

Automatic face identity encoding at the N170

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Abstract

The N170 event-related potential component is currently under investigation for its role in face identity processing. Using a location-matching paradigm, in which face identity is task irrelevant, we observed a progressive decrease in N170 amplitude to multiple repetitions of upright faces presented at unattended locations. In contrast, we did not observe N170 habituation for repeat presentations of inverted faces. The findings suggest that the N170 repetition effects reflect early face identity processes that are part of familiarity acquisition of new faces.

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1. Introduction

A considerable amount of research has been devoted to contrasting familiar and unfamiliar face processing, yet little research has investigated the mechanisms by which novel faces become familiar. Currently, the event-related potential (ERP) component N170 is under investigation for its role in the acquisition of face familiarity.

The N170 is thought to reflect the detection and global processing of facial images. Larger N170 responses are evoked in response to facial stimuli than non-face objects and scrambled faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Carmel & Bentin, 2002; Eimer, 2000b; George, Evans, Fiori, Davidoff, & Renault, 1996; Rossion et al., 2000; Sagiv & Bentin, 2001). The N170 component is attenuated and delayed in response to facial images lacking internal (e.g. eyes, nose, mouth) or external features (e.g. head contour, hair) (Eimer, 2000b). Inverting a face image impairs normal face recognition abilities via the disruption of configural information (e.g. Yin, 1969; for a review see Maurer, LeGrand, & Mondloch, 2002). Consequently, N170 responses evoked by inverted faces are delayed and

enhanced (Eimer, 2000a, 2000b, 2000c; Itier & Taylor, 2002; Rossion et al., 1999; Rossion et al., 2000), possibly revealing the greater effort required to recognize inverted faces or recruitment of additional neurons that respond to non-face objects.

Initial reports suggested face recognition processes were captured by later ERP components only. Differences between novel and famous faces were observed at N400 and P600, such that the responses were enhanced for famous versus unfamiliar faces (Bentin & Deouell, 2000; Eimer, 2000a). Famous face repetition effects were also observed at these later ERP components (Eimer, 2000c; Pfutze, Sommer, & Schweinberger, 2002; Schweinberger, Pickering, Burton, & Kaufmann, 2002a; Schweinberger, Pickering, Jentsch, Burton, & Kaufmann, 2002b; Schweinberger, Huddy, & Burton, 2004). These studies did not show repetition effects for unfamiliar face repetition at these late components (Eimer, 2000c; Schweinberger et al., 2002a).

A comparison of repeated presentations of unfamiliar and famous faces revealed earlier N170 repetition effects for unfamiliar faces. Caharel, Poiroux, and Bernard (2002) measured ERP modulation during passive viewing of one's own face, a famous face and an unfamiliar face, with each image repeated 100 times in random order. Familiarity effects were observed at the N170 such that the N170 amplitude was significantly attenuated in response to repetitions

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of an unfamiliar face but not for repetitions of one's own face or a famous face. Similar results were found by Henson et al. (2003) who showed repetition effects at the N170 for unfamiliar faces, and not for famous faces. Note the contrast with later components in which repetition effects were observed at later ERP components for famous faces, and not for unfamiliar faces as described above. These early versus late ERP effects demonstrate processing differences between highly familiar faces and newly learned faces.

A general finding is that the amplitude of the N170 decreases in response to repeat versus solitary presentations of unfamiliar faces (Campanella et al., 2000; George, Jemel, Fiori, & Renault, 1997; Guillaume & Tiberghien, 2001; Heisz, Watter, & Shedden, 2006; Itier & Taylor, 2002; Itier & Taylor, 2004). The N170 repetition effects are observed across short (e.g. Itier & Taylor, 2002) and long (George et al., 1997) repetition lags. Repetition effects at the N170 are observed for repeat presentation of photos portraying the same individual even when the same face is presented with different facial expressions (Guillaume & Tiberghien, 2001), different image backgrounds (Guillaume & Tiberghien, 2001), or different physical images (Campanella et al., 2000). N170 repetition effects are typically observed when the experimental task requires explicit evaluation of face identity (Campanella et al., 2000; George et al., 1997; Guillaume & Tiberghien, 2001; Itier & Taylor, 2002; Itier & Taylor, 2004) but are also observed when face identity is task irrelevant (Heisz et al., 2006). Taken together these findings suggest that N170 amplitude modulation for unfamiliar face repetitions is part of early identity processes and may reflect mechanisms that underlie familiarity acquisition for new faces.

Using an identity-matching task, Itier and Taylor (2002) reported N170 amplitude attenuation to repeated face images compared to new images regardless of whether the images were upright, inverted or contrast-reversed. This effect was reproduced in a follow-up study (Itier & Taylor, 2004) which used upright, inverted and contrast-reversed facial images in a target identification task. Their task consisted of a learning phase in which a target face was presented 10 times. The learning phase was immediately followed by a test phase in which the target was repeated 12 times amongst 20 new facial images of the same type and participants' task was to identify the targets. For upright, inverted and contrast-reversed images, there was a decrease in N170 amplitude in response to the last half of target face repetitions relative to non-target faces, and a decrease in N170 latency in response to all target face repetitions relative to non-target faces.

The observation of N170 habituation to repeated inverted and contrast-reversed images may seem counter to the hypothesis that the N170 repetition effects reflect early identity processing. Both inversion (Yin, 1969) and contrast-reversal (Galper, 1970) of facial images disrupt normal face recognition processes. Specifically, these image manipulations disrupt perception of configural relationships among features (Lewis & Johnston, 1997; Rhodes,

Brake, & Atkinson, 1993). In addition, evidence suggests that inverted faces are recognized via featural processing rather than via holistic face recognition processes (Rhodes, 1988; Rhodes et al., 1993; Searcy & Bartlett, 1996; Tanaka & Sengco, 1997).

However, it is possible that the N170 repetition effects for inverted and contrast-reversed faces are a consequence of the task demands. Specifically, when identity is part of the task, effort is made to extract identity from the image. Thus, a task which requires identity matching may show repetition effects for faces even when they are inverted or contrast-reversed. Previous experiments have demonstrated that attending to the identity of the face does modify processing at the N170. One study compared tasks involving face recognition versus digit detection (with digits superimposed on the face image) (Eimer, 2000a, 2000c). N170 peak latency was delayed for both upright and inverted faces in the digit detection task compared to the face recognition task. Moreover, when spatial attention was directed toward the face the N170 amplitude response was enhanced relative to when attention was directed away from the face toward the digit (Holmes, Vuilleumier, & Eimer, 2003).

If the repetition effect for inverted faces is due to identity processing that is imposed by task demands that direct attention to face identity, then it might be possible to reduce the repetition effect by drawing attention away from face identity. We know that identity of upright faces is processed automatically (Tanaka, 2001) and that inverted faces do not show the same advantage (Maurer et al., 2002). Therefore, a task in which face identity is not relevant might reveal repetition effects for upright faces that do not occur for inverted faces which are more difficult to identify. This would lend support to the hypothesis that the N170 repetition effects are related to face identity processing.

Heisz et al. (2006) used a location-matching task in which face identity was not relevant. A face was presented on each trial in one of four possible spatial locations and the task was to indicate whether the current face occurred in the same or different visuospatial location as the face on the previous trial. Behavioural responses and P3 amplitudes showed sensitivity to face identity when faces were presented at attended visuospatial locations but not when faces were presented at unattended visuospatial locations. The N170 repetition effect was also sensitive to visuospatial attention, showing a more progressive habituation when faces were presented in unattended locations (amplitude decreased for each repeated face up to four sequential repeats) versus attended locations (amplitude decreased for the first repeated face only). The claim was made that the N170 reflected automatic face identity processing and that amplitude reductions reflected increased ease of processing when faces were repeated. Heisz et al. (2006) suggested that in attended visuospatial locations, the identity process reflected by the N170 reengaged after the initial repeated face because attention to the spatial location of the face resulted in attention to the identity of the

face even though identity was not task relevant. However, in unattended visuospatial locations this reengagement of identity processing did not occur, revealing the progressive habituation of the N170.

We used the same location-matching task as Heisz et al. (2006) with an additional set of inverted face stimuli. Alternating runs of novel and repeat faces in upright and inverted form were presented. On each trial, a face was presented in one of four possible locations, and the task was to indicate whether the face appeared in the same or different visuospatial location as the previous face. We found a progressive habituation of the amplitude of the N170 to repeated upright faces in unattended locations, consistent with Heisz et al. (2006). An amplitude decrease for the first repeated upright face only was observed in attended locations, similar to other work (Campanella et al., 2000; George et al., 1997; Guillaume & Tiberghien, 2001; Heisz et al., 2006; Itier & Taylor, 2002, 2004). Finally, no N170 amplitude habituation occurred when repeated faces were inverted regardless of whether they were presented in attended or unattended visuospatial locations.

2. Methods

2.1. Participants

Thirty-four volunteers (31 female, mean age 19 years) from the McMaster University community participated in the study. Five subjects were eliminated due to excessively noisy EEG. All but two subjects were right handed and all subjects reported normal or corrected-to-normal vision. Informed consent was obtained from each participant. Eligible participants received course credit for their participation, and the remainder volunteered without compensation.

2.2. Apparatus and stimuli

Stimulus presentation and manual response measurement were controlled with Presentation[®] experimental software (Version 0.80, www.neurobs.com), running on a Pentium 4 computer under the Windows 2000 operating system with a 17-in. color CRT display at a resolution of 1024 × 768 pixels and a frame rate of 75 Hz. The experiment was run in a dimly lit room, with a fixed chin rest to maintain a constant viewing distance of 80 cm. Stimuli were 177 black-and-white pictures of Caucasian male (85) and female (92) faces with neutral expressions. These stimuli were adapted from a larger set of stimulus photographs courtesy of Dr. Daphne Maurer's Visual Development Laboratory, Department of Psychology, Neuroscience and Behaviour, McMaster University, originally acquired and processed as described in Mondloch, Geldart, LeGrand, and Maurer (2003). All the faces were unknown to the subjects and the faces were without glasses, jewelry, or other extraneous items. An elliptical image mask was used to isolate each face from mid forehead to lower chin (including eyebrows and outer margins of the eyes, as shown in Fig. 1). The 8-bit (256-level) grey scale images had a mean pixel luminance value of 166.0, with a standard deviation (contrast equivalent) of 12.3. Faces were presented within an ever-present placeholder box, with width of 85 mm and height of 104 mm centered on the display. Within the center of the box was a 1 mm square fixation point, which was occluded by the face stimuli when they were presented. Elliptical face stimuli with a width of 60 mm and height of 90 mm were presented on a white background, in one of the four corners of the constant box, with 2 mm vertical and horizontal separation from the nearest sides of the box. The spatial extent of the faces within the placeholder box was large enough that they overlapped adjacent locations by 19.5 mm in width and 40 mm in height. With the constant

viewing distance of 80 cm, face stimuli were ≈ 6.4 degrees of visual angle high and 4.3 degrees of visual angle wide.

2.3. Procedure

The experimental procedure is depicted in Fig. 1. The experiment consisted of four experimental sessions each lasting ≈ 10 min. Each session contained all 177 face stimuli divided into two subsets: upright and inverted; all faces maintained the same orientation for the entire experiment. Blocks of upright and inverted face trials were alternated throughout each session. Within each block, runs of repeat faces (e.g., four or five presentations of the same face) were alternated with runs of novel faces (e.g., three or four presentations of different faces). Stimulus order was randomized for each session so that a repeated face in one session might be presented only once as a novel face in the following session (and vice versa). Because the same 177 faces were used in all three sessions, familiarity with the set increased accordingly. Each session contained ≈ 300 trials, with self-paced breaks provided every 80 trials, dividing each session into four approximately equal blocks.

Prior to each session, participants received a brief training block in which the same upright face was presented for 16 trials. Participants were instructed to keep their eyes fixated on the central fixation point. Faces were presented in one of the four corners of the placeholder box for 200 ms, with an interstimulus interval that was randomly jittered from 1000 to 1300 ms. Participants performed a continuous, running 1-back location-matching task, determining whether the current face stimulus was in the same visuospatial location or a different visuospatial location as the immediately preceding face. Visuospatial location of each face stimulus was determined randomly with equal probability of occurrence in each of the four possible visuospatial locations, giving expected probabilities of same-location and different-location trials of 25% and 75%, respectively. Subjects responded with their right index and middle fingers on the “1” and “2” keys of the keypad on a standard computer keyboard to denote same-location and different-location responses, with response key mapping counterbalanced across subjects. Participants were required to respond to every face stimulus except the first one of a continuous-performance block. Subjects were instructed to ignore face identity, and both speed and accuracy were emphasized.

2.4. Electrophysiology

The continuous EEG (132 channels, BioSemi ActiveTwo, www.biosemi.com) was sampled at 512 Hz, using a left hemisphere parietal electrode (CMS) as reference. ERP averaging and analyses were performed using EEProbe software (ANT, www.ant-software.nl). The continuous EEG file for each subject was digitally filtered from 0.03 to 30 Hz. The EEG file was re-referenced to a common average reference for the N170 component and re-referenced to linked mastoids for analysis of the P3 component. Eye-blinks were identified and corrected using both automated and manual detection procedures via EEProbe software. Epochs contaminated with other eye movements and large artifacts were rejected. A 1000 ms recorded EEG epoch, including a 100 ms pre-stimulus baseline and a 900 ms interval following stimulus onset, was chosen for ERP averaging. ERP waveforms were then averaged separately for each condition. Only trials with correct responses were included.

2.5. Data analysis

Repeated measures analyses of variance (ANOVA) were conducted for both mean reaction time for correct responses and mean error rate in a 3-way design with the following conditions: stimulus orientation (upright, inverted), visuospatial location (different, same), and face identity (novel, repeat). Behavioural data were collapsed over experimental sessions and serial position.

The P1 component was isolated using a time window ranging from 50 to 150 ms, obtained via inspection of the grand average waveforms. Analysis of the P1 component was conducted on the same electrode set as in

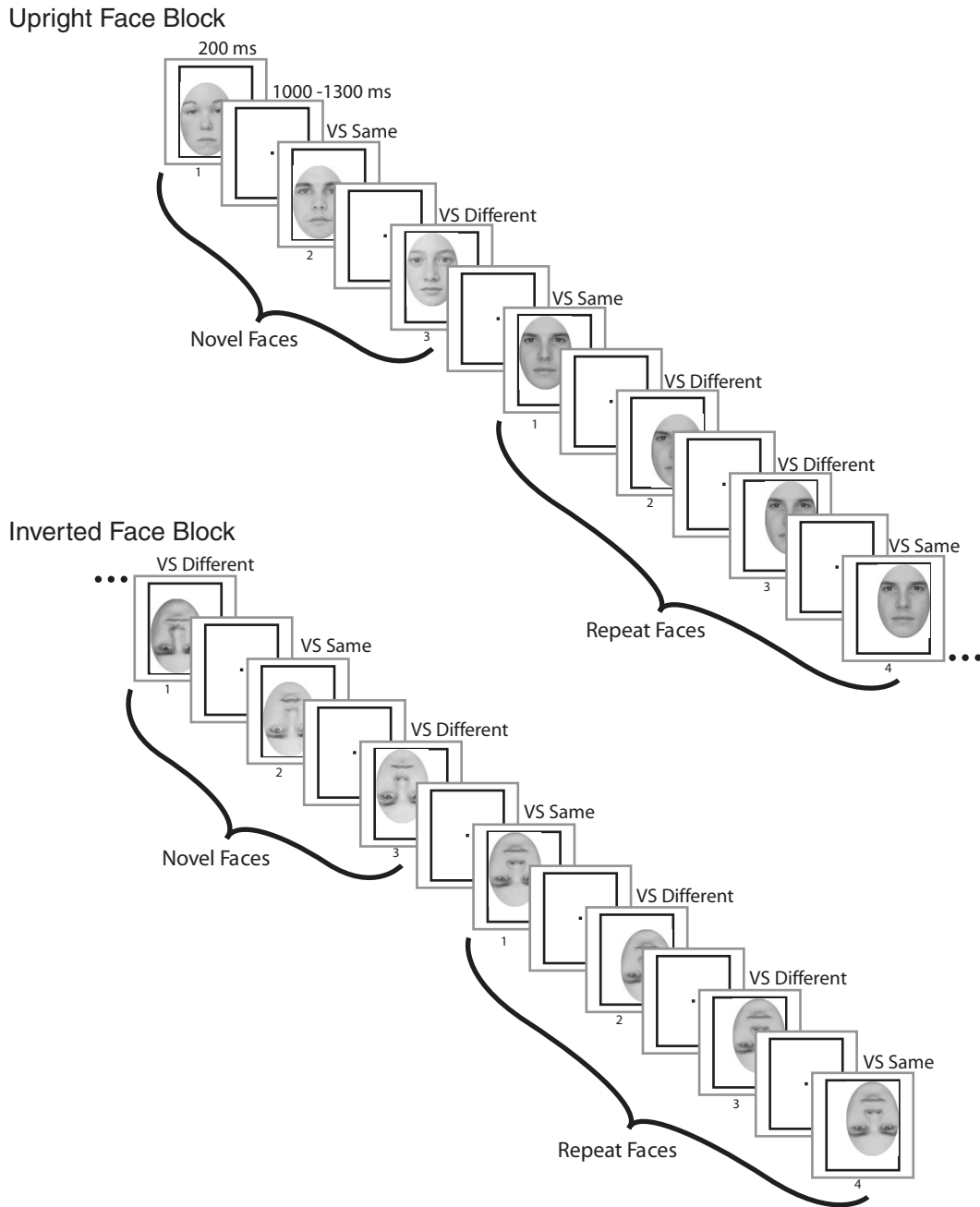


Fig. 1. The figure depicts some of the possible combinations of face orientation (upright vs. inverted), face identity (novel vs. repeat), visuospatial (VS) location (same vs. different) and serial position that participants experienced throughout the experiment. Faces were presented randomly at one of the four corners of an ever-present box on the computer screen, with subjects judging whether the current face stimulus was in the same or a different visuospatial location compared with the location of the previous face. Faces were presented for 200 ms in blocks of upright and inverted faces alternating runs of three or four novel faces and four or five repeated presentations of the same face, with 1000–1300 ms between stimuli.

N170 analysis. Repeated measures ANOVA with Greenhouse-Geisser correction applied when necessary was conducted for P1 peak amplitude in a 5-way design with the following conditions: hemisphere (left, right), stimulus orientation (upright, inverted), visuospatial location (different, same), face identity (novel, repeat), serial position (1, 2, 3, 4).

ERP analysis of the N170 components focussed on an occipital-parietal region of interest which exhibited maximal N170 amplitude. A set of eight electrodes were assessed, four electrodes from each of left and right hemispheres. For each subject individual waveforms were inspected to determine the optimal location at which to capture maximal N170 amplitude effects and the analysis of all N170 conditions was conducted for that

electrode pair. Electrode locations corresponding to locations defined by the 10–20 system: P03/P04, P05/P06, an electrode pair slightly lateral in location to P03/P04, and an electrode pair slightly medial in location to P05/P06. The N170 component was isolated using a time window ranging from 120 to 200 ms, obtained via inspection of the grand average waveforms. Repeated measures ANOVAs with Greenhouse-Geisser correction when needed were conducted on N170 amplitudes and latencies to examine differences across serial positions for runs of novel and repeated upright faces as well as runs of novel and repeated inverted faces. Initially, a five factor $2 \times 2 \times 2 \times 2 \times 4$ ANOVA with factors of hemisphere (left, right), stimulus orientation (upright, inverted), visuospatial location

(different, same), face identity (novel, repeat), and serial position (1, 2, 3, 4) was run, and based on a significant 5-way interaction, ANOVA analyses were done on the following effects. Two factor 2×4 ANOVAs with factors of hemisphere (left, right) and serial position (1, 2, 3, 4) were done separately for upright novel and repeat faces, and inverted novel and repeat faces, at same and different locations.

Effects of face identity and visuospatial location on P3 component amplitudes were assessed over a parietal region of interest, comprised of electrodes Pz (corresponding to the 10–20 system coordinates) and two neighbouring electrodes on either side of the midline. P3 mean amplitude effects (average amplitudes across a 450–580 ms window, obtained via inspection of the grand average waveforms) were assessed with a 3-way repeated measures ANOVA with factors of stimulus orientation (upright, inverted), visuospatial location (different, same), and face identity (novel, repeat). ERP data were collapsed over experimental sessions and serial position.

FCz amplitudes were assessed over a frontal region of interest, comprised of electrodes FCz (corresponding to the 10–20 system coordinates) and two neighbouring electrodes on either side of the midline. FCz (average amplitudes across a 450–580 ms window, obtained via inspection of the grand average waveforms) were assessed with a 3-way repeated measures ANOVA with factors of stimulus orientation (upright, inverted), visuospatial location (different, same), and face identity (novel, repeat). ERP data were collapsed over experimental sessions and serial position.

3. Results

3.1. Behavioral results

Fig. 2 illustrates mean error rate and reaction time performance for upright and inverted face stimuli, presented as repeat and novel face stimuli at different and same visuospatial locations. Behavioral performance was impaired for novel faces presented at the same visuospatial location: there were increases in both error rate and response time for novel faces at same location relative to repeat faces at same location, and novel and repeat faces at different locations. These observations were supported by a 2-way interaction of location and face identity for errors: $F(1,28) = 14.319$, $p < 0.01$; and reaction time: $F(1,28) = 6.345$, $p < 0.05$. The 3-way interaction between face orientation, location, and face identity was not significant for either error rate ($F < 1$) or reaction time performance ($F(1,28) = 2.159$, $p = \text{n.s.}$).

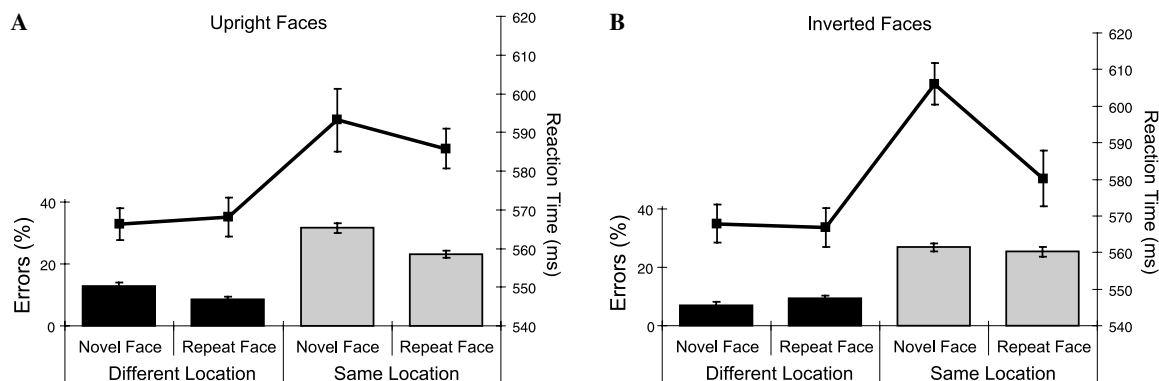


Fig. 2. Mean reaction time and mean percentage errors for (A) upright and (B) inverted, novel vs. repeat faces presented at same vs. different visuospatial locations. Mean reaction time is represented by the line graph, left axis and mean percentage errors is represented by the bar graph, right axis. Error bars indicate standard errors. Overall, performance was impaired for novel faces presented in the same visuospatial location.

3.2. P1 results

Fig. 3 illustrates mean P1 responses. Mean P1 amplitudes were larger for inverted relative to upright face stimuli, $F(1,28) = 21.134$, $p < 0.05$. Larger P1 amplitudes were observed for face stimuli presented at same relative to different visuospatial locations, $F(1,28) = 18.526$, $p < 0.05$. This observation is consistent with greater allocation of attention to “same” locations compared to “different” locations. There was also a significant 3-way interaction between hemisphere, orientation and face identity, $F(1,28) = 5.515$, $p < 0.05$. This effect was due to larger P1 amplitudes for novel than repeat upright faces detected at the right hemisphere electrode sites, suggesting an early sensitivity to novel upright (but not novel inverted) faces (Bonferroni $t(28) = 2.625$, $p < 0.01$ and $t(28) = 0.299$, $p = \text{n.s.}$, for upright and inverted, respectively). There were no significant interactions involving serial position.

3.3. N170 results

Fig. 3 (waveforms) and Fig. 4 (line graphs) illustrate mean N170 responses. Based on a significant 5-way interaction, $F(3,84) = 3.615$, $p < 0.05$, analyses were conducted to examine hemisphere by serial position for each of upright novel and repeat faces, and inverted novel and repeat faces, at same and different visuospatial locations. A progressive decrease in N170 amplitudes occurred for upright repeated faces at different (unattended) visuospatial locations, main effect of serial position: $F(3,84) = 3.135$, $p < 0.05$. The progressive decrease in N170 amplitude was most predominant in the right hemisphere compared to the left hemisphere, 2-way interaction between serial position and hemisphere: $F(3,84) = 8.020$, $p < 0.001$. This observation was supported by a significant linear trend of serial position, $F(1,28) = 6.739$, $p < 0.05$, and a significant linear trend of serial position by hemisphere, $F(1,28) = 22.414$, $p < 0.001$. In contrast, we did not observe a progressive habituation of the N170 amplitude for inverted repeated faces at different visuospatial locations, $F(3,84) = 0.723$, $p = \text{n.s.}$ N170

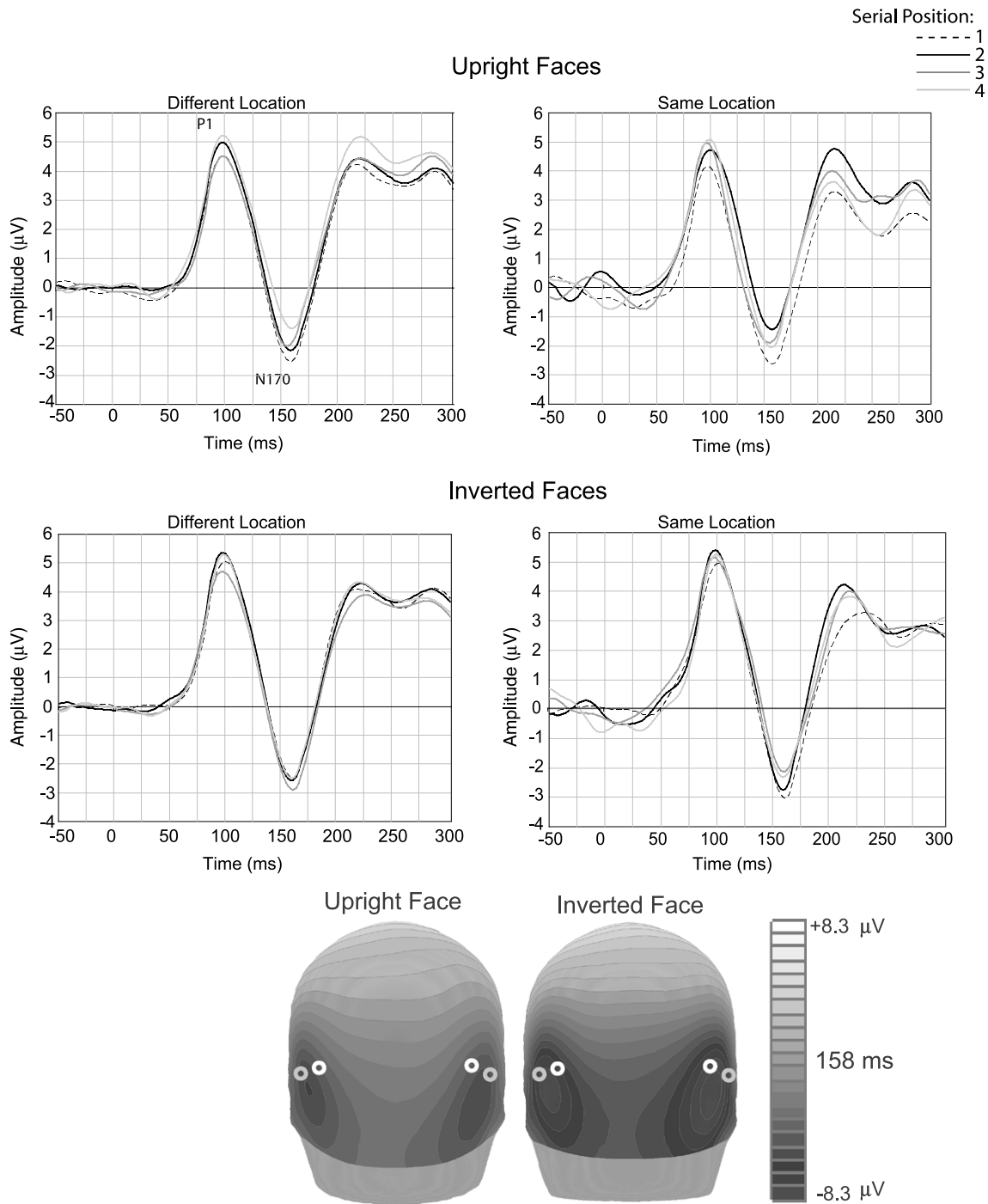


Fig. 3. Grand mean N170 component morphology for upright and inverted repeated face stimuli at different vs. same visuospatial locations. Grand mean scalp topographies illustrating N170 amplitude effects at 158 ms. Scalp voltage distributions are displayed for upright and inverted repeat faces presented at same locations. The white dots denote the location of electrodes used in N170 analysis, which are slightly medial and superior to P6/P7. The grey dots denote the electrode locations P6/P7 for reference.

habituation was not observed for novel upright faces presented at different locations, $F(3, 84) = 0.099, p = n.s.$, or for novel inverted faces presented at different locations, $F(3, 84) = 2.228, p = n.s.$

There was also a decrease in N170 amplitude for the initial (but not subsequent) upright face repetition at same visuospatial locations in both hemispheres; the effect was significant in the right hemisphere and supported by a sig-

nificant 2-way interaction between serial position and hemisphere: $F(3, 84) = 3.640, p < 0.05$. N170 habituation was not observed for repeat upright face presented at same locations, this observation supported by a null result of linear trend for serial position, $F(1, 28) = 0.696, p = n.s.$ We did not observe a decrease in N170 amplitude for the initial inverted face repetition at same visuospatial locations, $F(3, 84) = 0.639, p = n.s.$ N170 habituation was not observed

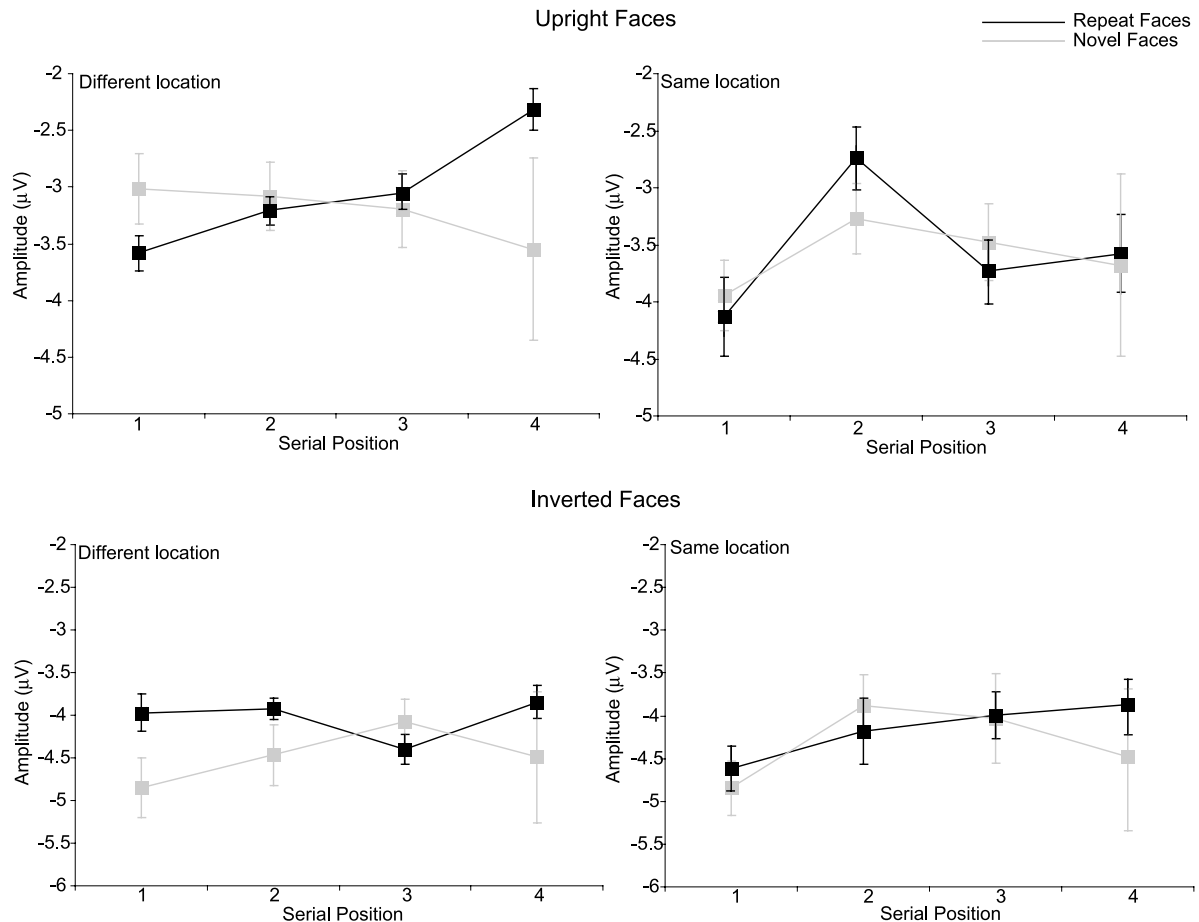


Fig. 4. Grand means of N170 amplitudes illustrating upright and inverted, novel vs. repeat face stimuli at different vs. same visuospatial locations. Repetition effects occurred for upright faces but not for inverted faces. Error bars indicate standard errors.

for novel upright faces presented at same locations, $F(3, 84) = 0.188$, $p = \text{n.s.}$, or for novel inverted faces presented at same locations, $F(3, 84) = 1.918$, $p = \text{n.s.}$

No significant N170 latency effects were observed.

3.4. P3 results

Fig. 5A illustrates mean P3 amplitude responses for upright and inverted face stimuli, presented as repeat and novel face stimuli at different and same visuospatial locations. Overall, greater P3 mean amplitude responses were elicited for upright relative to inverted faces, $F(1, 28) = 6.876$, $p < 0.05$. P3 mean amplitude was larger for faces presented at same versus different locations, $F(1, 28) = 64.257$, $p < 0.05$. Amplitudes were larger for novel compared to repeated faces, $F(1, 28) = 6.425$, $p < 0.05$, and this interacted with location and orientation $F(1, 28) = 5.244$, $p < 0.05$. This 3-way interaction can be explained as follows. P3 amplitudes were larger for upright novel faces ($10.8 \mu\text{V}$) relative to repeat faces ($9.0 \mu\text{V}$) presented at same (attended) visuospatial locations (Bonferroni $t(28) = 3.600$, $p < 0.01$), whereas no differences were observed between novel ($6.3 \mu\text{V}$) and repeat ($6.2 \mu\text{V}$) faces presented at different locations (Bonferroni $t(28) = 0.576$,

$p = \text{n.s.}$). P3 amplitudes were equivalent for inverted novel versus repeat faces presented at same visuospatial locations ($9.3 \mu\text{V}$ vs. $9.2 \mu\text{V}$, respectively; Bonferroni $t(28) = 0.256$, $p = \text{n.s.}$) and for inverted novel versus repeat faces presented at different locations ($5.9 \mu\text{V}$ vs. $5.7 \mu\text{V}$, respectively; Bonferroni $t(28) = 0.875$, $p = \text{n.s.}$). These observations suggest that upright and inverted faces are treated differently at this stage of processing. In particular, P3 amplitude at Pz is sensitive to the difference between repeat and novel faces when the faces are upright and in the attended visuospatial location, but not when they are inverted or in the unattended visuospatial location.

3.5. FCz results

At FCz there was an identity effect observed that was in the same time window as the identity effect at Pz. The pattern was the same as that observed at Pz in that the identity effect occurred at same but not different locations. The pattern was different than that observed at Pz in that at same locations, novel faces produced larger amplitudes than repeat faces for both upright and inverted faces, whereas at Pz this occurred for upright faces only. Fig. 5B shows the waveforms at FCz and Fig. 6 shows the topographies of the

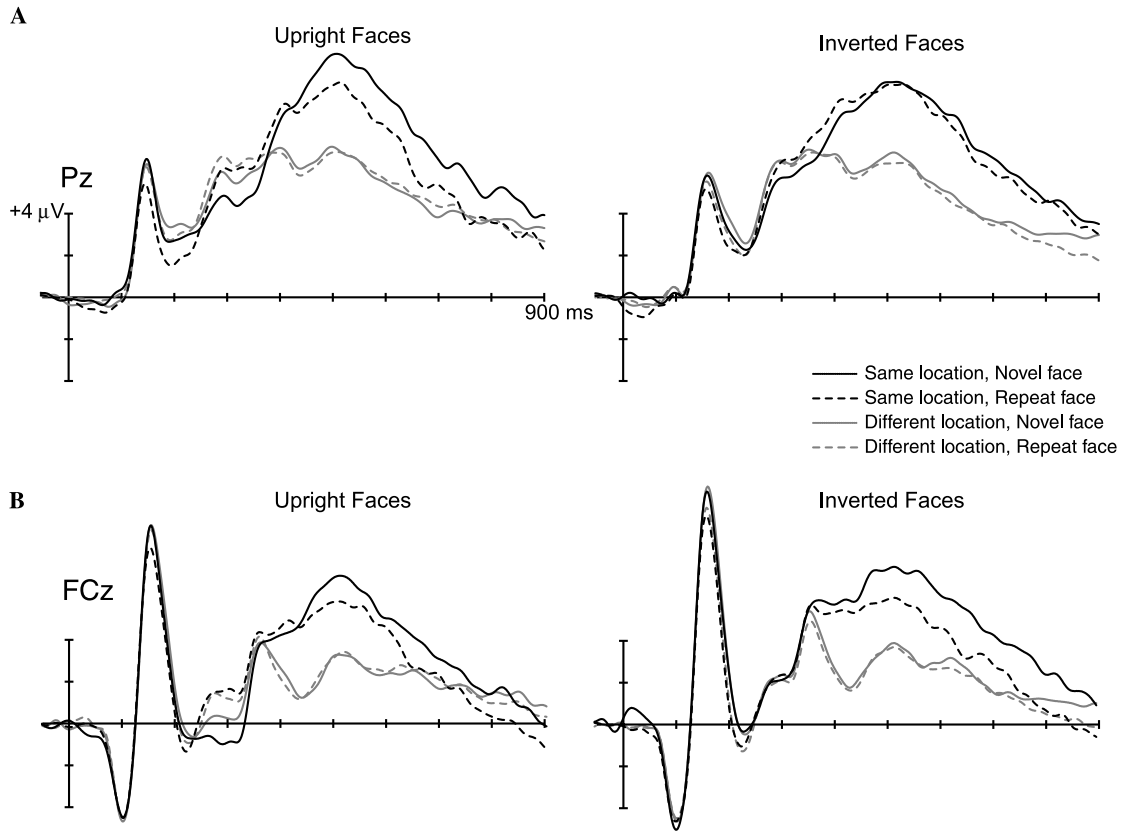


Fig. 5. (A) Grand mean waveforms observed at electrode Pz illustrating P3 morphology for upright and inverted face stimuli presented as novel vs. repeat faces at same vs. different visuospatial locations. Overall, faces presented at same visuospatial locations elicited larger P3 mean amplitudes than faces presented at different visuospatial locations. At same visuospatial locations, novel faces elicit larger P3 responses than repeat faces for upright faces only, and not for inverted faces. (B) Grand mean waveforms at electrode FCz showing positivity in same time window as P3. At same visuospatial locations only, upright and inverted faces produced a more positive component for novel compared to repeated faces.

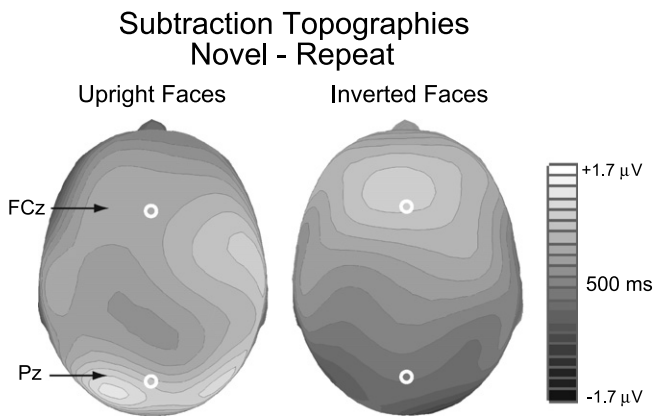


Fig. 6. Grand mean subtraction topographies illustrating novel—repeat difference at parietal and frontal sites at 500 ms (see Fig. 5 for the associated waveforms).

novel minus repeated faces difference for upright and inverted orientations at 500 ms. Mean FCz amplitude was larger for faces presented at different relative to same locations, $F(1, 28) = 58.591, p < 0.05$. Amplitudes were larger for novel compared to repeated faces, $F(1, 28) = 6.088, p < 0.05$, and this interacted with location, $F(1, 28) = 11.809, p < 0.05$. This 2-way interaction can be explained as follows. Larger FCz amplitudes were observed for novel faces relative to

repeat faces presented at same (attended) visuospatial locations (Bonferroni $t(28) = 3.165, p < 0.01$), whereas no differences were observed between novel and repeat faces presented at different locations (Bonferroni $t(28) = -1.062, p = \text{n.s.}$). Importantly, a 3-way interaction between face orientation, location and face identity was not significant, $F(1, 28) = 0.526, p = \text{n.s.}$ The topographies illustrate the contrast between the P3 results at Pz (for which the novel versus repeat difference occurs only for upright faces) and the FCz results (for which both upright and inverted faces show a novel versus repeat difference).

4. Discussion

The N170 ERP component is currently under investigation for its sensitivity to novel face repetitions and the acquisition of familiarity with particular faces. Recent studies have reported a decrease in the amplitude of the N170 in response to face repetitions (Campanella et al., 2000; George et al., 1997; Guillaume & Tiberghien, 2001; Heisz et al., 2006; Itier & Taylor, 2002, 2004). A particularly sensitive measure of the N170 habituation effect is observed when attention is directed away from face identity. For example, using a visuospatial location matching task in which face identity was not relevant, Heisz et al. (2006) reported a progressive

decrease in the N170 amplitude for up to three repetitions of the same face presented in unattended locations. These findings were interpreted as support for a hypothesis that the N170 activity represents relatively early and automatic face identity processing. Indeed, it has been suggested that tasks that do not require explicit evaluation of the face identity, provide a more pure measure of the automaticity of face processing (Gauthier et al., 2000). However, it was not clear from the Heisz et al. (2006) study whether the N170 habituation was due primarily to face identity priming or had a large component of perceptual priming, because the repeated faces were also perceptually identical. In the present study, we used inverted faces to test the hypothesis that the N170 habituation reflects a change in face identity processing mechanisms. If the N170 habituation was due to identity processing, then in the current experiment inverted faces would not produce the same progressive habituation as upright faces because extracting identity from inverted faces is relatively difficult (Eimer, 2000a, 2000b, 2000c; Rossion et al., 1999).

Using the same 1-back visuospatial location matching paradigm we replicated the Heisz et al. (2006) results showing a progressive decrease in N170 amplitude for each repetition of the same face when the repetitions occurred in unattended visuospatial locations. To demonstrate that face identity was not being explicitly evaluated at different locations, Heisz et al. (2006) analyzed the P3 ERP component. The amplitude of the P3 has been reported to effectively index allocation of cognitive resources (Kramer & Strayer, 1988; Kramer, Strayer, & Buckley, 1991; Watter, Geffen, & Geffen, 2001; Wickens, Kramer, Vanasse, & Donchin, 1983). The present P3 findings for upright faces replicated those of Heisz et al. (2006) by revealing a larger P3 for novel versus repeat faces when they appeared in the same location as the previous trial, but the P3 amplitude was not sensitive to face repetition when the faces appeared in different visuospatial locations. Some studies report larger P3 amplitudes for repeated versus novel faces (Itier & Taylor, 2002, 2004; Paller, Bozic, Ranganath, Grabowecky, & Yamada, 1999; Paller, Gonslaves, Grabowecky, Bozic, & Yamada, 2000), however in those studies the tasks required responses to repeated face identity, and in our study the faces were not relevant to the response, so this difference in response processing may have contributed to the different pattern we observed. We posit that the larger P3 for novel versus repeat faces indicates that attention was captured by the identity properties of the novel face stimulus and that this greater attention to identity did not occur when the face was presented in a different visuospatial location.

Inverted face stimuli produced similar P3 amplitude differences such that P3 amplitude for same visuospatial locations was much larger than different visuospatial locations. However, the novel versus repeat difference at same visuospatial locations did not occur for inverted faces at the parietal P3,¹ suggesting that even at attended locations,

attention was not captured by identity of the inverted faces to the same extent that this occurred for upright faces.

The behavioural responses were consistent with the P3 results. Both upright and inverted faces produced more errors and longer reaction times when faces were presented in the same visuospatial location as the stimulus on the previous trial, supporting the idea that the perceptual properties of same-location stimuli interfered with behavioural performance despite being irrelevant to the task. Similar to the behavioural results of Heisz et al. (2006), this effect was larger for novel faces. It is possible that attention was captured by the novel stimulus which interfered more with response processing than the repeated stimulus. In general, the effects of stimulus properties on response time, accuracy, and the P3 were much larger when stimuli were presented to the same (attended) visuospatial location.

The establishment of unattended face processing at different locations via P3 and behavioral data, and replication of the N170 habituation to upright face repetition, allowed us to test the N170 habituation effect in response to face inversion. Our claim is that when face identity is not relevant to the task, face processing at unattended locations reflects a relatively purer representation of habituation of automatic face processing, consistent with the conclusion made by Heisz et al. (2006). Attention to a face stimulus, whether it is due to task relevance or focus of spatial attention, results in substantial optimal engagement of face identity processes, and these processes reengage with each repetition of the face. In this situation, a decrease in N170 amplitude is observed only for the first repetition (that is, the second presentation) of a previously novel face. When attention is directed away, as it was in our study by making face identity task irrelevant and by presenting faces outside the locus of spatial attention, face identity processes do not reengage with each face and habituation of the N170 occurs, with N170 amplitude observed to decrease progressively over several repetitions of the same face.

In contrast to the progressive decrease in the N170 amplitude for upright faces presented at unattended locations, we did not observe N170 habituation for inverted faces. Inverted faces do not share some of the processing advantages afforded to upright faces (Rossion et al., 1999; Yin, 1969). The processing difference of upright versus inverted faces likely reflects greater expertise for upright faces, including the relative ease with which upright faces are perceived and processed at an individual level (Tanaka, 2001). The identity processing impairment for inverted faces is thought to result from the disruption of second-order relations—the spatial relationships among the features of the face (Leder & Bruce, 2000; Yin, 1969; for reviews see: Maurer et al., 2002; Valentine, 1988). Extraction of second-order relational information from a face is thought to occur early in face processing (Freire, Lee, & Symons, 2000) and may possibly be reflected in the N170. The N170 response to inverted faces is characteristically later and larger compared with upright faces, suggesting

¹ There was a novel—repeat difference at frontal sites, which may suggest an additional generator sensitive to stimulus repetition.

greater N170-related processing is required when information is more difficult to extract (Eimer, 2000a, 2000b, 2000c; Itier & Taylor, 2002; Rossion et al., 1999).

Our observed lack of N170 habituation for repeated inverted face stimuli fits well with these prior findings. Compared to upright faces, poorer extraction of physical second-order relations would lead to impaired processing of identity properties of inverted faces. We suggest that identity representations for upright faces are established relatively efficiently, requiring less N170-related processing on subsequent viewings of the same stimulus. In contrast, identity representations of inverted faces are established relatively inefficiently. Without a strong identity representation of a face stimulus, the N170 response to the repetition of an inverted face would not habituate until a sufficient identity representation had been established.

This study was designed to address the question of whether identity processing underlies the N170 habituation effect. The critical point for this paper is that N170 habituation at unattended locations was observed for repeated upright faces, but did not occur for repeated inverted faces, supporting the idea that N170 habituation is related to face identity. Campanella et al. (2000) found that contiguous presentations of photographs that preserved face identity but not the physical properties of the face stimulus caused a decrease in the N170 amplitude, inferring that the N170 repetition effect reflects identity processing rather than perceptual priming.² However, Itier and Taylor (2002) reported a decrease in N170 amplitude in response to single repetitions of both upright, inverted, and contrast reversed faces. This suggests that the N170 repetition effect may reflect perceptual priming because inversion and contrast reversal impairs identity processing. Inverted faces are processed differently from upright faces in part because processing face identity is less fluent for inverted faces than upright faces. However, the automatic face identity process still operates when an inverted face is presented, and habituation of the N170 may be observed if this process is allowed to complete. For example, other studies have observed N170 habituation for repeated inverted faces (Itier & Taylor, 2002, 2004). The difference between those studies and the current study is the nature of the task. When face identity is task relevant, N170 habituation to repeated inverted faces is observed. When face identity is not task relevant, we do not observe N170 habituation to repeated inverted faces. The present study extends these findings and explains the conflict in the published results by showing that the N170 repetition effect does not occur for inverted faces when identity of the face stimulus is not task relevant, lending support to the hypothesis that the N170 repetition effect reflects habituation of face identity processing.

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² It would be interesting to test whether the results from our study would replicate with different photographs of the same individual.

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