, M., 2000b. Effects of face inversion on the structural encoding and recognition of faces—evidence from event-related brain potentials. *Cogn. Brain Res.* 10, 145–158.
- Eimer, M., Kiss, M., Nicholas, S., 2010. Response profile of the face-sensitive N170 component: a rapid adaptation study. *Cereb. Cortex* 20, 2442–2452.
- Ekman, P., Friesen, W., 1976. *Pictures of Facial Affect*. Consulting Psychologists Press, Palo Alto, CA.
- George, N., Jemel, B., Fiori, N., Chaby, L., Renault, B., 2005. Electrophysiological correlates of facial decision: Insights from upright and upside-down Mooney-face perception. *Cogn. Brain Res.* 24, 663–673.
- Halgren, E., Raji, T., Marinkovic, K., Jousmäki, V., Hari, R., 2000. Cognitive response profile of the human fusiform face area as determined by MEG. *Cereb. Cortex* 10, 69–81.
- Harris, A.M., Nakayama, K., 2008. Rapid adaptation of the M170 response: importance of face parts. *Cereb. Cortex* 18, 467–476.
- Henson, R.N., 2003. Neuroimaging studies of priming. *Prog. Neurobiol.* 70, 53–81.
- Itier, R.J., Batty, M., 2009. Neural bases of eye and gaze processing: the core of social cognition. *Neurosci. Biobehav. Rev.* 33, 843–863.
- Itier, R.J., Taylor, M.J., 2004. Source analysis of the N170 to faces and objects. *NeuroReport* 15, 1261–1265.
- Itier, R.J., Alain, C., Sedore, K., McIntosh, A.R., 2007. Early face processing specificity: it's in the eyes! *J. Cogn. Neurosci.* 19, 1815–1826.
- 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.
- Jacques, C., Rossion, B., 2009. The initial representation of individual faces in the right occipito-temporal cortex is holistic: Electrophysiological evidence from the composite face illusion. *J. Vis.* 9(6):8, 1–16.

- Jeffreys, D.A., 1996. Evoked potential studies of face and object processing. *Vis. Cogn.* 3, 1–38.
- 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.
- Latinus, M., Taylor, M.J., 2005. Holistic processing of faces: learning effects with Mooney faces. *J. Cogn. Neurosci.* 17, 1316–1327.
- Latinus, M., Taylor, M.J., 2006. Face processing stages: impact of difficulty and separation of effects. *Brain Res.* 1123, 179–187.
- Maurer, D., Le Grand, R., Mondloch, C.J., 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.
- McKone, E., Yovel, G., 2009. Why does picture-plane inversion sometimes dissociate perception of features and spacing in faces, and sometimes not? Toward a new theory of holistic processing. *Psychon. Bull. Rev.* 16, 778–797.
- Mooney, C.M., 1957. Age in the development of closure ability in children. *Can. J. Psychol.* 11, 219–226.
- Pitcher, D., Walsh, V., Yovel, G., Duchaine, B., 2007. TMS evidence for the involvement of the right occipital face area in early face processing. *Curr. Biol.* 17, 1568–1573.
- Rossion, B., Gauthier, I., 2002. How does the brain process upright and inverted faces? *Behav. Cogn. Neurosci. Rev.* 1, 63–75.
- 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., Gauthier, I., Tarr, M.J., 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., Joyce, C.A., Cottrell, G.W., Tarr, M.J., 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, J.W., Farah, M.J., 1993. Parts and wholes in face recognition. *Q. J. Exp. Psychol.* 46A, 225–245.
- Yin, R.K., 1969. Looking at upside-down faces. *J. Exp. Psychol.* 81, 141–145.