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Progressive N170 habituation to unattended repeated faces

Jennifer J. Heisz, Scott Watter, Judith M. Shedden *

Department of Psychology, McMaster University, Canada

Abstract

This study utilized a location-matching task to investigate whether the face-sensitive N170 event-related potential component would habituate in its response to the repeated presentation of same face stimuli when face identity was irrelevant to the experimental task. N170 amplitude decreased progressively with repeated presentation of the same face vs. sequential presentation of novel faces. This N170 habituation to face identity repetition occurred only for faces at unattended spatial locations, likely representing a relatively pure observation of automatic early face processing.
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1. Introduction

Face recognition plays a paramount role in establishing human relationships, acting as a retrieval cue for person-specific information. Despite structural similarity, people have little trouble recognizing familiar faces. Attaining familiarity for new faces also seems relatively effortless—even a single exposure to a novel face often leads to familiarity. Recently, an fMRI study demonstrated that in the fusiform face area (FFA) of the brain—thought to play a key role in the representation of face identity—activity progressively decreased with repeated presentation of the same face, compared with presentation of different faces and letters (Gauthier et al., 2000; see also Gill-Spector & Malach, 2001). Gauthier et al. (2000) suggested that this rapid selective habituation to repeated faces implies the fusiform face area's involvement in representing faces at an individual level, not merely distinguishing faces from other non-face stimuli. In addition to the hemodynamic response of the FFA, the N170 event-related potential (ERP) component has also been shown to be sensitive to faces, though the role of the N170 in identity coding has not been established.

This experiment sought to determine whether the N170 component may reflect processing of individual face representations and whether the N170 component would habituate to repeated presentations of the same face.

The N170 is thought to represent neural activity involved in the structural encoding of faces because of its large amplitude for faces with respect to non-face objects and scrambled face stimuli (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Carmel & Bentin, 2002; George, Evans, Fiori, Davidoff, & Renault, 1996; Rossion et al., 2000). Also, inverted faces elicit a larger and later N170 component, which may be indicative of the difficulty involved in abstracting structural components of an inverted face (Eimer, 2000a, 2000b; Itier & Taylor, 2002; Rossion et al., 1999, 2000).

Other evidence suggests that N170 activity represents object processing at a subordinate representational level. One recent investigation by Tanaka (2001) suggests that faces are typically processed automatically at an individual level. This study reported that adults were as fast at identifying faces at the subordinate level (e.g., Bob) as they were at the basic level (e.g., Human). Similarly, research shows that experts in a field (e.g., experienced birdwatchers) also demonstrate automatic processing of their "objects of expertise" (e.g., birds) at the individual or subordinate level, where novices do not (Gauthier & Tarr, 1997; Johnson & Mervis, 1997). Heightened visual experience with a particular

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* Corresponding author. Tel.: +1 905 525 9140x24345; fax: +1 905 529 6225.
  E-mail address: shedden@mcmaster.ca (J.M. Shedden).

class of visual stimuli also modifies the response of the N170. The N170 response to expert objects it is more comparable to that of faces than other objects, characterized by a larger amplitude response (Gauthier, Curran, Curby, & Collins, 2003; Tanaka & Curran, 2001) and sensitivity to stimulus inversion (Busey & Vanderkrolk, 2005; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002). Additionally, the N170 amplitude is enhanced when an object is processed at a subordinate vs. a basic representational level (Tanaka, Luu, Weisbrod, & Kiefer, 1999). This subordinate level processing of both faces and expert objects reflected in the N170 response suggests that the activity of the N170 component is sensitive to the detection of identity, and may reflect processes involved in establishing face familiarity.

Recent ERP studies have used identity-matching tasks to investigate the response of the N170 to the acquisition of face familiarity. These ERP studies reported larger N170 amplitudes for novel vs. familiar face stimuli (Guillaume & Tiberghien, 2001; Itier & Taylor, 2002). The amplitude of the N170 is reported to be unaffected by changes in facial expression or background (Guillaume & Tiberghien, 2001). However, research shows the N170 can be affected by repeated presentation of an initially novel face. Itier and Taylor (2002) demonstrated that immediate repetition of a novel face stimulus, in upright, inverted or negative form, generated a smaller and earlier N170 component than the initial presentation of the face. Additionally, when a novel face was repeated after the presentation of another intervening face stimulus, an earlier N170 was evoked compared to the initial exposure to the face. Itier and Taylor (2002) interpreted these findings as perceptual priming. However, another study demonstrates that the N170 repetition effect to repeated faces can be attributed to identity priming (Campanella et al., 2000). The study employed a 1-back identity matching task in which three different pairs of matching stimuli were presented: same identity, same percept; same identity, different percept; and different identity, different percept. They reported similar N170 repetition effects for repeated faces with the same identity regardless of percept.

Like the N170 response to single face repetitions, the activity of the FFA also decreases with immediate repetition of the same face (Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004). The reduction in FFA activity to repeat faces has been attributed to the processing of the face's identity rather than physical properties or expression. Rotshtein et al. (2005) dissociated neural processing of identity and physical properties by demonstrating selective sensitivity of the right FFA to a face's identity and not to the physical properties, and selective sensitivity of the inferior occipital gyrus to physical properties and not to identity. Similarly, Winston et al. (2004) dissociated neural processing of identity and expression by demonstrating selective sensitivity of the right FFA and right posterior superior temporal sulcus (STS) to a face's identity and not to expression, and selective sensitivity of the right anterior STS to a face's expres-

sion and not to identity. The selective sensitivity of the FFA to face identity akin to that of the N170 ERP component suggests that both the N170 and the FFA may play a comparable role in recognizing faces.

Though Itier and Taylor (2002) provide some initial evidence for this argument, their study only assessed a single repetition of a given stimulus. Their study also employed an experimental task which focused on evaluating the identity of presented face stimuli, as did all ERP and fMRI studies discussed here. Gauthier et al. (2000) suggested that such overt, identity-focused tasks may involve a more constant level of activation of neurons responsive to faces, potentially eliminating, reducing or masking any gradual habituation of face-sensitive processing activity in response to repeated face stimuli. In contrast, Gauthier et al.'s (2000) fMRI study demonstrated a progressive decrease in activity of the fusiform face area over several repetitions of the same face stimulus, when subjects performed a location-matching task with repeated vs. novel face stimuli, where face identity was irrelevant to task demands. Gauthier et al. (2000) argued that having participants perform a task that did not involve the evaluation of face identity, as previous studies had done, allowed a more sensitive measure of habituation of face-specific processing areas to repeated face stimuli.

To better observe the potential habituation of N170-related face processing to identity repetition, the present study employed a 1-back location-matching task, removing overt attention from the evaluation of face identity. Runs of three or four unique face stimuli were alternated with runs of four or five presentations of the same face stimulus, with face stimuli presented randomly at one of four positions on a computer screen. The task asked participants to judge whether or not the current stimulus appeared at the same screen location as the previous one. Substantial spatial overlap of face stimuli at the four different screen positions was used to minimize the tendency for eye movements. Face identity was irrelevant to task performance.

To counteract bias to predict subsequent stimulus location, face stimuli were equally likely (25%) to appear at each of the four spatial screen locations on any trial. Stimulus location information was the only task relevant information required in this 1-back location-matching task, and thus, there are two principal ways participants might perform the task: either using a visuospatial approach or a verbal approach. A visuospatial approach would require participants to encode and maintain the spatial location of the current trial in working memory, using this information to make response decisions relative to the spatial location of the next trial. Alternatively, a verbal approach would require participants to encode spatial positions as an informationally equivalent verbal code (e.g., "top left"), performing the task via a comparison of verbal codes for the appropriate trials. Of course, a combination of these styles of performance would also be possible. Given the strong direct compatibility between stimulus set and task requirements

on visuospatial working memory, we would suggest that participants primarily approached this task by way of visuospatial working memory codes. If participants were to perform this task using a verbal approach, they must first recode visuospatial location information as verbal information and then compare verbal codes for each trial, consequently imposing a substantially greater working memory load in comparison to a visuospatial approach. The visuospatial approach is more direct and less effortful than the verbal approach, and thus the likely method employed by participants for the task at hand.

Given the close functional and mechanistic relationship between spatial attention and spatial working memory (see Awh & Jonides, 2001; for a review), maintaining the 1-back stimulus location information in a visuospatial working memory code is likely to directly impact the distribution of spatial attention on a trial-by-trial basis. In this case, it is likely that maintaining a given spatial position in spatial working memory—as this task requires every trial—would involve a greater allocation of spatial attention to this location compared with other screen positions. Considering this likely bias of spatial attention to the most recently presented stimulus position, we can use this influence on spatial attention as an investigative tool. In the present experiment, participants overtly categorized stimuli presented in the same spatial location as the previous stimulus as *same*, and those presented at locations other than that of the previous stimulus as *different*. This allowed the N170 response to novel vs. repeated face stimuli to be assessed at attended visuospatial locations (*same* locations), and compared within-subjects to the identical stimulus manipulations presented at unattended visuospatial locations (*different* locations). Under these conditions, effects of novel vs. repeated face stimuli on the N170 response at *different* locations would represent the best measure of relatively unattended processing of face identity, and thus may reflect relatively automatic processing of face identity information. Given the bias of selective attention to *same* locations, it may be easier to detect face identity effects at unattended vs. attended location conditions. Observing such effects would strengthen our interpretation of likely task performance, and support the notion of differential N170 face identity effects in *different* spatial location trials representing relatively automatic face identity processing.

2. Methods

2.1. Participants

Eleven volunteers (7 male, aged 18–31 years, mean age 22.3 years) from the McMaster University community participated in the study. All subjects were right handed and 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 performed with Presentation experimental software (Version 0.80, www.neuro-bs.com), running on a Pentium 4 computer under the Windows 2000 operating system. The display used was a 17-inch color CRT display, at a resolution of 1024×768 pixels at a frame rate of 75 Hz. The experiment was run in a dimly lit room, with a fixed chin rest used to maintain a constant viewing distance of 80 cm. Stimuli were 177 black-and-white pictures of Caucasian male (82) and female (95) faces with neutral expressions. Stimuli were adapted from a larger set of stimulus photographs courtesy of Dr. Daphne Maurer's Visual Development Lab, Department of Psychology, McMaster University, originally acquired and processed as described in Mondloch, Geldart, Maurer, and Le Grand (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). The 8-bit (256-level) gray 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 box, with height of 104 mm and width of 85 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. With the constant viewing distance of 80 cm, face stimuli were approximately 6.4 degrees of visual angle high and 4.3 degrees of visual angle wide.

2.3. Procedure

Fig. 1 demonstrates the experimental design, illustrating the contrasts between face identity, visuospatial location, and run position. The experiment consisted of three sessions, each approximately 10 min in length. Each session contained blocks of repeat faces and novel faces, which were alternated throughout the session until all 177 stimuli had been used. Blocks of repeat faces contained four or five presentations of the same face, and blocks of novel faces contained three or four presentations of different faces, all randomly assigned. 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 approximately 300 trials, with self-paced breaks provided every 80 trials, dividing each session into four approximately equal blocks.

Participants received a brief training block in which the same face was presented for 16 trials. Participants were
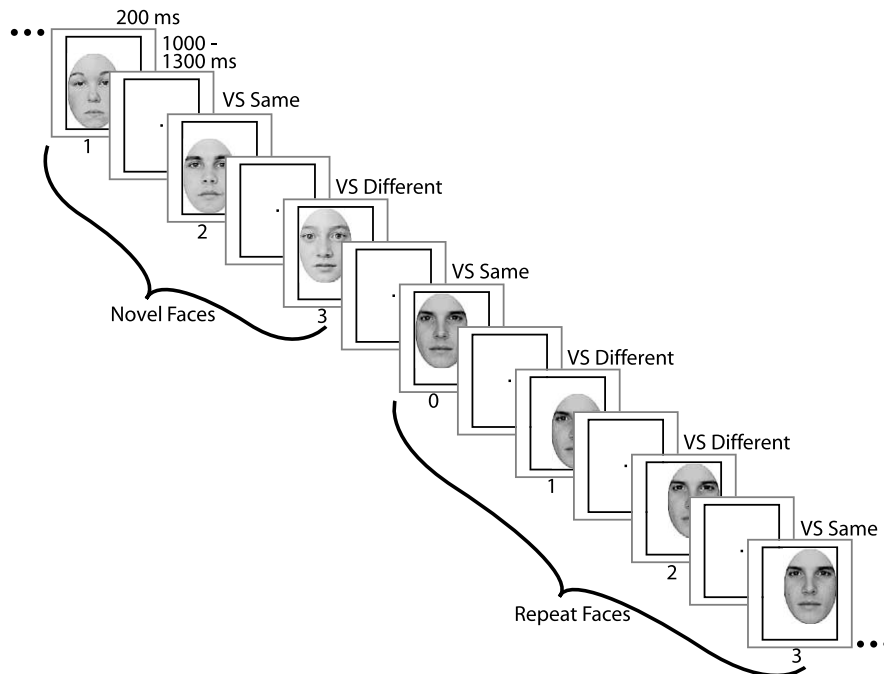
Fig. 1. The figure depicts the possible combinations of face identity (novel vs. repeat), visuospatial (VS) location (same vs. different) and run position that participants experienced throughout the experiment. Faces were presented randomly at one of the four corners of an ever-present box on the computer 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 alternating runs of 3 or 4 novel faces and 4 or 5 repeated presentations of the same face, with 1000–1300 ms between stimuli.

instructed to keep their eyes fixated on central fixation point. Faces were presented in one of the four corners of an ever-present box (as described above) 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 (128 channels, BioSemi Active-Two) 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 and

re-referenced to a right mastoid reference (for P3b) and digitally filtered from 2 to 30 Hz and re-referenced to a common average reference (for N170). Eye-blinks were identified, and corrected using both automated and manual detection procedure 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 and session. Only trials with correct responses were included.

2.5. Data analysis

Mean reaction time for correct responses and mean accuracy was computed for all combinations of conditions: session (1, 2, 3), visuospatial location (different, same), face identity (novel, repeat), and run position (1, 2, 3). Repeated measures analyses of variance (ANOVA) were conducted for both mean reaction time and mean accuracy with the conditions above.

ERP analysis of the N170 component focussed on an occipitotemporal region of interest which exhibited maximal N170 amplitude, using electrodes corresponding to the following locations defined by the 10–20 system: O9, O10, Oz, POz, O1, and O2, plus one additional electrode in each of the left hemisphere, right hemisphere and midline, creating a 3 × 3 electrode matrix. The N170 component was isolated using a time window ranging from 120

to 200 ms, obtained via inspection of the grand average waveforms. Four-way repeated measures ANOVA with Greenhouse-Geisser correction for both N170 mean amplitude and peak latency measures were conducted, with factors of hemisphere (left, midline, right), electrode (3 sites), visuospatial location (different, same), face identity (novel, repeat), and run position (1, 2, 3), with ERP data collapsed over session.

Inspection of grand mean waveforms suggested the presence of a P3b component over the centroparietal area. Effects of face identity and visuospatial location on P3b component amplitude were assessed over a small region of interest centered on the Cz electrode (corresponding to the 10–20 system coordinates), including one electrode laterally on either side. P3b mean amplitude effects (mean waveform amplitude within a 500–600 ms window) were assessed with a four-way repeated measures ANOVA with Greenhouse-Geisser correction, with factors of visuospatial location (different, same), face identity (novel, repeat), run position (1, 2, 3), and electrode (3 sites).

3. Results

Participants' overall mean accuracy for the 1-back location-matching task was greater when face stimuli were presented in different-location (94.8% correct) vs. same-location positions (83.9% correct), $F(1, 10) = 26.95$, $p < 0.001$. Mean accuracy was also greater overall for repeated faces (91.7% correct) than for novel faces (87.5% correct), $F(1, 10) = 15.61$, $p < 0.01$. Participants were less accurate for novel faces presented in same location (81.1%) compared to repeat faces in the same location (86.7%), and novel faces (93.9%) and repeat faces (95.9%) in different locations. This observation was supported by a marginal interaction between visuospatial location and face identity, $F(1, 10) = 3.430$, $p = 0.094$. Participants were less accurate for faces presented in run position 1 (86.5% correct) compared with later run positions (91.3% and 90.3% correct for run positions 2 and 3, respectively), $F(2, 20) = 6.52$, $p < 0.05$. Participants also made more errors for the first novel face following a series of repeated faces. Novel faces in run position 1 were less accurate (86.1%) than novel faces presented in run position 2 (93.4%) and 3 (92.9%) or repeat faces presented in run position 1 (93.8%), 2 (93.6%), and 3 (93.6%), supported by an interaction of face identity and run position, $F(2, 20) = 3.572$, $p < 0.05$.

Participants' mean reaction times decreased from session 1 (626 ms) through session 2 (589 ms) and session 3 (578 ms), $F(2, 20) = 4.491$, $p < 0.05$. Mean reaction times for faces presented at different locations were faster than those at same locations in sessions 2 (586 ± 6.2 ms SEM vs. 604 ± 8.6 ms) and 3 (574 ± 7.2 ms vs. 594 ± 9.8 ms), with the inverse of this pattern observed in session 1 (628 ± 10.1 ms vs. 620 ± 11.5 ms). This observation was supported by a significant interaction between session and visuospatial location, $F(2, 20) = 7.284$, $p < 0.01$. The main effect of location was not significant, $F(1, 10) = 1.33$, $p = ns$.

Fig. 2 shows the mean reaction time data for repeat vs. novel face identity stimuli at same vs. different locations, collapsed over run position and session. For faces presented at different locations relative to the previous stimulus, face identity appeared to have no effect on reaction time. For faces presented at the same location relative to the previous stimulus, novel face stimuli appeared to elicit a substantial RT cost relative to the different-location stimuli, with repetition of face identity in the same location showing no such influence. These observations were supported by a significant interaction between face identity and visuospatial location, $F(1, 10) = 5.33$, $p < 0.05$.

Fig. 3 shows the grand average ERP waveforms from the electrode at the midpoint of the O2 and O10 positions (10–20 system coordinates), comparing N170 activity over sequential run positions for novel vs. repeated faces at different vs. same locations. This electrode well illustrates the pattern of N170 responses observed across electrodes. Fig. 4 illustrates the scalp topographies of the N170 effects at mean peak latency of 155 ms, for faces presented at different locations. The focal negativity observed bilaterally at this trial latency was consistent with previously reported distributions of the N170 component. Mean N170 peak amplitudes were generally consistent across hemisphere, electrodes and conditions, with no main effects observed for hemisphere, $F(2, 20) = 1.57$, $\varepsilon = 0.58$, $p = ns$, electrode, $F(2, 20) = 0.34$, $\varepsilon = 0.58$, $p = ns$, nor for visuospatial location, face identity, or run position, all Fs < 1. Repeat faces presented at different locations produced a progressive decrease in the amplitude of the N170 predominately observed in electrodes located over the right hemisphere. In contrast, repeat faces presented at same locations did not produce a progressive decrease in the amplitude of the N170, but rather an initial decrease in N170 amplitude was observed from run position 0 to run position 1 followed by
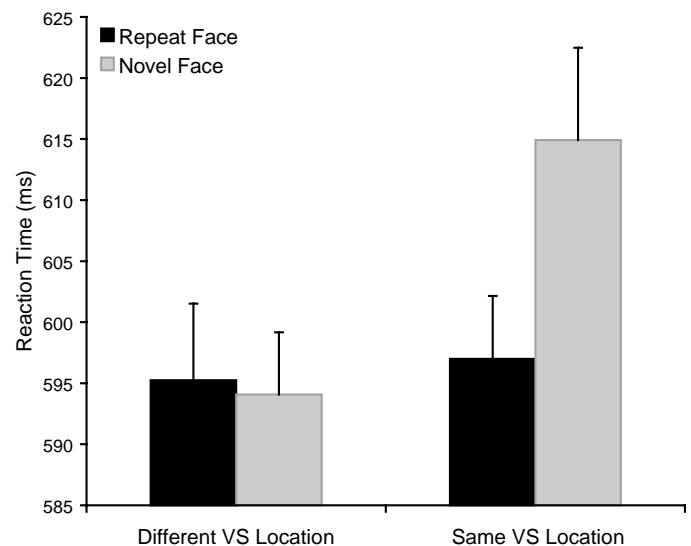

Fig. 2. Mean reaction time for same vs. different visuospatial (VS) location and novel vs. repeated face identity. Subjects were slower to respond to novel faces compared to repeated faces at same visuospatial locations, and compared with all faces at different VS locations. Error bars indicate SE.
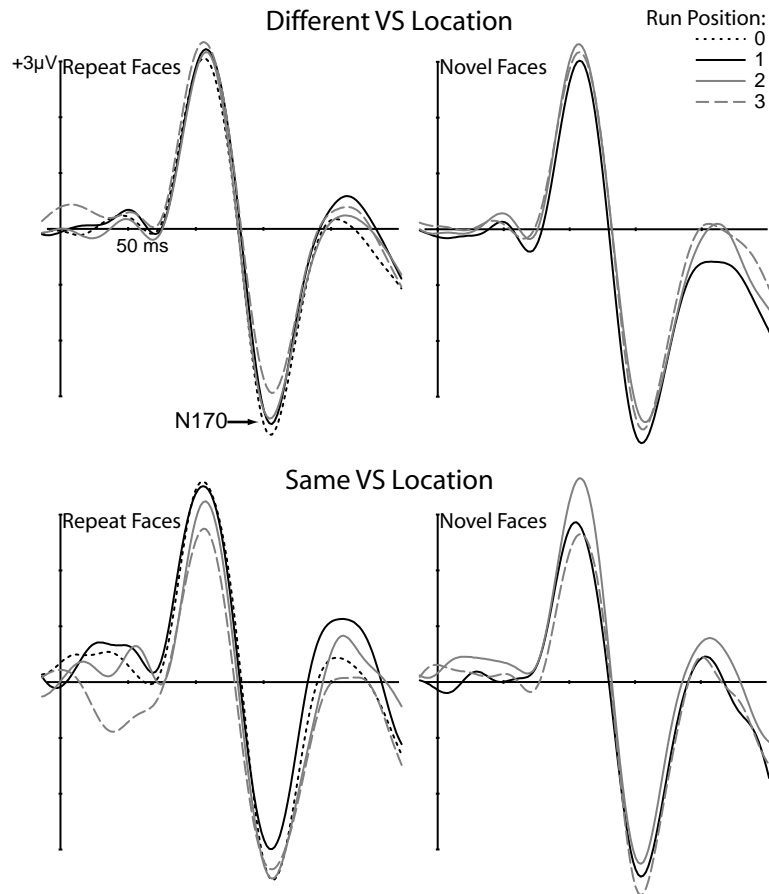
Fig. 3. Grand mean N170 component morphology for a representative example electrode (midpoint of O2 and O10 sites in the 10–20 system) for repeat vs. novel faces at same vs. different visuospatial (VS) locations, over sequential run positions. Run position 0 for repeated faces represents the first presentation of a subsequently repeated face stimulus, and represents an equivalently novel face to those in all run positions of the novel face conditions. A progressive decrease in N170 amplitude over run position was observed for repeated faces at different visuospatial locations, but not for other conditions. N170 latency was unaffected by face identity and visuospatial location.

an increase in N170 amplitude for run position 2. These observations were supported by a three-way interaction of hemisphere, face identity, and location, $F(2,20) = 4.20$, $\varepsilon = 0.87$, $p < 0.05$, and a marginal interaction between hemisphere, visuospatial location, and run position, $F(4,40) = 3.16$, $\varepsilon = 0.63$, $p = 0.05$.

Additional analyses were conducted to better explore the effect of sequential presentations of novel vs. repeated face stimuli on N170 peak amplitude. Two-way repeated-measures ANOVAs were conducted separately for combinations of location and face identity conditions with factors of electrode and run position. Only electrodes over the right hemisphere were included in this analysis. For repeated face identity conditions, N170 peak amplitude data from position 0 were included (the first presentation of a subsequently repeated face), to provide a baseline state equivalent to novel face presentation. Assessment of repeated face stimuli at different locations showed a significant decrease in the N170 peak amplitude response across run positions, $F(3,30) = 3.80$, $\varepsilon = 0.75$, $p < 0.05$. The linear contrast of run position was also significant, $F(1,10) = 7.34$, $p < 0.05$. Despite observable differences in the grandaverage waveforms for the initial repetition of

repeat face presented at the same locations, there was no significant run position effect for repeated face stimuli at same location across run position 0 through 4, $F(3,30) = 0.38$, $\varepsilon = 0.78$, $p = $ ns. To directly compare the decrease in N170 amplitude from run position 0 to run position 1, we performed a separate ANOVA on run position 0 and 1 with factors of hemisphere (left, right) and electrode (3). The decrease in N170 amplitude for the initial repetition of the face in the same location in the right hemisphere was supported by a marginal interaction between hemisphere and run position, $F(1, 10) = 3.99$, $\varepsilon = 1.00$, $p = 0.07$. In contrast, N170 peak amplitude did not reliably differ across run positions for novel faces presented at different locations, $F(2,20) = 0.17$, $\varepsilon = 0.99$, $p = $ ns, or same locations, $F(2,20) = 0.46$, $\varepsilon = 0.92$, $p = $ ns. Analyses of novel face conditions were repeated with data from an additional fourth run position included, and did not differ from the above results.

Peak latency measures of the N170 component, also well illustrated by the example electrode in Fig. 3, were also assessed. No main effects or interactions were observed for any combination of electrode, face identity, visuospatial location or run position.
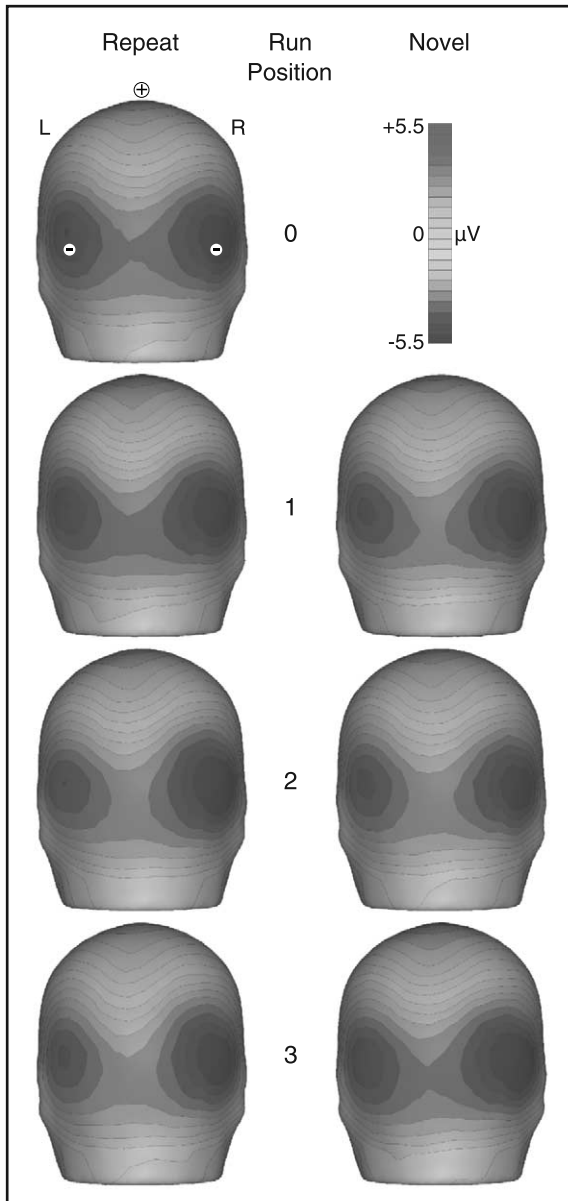
Fig. 4. Grand mean scalp topographies illustrating N170 amplitude effects at mean N170 peak latency of 155 ms. Scalp voltage distributions are displayed for sequential run positions for repeat vs. novel faces for stimuli presented at different visuospatial locations. This figure represents scalp distribution data corresponding to the top half of Fig. 3.

Fig. 5 shows the grand average ERP waveforms demonstrating the P3b component at electrode Cz, for repeat and novel faces presented at same and different locations. Overall, greater P3b mean amplitudes were elicited for faces presented in the same location (15.4 μV) than faces presented in different locations (8.1 μV), regardless of face identity, $F(1, 10) = 38.242$, $p < 0.001$. For face stimuli presented in same locations, a larger P3b mean amplitude response was observed for novel faces (16.9 μV) compared to repeated faces (13.9 μV). This effect was not observed for novel (7.9 μV) or repeat (8.2 μV) faces presented at different locations. This observation was supported by an interaction of face identity and visuospatial location, $F(1, 10) = 5.166$, $p < 0.05$.
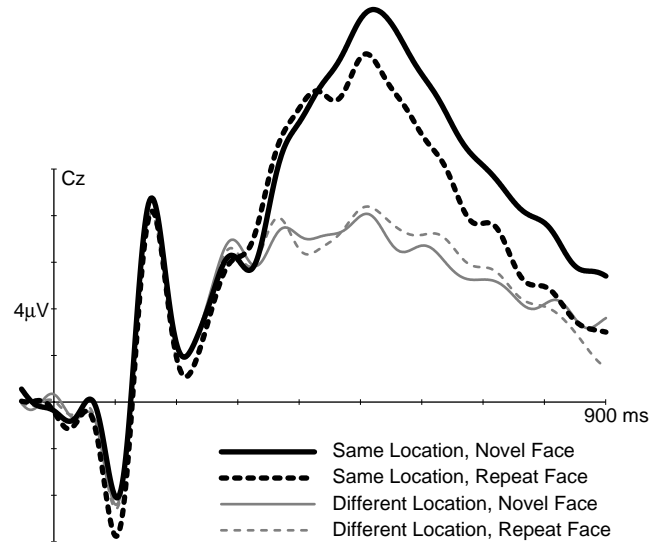

Fig. 5. Grand mean waveforms for electrode Cz demonstrating P3b morphology for novel vs. repeated faces at same vs. different visuospatial locations. Faces presented at same visuospatial locations elicited greater P3b amplitudes than stimuli at different spatial locations, with maximal amplitudes over the centroparietal midline. The P3b response differed selectively for novel vs. repeated faces presented at same visuospatial locations, with larger mean amplitudes for novel vs. repeated faces.

4. Discussion

The primary goal of this study was to determine whether the N170 ERP component response habituates with repeated face identity, akin to the response of the fusiform face area to identity repetition reported by Gauthier et al. (2000), and to control for and examine the effect that selective attention may have on such identity-specific face processing. Itier and Taylor (2002) previously observed a decrease in both N170 amplitude and latency for the immediate repetition of repeat face stimulus when face identity was the focus of the experimental task. In our study, subjects performed a 1-back location-matching task, similar to Gauthier et al. (2000), where face identity was irrelevant to the experimental task. Using an experimental paradigm that focused participants' controlled performance away from face identity, we observed a progressive decrease in N170 amplitude over four consecutive presentations of the repeat face stimulus, compared with no such decrease for sequentially presented novel faces. This progressive N170 habituation to repeated face identity only occurred when face stimuli were presented in different visuospatial locations relative to the previous stimulus.

Repeated exposure to an initially novel face appears to cause both a progressive habituation of FFA activity (as observed by Gauthier et al., 2000) as well as a similar habituation of the N170 amplitude response, when participants' attention is focused away from overtly considering face identity. This effect appears to be more difficult to observe when participants' attention is directed to the spatial location of a face stimulus, despite face identity being irrelevant to task demands. This is in keeping with Gauthier et al.'s (2000) suggestion that studying the effects of face familiarity

using identity-focused task demands may reduce or mask such habituation effects, and that task demands that do not require the overt evaluation of face identity may provide a more sensitive measure of face-specific processing. Indeed, simply attending to the location of a repeated face stimulus, despite performing a cognitive task unconcerned with face identity, appeared to be enough to reduce the habituation effect in the present study.

Although a progressive decrease in N170 amplitude over numerous stimulus repetitions was not observed at same spatial locations, an initial N170 peak amplitude decrement was observed for the first face repetition. This effect replicates the findings of previous studies of face repetition on the N170 (Campanella et al., 2000; Itier & Taylor, 2002) and FFA (Rotshtein et al., 2005; Winston et al., 2004) in tasks in which face evaluation was mandatory. Given that our task did not require evaluation of face identity, yet face identity appeared to selectively influence task performance at attended locations, our results suggest that faces appearing at selectively attended locations may engender some greater degree of identity processing independent of prevailing task demands. The absence of progressive habituation at attended locations adds further support to the idea that habituation caused by face repetition may be better observed when face identity is relatively unattended. Although it is likely that such habituation does occur for repeated faces at attended locations, the effects may be masked by an increased bias towards processing of face identity information, as discussed above.

These data also present a number of possibilities for the relationship between N170-related processes and the fusiform face area. It is possible that the progressive decrease in FFA activity with repeated face identity observed by Gauthier et al. (2000) may be due to habituation of earlier late-perceptual processing of structural face information indexed by the N170, providing a progressively decreasing input to more abstract semantic processing of face information in FFA, and not due to primary habituation of FFA processing itself. Alternately, processing in FFA may habituate with face repetition independent of reduced N170-related input, suggesting the possibility of a proportionately faster decline in FFA activity than in N170 amplitude response.

Although substantial N170 amplitude effects were observed in this study, no effects of face identity or location (or any other factor) were observed on N170 peak latency. This is in contrast to Itier and Taylor's (2002) findings of both smaller N170 amplitude and shorter N170 peak latency with the repetition of a previously novel face. These data initially suggest that task demands involving the selective evaluation of face identity may be necessary to produce the facilitation of face processing reflected by Itier and Taylor's (2002) shorter N170 latency with immediate identity repetition. Substantial changes in the speed of early face information processing, as reflected by N170 latency, may only be possible with selective, controlled performance (as in Itier & Taylor, 2002), while the current N170 latency

results reflect relatively constant processing efficiency in the absence of deliberate identity-focused task demands, regardless of the extent to which face identity information is processed for spatially attended vs. unattended faces. This lack of N170 peak latency differences, in the presence of substantial N170 amplitude effects, provides an independent indication of the success of our experimental design in focusing participants' selective attention away from evaluating face identity.

Both mean reaction time and P3b ERP component effects suggested that participants' selective attention was directed away from different-location face stimuli, further supporting our interpretation of N170 amplitude effects in these conditions. The mean reaction time data for novel vs. repeated faces at different vs. same positions, illustrated in Fig. 2, show that location-matching task performance was uninfluenced by face identity when face stimuli were presented at different locations, but that novel faces imparted a small but significant RT cost (18 ms) relative to repeated faces when face stimuli were presented at the same location. Additionally, a similar performance pattern observed for mean reaction time was observed for accuracy performance. This pattern of RT data supports the idea that participants were selectively attending to the most recent stimulus location, leading to same-location stimuli being consistently presented at the locus of spatial attention, while different-location stimuli were consistently presented at locations other than the locus of spatial attention. Such a cost to RT may be due to some degree of capture of selective attention by novel faces, given participants' pre-existing orientation to the location where the face stimulus was presented. Alternately, the source of such an RT cost for novel faces could possibly involve some degree of mismatch or conflict between the semantic representation of the task-relevant response *same* (same/different location decision) and the representation of face novelty (vs. repetition) at such an attended location—this *same-novel* mismatch relationship (where *novel* is conceptually akin to *different*), compared to a *same-repeat* match (where *repeat* is conceptually akin to *same*), might be considered similar to costs due to S-R incompatibility effects (e.g., Hedge & Marsh, 1975), or visual feature conjunction mismatches (Wang, Cui, Wang, Tian, & Zhang, 2004). Whatever the mechanism, the dissociation of RT effects between different and same visuospatial locations, coupled with the task-relevant demands of spatial location, suggests that selective attention was likely directed towards same visuospatial locations and away from different visuospatial locations during this task.

A notable P3b ERP component was also observed in this study and is illustrated in Fig. 5. The P3b amplitude effects support the interpretation of the reaction time data above. Substantially larger P3b amplitudes were observed for same-location trials compared with different-location trials, in keeping with typical expectations of the informational value and relative probability of target trials on P3b amplitude (e.g., Johnson, 1986, 1993). It is important to

note that the relative 1:3 occurrence of same vs. different response categories to which P3b is sensitive, is related to—but in practice very different from—same vs. different location stimulus probabilities. In the latter case, having three times as many spatial locations at which different-location trials may display stimuli vs. same-location trials leads to an equal (25%) stimulus expectancy at each of the four possible stimulus locations. In contrast, there is a 25% vs. 75% probability for subjects to make a keypress response to indicate a same vs. different stimulus category, as determined by task context.

In addition to this typical P3b effect, novel faces produced larger P3b amplitudes than repeated faces at the same spatial location, while no such difference was observed for different-location trials. This selective P3b amplitude effect of face identity at same locations suggests that novel faces were somehow more salient and/or processed to a greater degree than repeated faces, considering interpretations of P3b amplitude as an index of allocated processing capacity (Kramer & Strayer, 1988; Kramer, Strayer, & Buckley, 1991; Watter, Geffen, & Geffen, 2001; Wickens, Kramer, Vanasse, & Donchin, 1983). This is in contrast to an absence of such effects for the novel vs. repeated faces at different locations, suggesting that novel faces presented at same locations had some privileged access to selective processing, despite task demands which did not involve, nor benefit from, processing of face identity. In the absence of overt or deliberate consideration of face identity in our task, participants' selective attention appears to have been partially and/or temporarily captured by novel face stimuli, when such stimuli were presented at the locus of spatial attention. This interpretation is in keeping with the observed RT data, where novel faces at same locations made responding to the location matching task significantly slower than in all other conditions.

Taken all together, these data appear to converge well on a single interpretation supporting the dissociation of overt task performance effects seen in P3b amplitude and RT data from the effects of habituation of more automatic processing of face identity information observed in the N170 amplitude data. Larger P3b mean amplitudes and slower mean RTs for novel vs. repeated faces at same spatial locations, but not different spatial locations, suggest that novel face identity information interfered with task-relevant location-matching performance only when such stimuli were presented at the locus of spatial attention, and that the locus of spatial attention on a given trial was biased towards the same spatial location as the stimulus location of the previous trial. Given this bias of selective attention away from different spatial locations, the observation of N170 amplitude habituation effects with repetition of face identity at different but not same spatial locations makes a strong case that such effects represent a likely measure of automatic processing of face information at an individual level.

In summary, we have demonstrated that the N170 is sensitive to the repetition of face identity, akin to the sensitiv-

ity of the fusiform face area demonstrated by Gauthier et al. (2000). Whether the sensitivity of FFA activation to identity repetition is a direct and primary result of decreased input from N170-related processing, or whether FFA activity habituates to such repetition independently is a topic for further study. Attentional effects in both reaction time and ERP data suggest participants selectively attended to the location of the most recently presented face stimulus. Under these conditions, we believe that the progressive decrease in N170 amplitude for repeated vs. novel faces presented at different visuospatial locations represents a relatively purer measure of early automatic face processing than data from comparative tasks involving overt judgments of face familiarity.

References

Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences, 5*, 119–126.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*, 551–565.

Busey, T. A., & Vanderkrolk, J. R. (2005). Behavioral and electrophysiological evidence for configural processing in fingerprint experts. *Vision Research, 45*, 431–448.

Campanella, S., Hanoteau, C., Dépy, D., Rossion, B., Bruyer, R., Crommelinck, M., et al. (2000). Right N170 modulation in a face discrimination in a face discrimination task: An account for categorical perception of familiar faces. *Psychophysiology, 37*, 796–806.

Carmel, D., & Bentin, S. (2002). Domain specificity versus expertise: Factors influencing distinct processing of faces. *Cognition, 83*, 1–29.

Eimer, M. (2000a). The face-specific N170 component reflects late stages in the structural encoding of faces. *NeuroReport, 11*, 2319–2324.

Eimer, M. (2000b). Effects of face inversion on the structural encoding and recognition of faces: Evidence from event-related brain potentials. *Cognitive Brain Research, 10*, 145–158.

Gauthier, I., Curran, T., Curby, K. M., & Collins, D. (2003). Perceptual interference supports a non-modular account of face processing. *Nature Neuroscience, 6*(4), 428–432.

Gauthier, I, & Tarr, M. J. (1997). Becoming a "greeble" expert: Exploring mechanisms for face recognition. *Vision Research, 37*(12), 1673–1682.

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

George, N., Evans, J., Fiori, N., Davidoff, J., & Renault, B. (1996). Brain events related to normal and moderately scrambled faces. *Cognitive Brain Research, 4*, 65–76.

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

Guillaume, F., & Tiberghien, G. (2001). An event-related potential study of contextual modification in a face recognition task. *Neuroreport, 12*, 1209–1216.

Hedge, A., & Marsh, N. W. (1975). The effect of irrelevant spatial correspondence on two-choice response-time. *Acta Psychologica, 39*, 427–439.

Itier, R. J., & Taylor, M. J. (2002). Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: A repetition study using ERPs. *NeuroImage, 15*, 353–372.

Johnson, R., Jr. (1986). A triarchic model of P300 amplitude. *Psychophysiology, 23*, 367–384.

Johnson, R., Jr. (1993). On the neural generators of the P300 component of the event-related potential. *Psychophysiology, 30*, 90–97.

Johnson, K. E., & Mervis, C. B. (1997). Effects of varying levels of expertise on the basic level of categorization. *Journal of Experimental Psychology: General, 126*(3), 248–277.

Kramer, A. F., & Strayer, D. L. (1988). Assessing the development of automatic processing: An application of dual-task and event-related brain potential methodologies. *Biological Psychology, 26*, 231–267.

Kramer, A. F., Strayer, D. L., & Buckley, J. (1991). Task versus component consistency in the development of automatic processing: A psychophysiological assessment. *Psychophysiology, 28*, 1425–1437.

Mondloch, C., Geldart, S., Maurer, D., & Le Grand, R. (2003). Developmental changes in face processing skills. *Journal of Experimental Child Psychology, 86*, 67–84.

Rossion, B., Delvenne, J. F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., et al. (1999). Spatio-temporal localization of the face inversion effect: An event-related potentials study. *Biological Psychology, 50*, 173–189.

Rossion, B., Gauthier, I., Goffaux, V., Tarr, M. J., & Crommelinck, M. (2002). Expertise training with novel objects leads to left-lateralized facelike electropsychological responses. *Psychological Science, 13*(3), 250–257.

Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., et al. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not inverted objects: An electrophysiological account of face-specific processes in the human brain. *NeuroReport, 11*, 69–74.

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

Tanaka, J. W. (2001). The entry point of face recognition: Evidence for the face expertise. *Journal of Experimental Psychology: General, 130*, 534–543.

Tanaka, J. W., & Curran, T. (2001). A neural basis for expert object recognition. *Psychological Science, 12*, 43–47.

Tanaka, J. W., Luu, P., Weisbrod, M., & Kiefer, M. (1999). Tracking the time course of object categorization using event-related potentials. *NeuroReport, 10*, 829–835.

Watter, S., Geffen, G. M., & Geffen, L. B. (2001). The n-back as a dual-task: P300 morphology under divided attention. *Psychophysiology, 38*, 998–1003.

Wang, Y., Cui, L., Wang, H., Tian, S., & Zhang, X. (2004). The sequential processing of visual feature conjunction mismatches in the human brain. *Psychophysiology, 41*, 21–29.

Wickens, C., Kramer, A., Vanasse, L., & Donchin, E. (1983). The performance of concurrent tasks: A psychophysiological analysis of the reciprocity of information processing resources. *Science, 221*, 1080–1082.

Winston, J. S., Henson, R. N. A., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and emotion in face perception. *Journal of Neurophysiology, 92*, 1830–1839.