

Activation of Preexisting and Acquired Face Representations: The N250 Event-related Potential as an Index of Face Familiarity

James W. Tanaka¹, Tim Curran², Albert L. Porterfield³,
and Daniel Collins²

Abstract

■ Electrophysiological studies using event-related potentials have demonstrated that face stimuli elicit a greater negative brain potential in right posterior recording sites 170 msec after stimulus onset (N170) relative to nonface stimuli. Results from repetition priming paradigms have shown that repeated exposures of familiar faces elicit a larger negative brainwave (N250r) at inferior temporal sites compared to repetitions of unfamiliar faces. However, less is known about the time course and learning conditions under which the N250 face representation is acquired. In the familiarization phase of the Joe/no Joe task, subjects studied a target “Joe” face (“Jane” for female subjects) and, during the course of the experiment, identified a series of sequentially presented faces as either

Joe or not Joe. The critical stimulus conditions included the subject’s own face, a same-sex Joe (Jane) face and a same-sex “other” face. The main finding was that the subject’s own face produced a focal negative deflection (N250) in posterior channels relative to nontarget faces. The task-relevant Joe target face was not differentiated from other nontarget faces in the first half of the experiment. However, in the second half, the Joe face produced an N250 response that was similar in magnitude to the own face. These findings suggest that the N250 indexes two types of face memories: a preexperimentally familiar face representation (i.e., the “own face”) and a newly acquired face representation (i.e., the Joe/Jane face) that was formed during the course of the experiment. ■

INTRODUCTION

During the course of the day, we encounter scores of new people and new faces, the identities of whom soon fade from memory and are quickly forgotten. However, some faces engage our attention and are encoded as more permanent representations that are accessed during recognition. Indeed, it has been estimated that by the time we reach adulthood, we can recognize hundreds, if not thousands of different individual faces (Bruce & Valentine, 1985). Although the human capacity for storing face memories is remarkable, relatively little is known about the learning conditions and neurophysiological mechanisms that precipitate the acquisition of new face representations. To address this question, we employed event-related potentials (ERPs) to compare the neurophysiological response to a preexperimentally familiar face (the subject’s own face), an unfamiliar face (Joe) whose individual identity is learned during the course of the experiment, and an unfamiliar (Other) face whose identity is not individuated. The goal of this re-

search is to identify the neurophysiological components that mediate the activation of preexisting face memories and the acquisition of new face representations.

In the ERP literature, it has been well established that an enhanced negative deflection in posterior recording channels is produced approximately 170 msec post-stimulus onset in response to face stimuli relative to other nonface objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Subsequent research has shown that the latency of the N170 can be delayed by inverting the face stimulus (Rossion et al., 2000) or by reversing its luminance values (Itier & Taylor, 2002). The amplitude of the N170 can be reduced by rearranging the internal facial features of a face (George, Evans, Fiori, Davidoff, & Renault, 1996) or filtering its low spatial frequency information (Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003).

Whereas manipulations of the physical properties of a face can alter the response characteristics of the N170, the psychological properties of a face regarding its familiarity have little impact on this component. Specifically, studies examining the influence of face familiarity have shown that the N170 response to faces of well-known celebrities and politicians (Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003; Bentin & Deouell, 2000;

¹University of Victoria, Canada, ²University of Colorado, ³Oberlin College

Eimer, 2000; Bentin et al., 1996) and familiar university professors (Herzmann, Schweinberger, Sommer, & Jentzsch, 2004) is equivalent to the N170 response to the faces of strangers. Given that the N170 does not differentiate familiar from unfamiliar faces, it has been proposed that this component indexes a structural representation of the general face category rather than a previously stored face representation (Bentin & Deouell, 2000; Eimer 2000; but see Caharel, Poiroux, & Bernard, 2002).

The earliest point at which memory-related face processes influence brain activity occurs at approximately 250 msec poststimulus onset. Results from repetition priming paradigms have shown that repeated exposures of familiar faces elicit a larger negative brainwave (N250r) at inferior temporal sites compared to repetitions of unfamiliar faces (Pfütze, Sommer, & Schweinberger, 2002; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002; Begleiter, Porjesz, & Wang, 1995; Schweinberger, Pfütze, & Sommer, 1995). The N250r is strongest when repetitions are immediate and use identical prime-target images (Schweinberger et al., 2002; Begleiter et al., 1995; Schweinberger et al., 1995) and its magnitude is significantly reduced when different views of the familiar face are presented or when the prime and target faces are separated by two or three intervening faces (Pfütze, et al., 2002). The face N250r effect is completely abolished when the prime and target faces are separated over many trials (Schweinberger, Huddy, & Burton, 2004). A more robust N250r effect is found if subjects view multiple presentations of the target face at study and this component is enhanced as the number of recognition trials increases at test (Itier & Taylor, 2004). ERP differences between familiar and unfamiliar faces have also been reported at a later time of about 400 msec poststimulus onset (Bentin & Deouell, 2000; Eimer, 2000; Paller, Gonsalves, Grabowecky, Bozic, & Yamada, 2000). These effects tend to have a broader scalp distribution than the temporal-occipital N250 and have been attributed to the semantic information associated with a familiar face (Paller et al., 2000). Thus, it has been proposed that the N250r is the earliest component that indexes a stored perceptual face representation in long-term memory (Pfütze et al., 2002; Schweinberger et al., 2002).

The Joe/No Joe Task

In the current study, the development of perceptual face memories was investigated in the Joe/no Joe task. Subjects studied an unfamiliar face (i.e., “Joe” for male subjects and “Jane” for female subjects) and were asked to monitor the target Joe (or Jane) face when presented with other unfamiliar faces and their own face (see Figure 1). The Own face was selected as a benchmark of preexperimental familiarity because it has been shown that relative to other familiar faces, one’s

own face is identified more quickly in a visual search task (Tong & Nakayama, 1999), shows greater hemispheric specialization (Keenan, Wheeler, Platek, Lardi, & Lassonde, 2003), and elicits enhanced fusiform gyrus activity (Kircher et al., 2001). To measure the potential acquisition of new face representations, the ERP response elicited by the task-relevant Joe (or Jane) face was compared to the response evoked by the Own and an unfamiliar Other face. Critically, the number of presentations of the Joe face, the subject’s own face, and the unfamiliar faces were equated in the Joe/no Joe task so that any differences between conditions can be attributed to either preexperimental familiarity or task relevancy rather than to differences in frequency of exposure within the experiment. To examine the acquisition of face representations over time, the N250 component in the first half of the experiment was compared to the N250 component in the second half across the Own, Joe, and Other conditions.

METHODS

Subjects

The 24 subjects (12 men) were undergraduate students at the University of Colorado at Boulder ranging in age from 18 to 28 years with a mean age of 20.79 years. The subjects were right-handed and had normal or corrected-to-normal visual acuity. Subjects were prescreened to ensure that they were not familiar with any of the other subjects in the study.

Materials

The stimuli were color images of the 24 subjects taken with a digital camera under fluorescent lighting conditions. Using the Adobe PhotoShop software package, the face stimuli were cropped, mounted on a neutral background, and scaled to an image size of 122 × 180 pixels. The images subtended visual angles of 3.0° × 4.8° in the horizontal and vertical dimensions, respectively. For counterbalancing purposes, the subjects/photographs were divided into two sets of 12 faces. The 12 faces within each set were rotated across the Own, Joe/Jane, and Other face conditions such that each face appeared only once in the Own, Joe/Jane, and Other conditions (see Figure 1A). Whereas the subject’s own face was the default assignment to the Own condition, faces in Joe/Jane and Other face conditions were assigned according to the subject’s sex (i.e., male faces were assigned to the Joe and Other conditions for male subjects and female faces were assigned to the Jane and “other” conditions for female subjects). The remaining nine face stimuli were used as filler trials and not used in analysis, but were equivalent to the Other condition from the subject’s perspective.

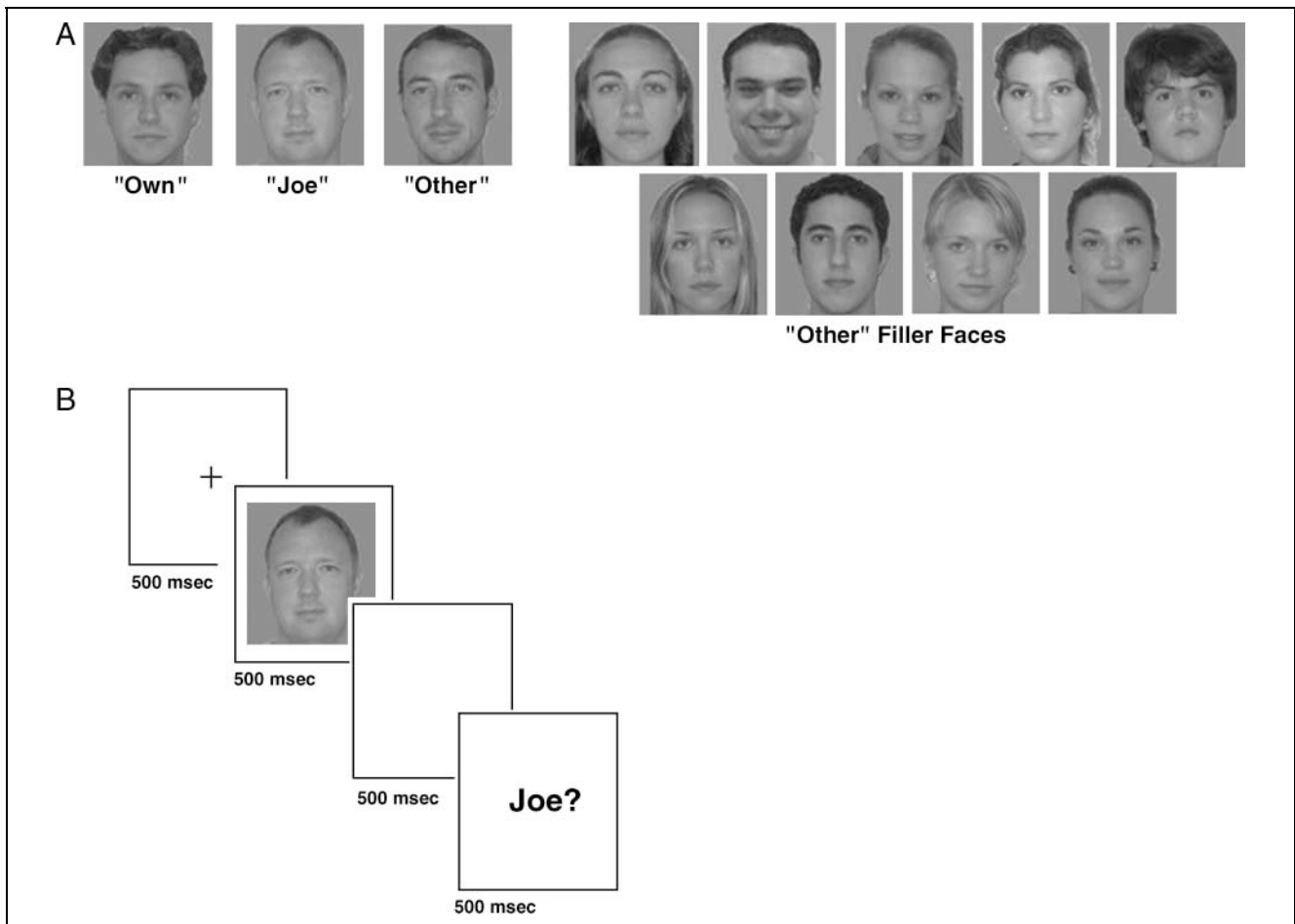


Figure 1. Description of the Joe/no Joe task. (A) In the learning phase, subjects studied a target Joe face (Jane for female subjects) and at test, categorized faces as either Joe or not Joe. The critical stimulus conditions included the subject's own face, a same-sex Joe (Jane) face and a same-sex Other face. The remaining nine Other face stimuli served as filler trials and were not used in analysis. (B) On each trial, subjects viewed a fixation cross followed by a face, a blank screen, and then a response screen at which point they were to respond via a keypress whether the face was the target Joe or not Joe.

Procedure

After the electroencephalogram (EEG) electrodes were applied, subjects viewed the 12 faces used in the study and were asked to verify that they were not familiar with any except their own face. Subjects were then shown the target Joe (Jane) face, matched according to their sex and asked to study it. They were told that their task was to decide whether each face presented during the experiment was or was not the target face.

Trial structure was as follows: A fixation cross was displayed (500 msec) followed by a face (500 msec) followed by a blank screen (500 msec). The "Joe?" ("Jane?") prompt then appeared at which subjects indicated their decision by pressing the appropriate key on the response pad (see Figure 1B). The delayed response paradigm was used to minimize motor-related effects in the ERP signal. Ten practice trials were completed before the experimental trials to ensure that the subjects understood the task.

Each subject completed 35 blocks of trials with self-paced rest breaks in between. Each block contained 24

trials—two presentations of each of the 12 faces. Before artifact rejection, each of the Own, Joe/Jane, and Other experimental conditions contained 70 critical trials.

EEG/ERP Methods

Scalp voltages were collected with a 128-channel Geodesic Sensor Net (Tucker, 1993) connected to an AC-coupled, 128-channel, high-input impedance amplifier (200 M Ω , Net Amps, Electrical Geodesics Inc., Eugene, OR). Amplified analog voltages (0.1–100 Hz band pass, –3 dB) were digitized at 250 Hz. Individual sensors were adjusted until impedances were less than 50 k Ω . The EEG was digitally low-pass filtered at 40 Hz. Trials were discarded from analyses if eye movements were detected (EOG greater than 70 μ V) or more than 20% of channels were bad (average amplitude greater than 100 μ V or transit amplitude greater than 50 μ V). Individual bad channels were replaced on a trial-by-trial basis with a spherical spline algorithm (Srinivasan, Nunez, Tucker, Silberstein,

& Cadusch, 1996). EEG was measured with respect to a vertex reference (Cz), but an average-reference transformation was used to minimize the effects of reference-site activity and accurately estimate the scalp topography of the measured electrical fields (Dien, 1998; Picton, Lins, & Scherg, 1995). Average-reference ERPs were computed for each channel as the voltage difference between that channel and the average of all channels. The average reference was corrected for the polar average reference effect (Junghöfer, Elber, Tucker, & Braun, 1999). ERPs were baseline corrected with respect to a 100-msec pre-stimulus recording interval.

RESULTS

Behavioral Results

Accuracy was at ceiling, with all conditions averaging 99% correct. Reaction time (RT), for accurate trials only, was analyzed in a Condition (Own, Joe, Other) \times Experiment Half (First, Second) repeated measures analysis of variance (ANOVA). When necessary in this and all subsequently reported ANOVAs, degrees of freedom were adjusted according to the conservative Greenhouse-Geisser procedure for sphericity violations (Winer, 1971). Recognition RT was significantly faster in the second ($M = 1297$ msec) than first ($M = 1363$ msec) half of the

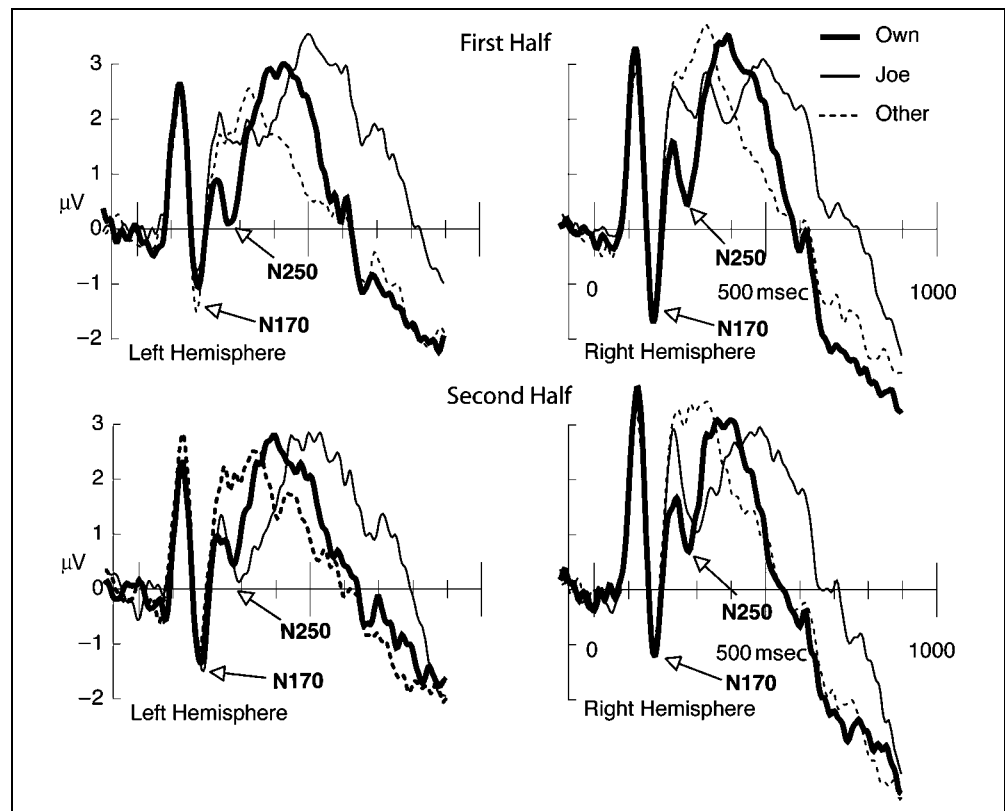
experiment, $F(1,23) = 43.36$, $MSE = 3619$, $p < .001$. The main effect of condition was also significant, $F(2,23) = 4.09$, $MSE = 1149$, $p < .05$. Follow-up contrasts indicated that only Joe ($M = 1320$ msec) and Other ($M = 1339$ msec) differed, with Own falling nonsignificantly in between ($M = 1330$ msec). The interaction did not approach significance.

ERP Results

N170 Results

Analyses focused on the locations where the N170 was maximal, channels 64 and 96 (see Figure 2). To allow for spatial variability across subjects and conditions, we averaged groups of channels surrounding the peak channels: left hemisphere, 57 (TP9), 58 (P9), 63, 64, 65, 69, 70; right hemisphere, 90, 91, 95, 96, 97 (P10), 100, 101 (TP10). These locations are consistent with previous N170 studies (e.g., Herzmann et al., 2004; Itier & Taylor, 2004; Schweinberger et al., 2002). N170 latency was determined as the time of the peak amplitude occurring within a 140- to 250-msec window and this value was entered into a Condition (Own, Joe, Other) \times Experiment Half (First, Second) \times Hemisphere repeated measures ANOVA. Mean latency was 176 msec, and no main effects or interactions approached significance.

Figure 2. Grand-average ERPs, averaged across channels used in the N170 and N250 analyses: left hemisphere, 57 (TP9), 58 (P9), 63, 64, 65, 69, 70; right hemisphere, 90, 91, 95, 96, 97 (P10), 100, 101 (TP10).



Amplitude analyses focused on these same regions. With peak amplitude as the dependent measure, no effects approached significance. There were also no significant effects when the dependent measure was mean amplitude between 145 and 206 msec ($M \pm 2SD$). In summary, the present conditions produced no detectable influence on N170 latency or amplitude.

N250 Results

The N250 analysis employed the same groups of channels as the N170 analysis (see Figure 2). Formal latency analyses were not possible because the N250 peak was not always discernable in individual subjects/conditions. Indeed, it is not discernable in even the grand averages of the Other condition. Thus, based on visual inspection of the grand averages, an analysis window of 230–320 msec was used to compute mean amplitude. The N250 was more negative in the left than right hemisphere, $F(1,23) = 8.17$, $MSE = 44.69$, $p < .01$. There were also differences between conditions, $F(2,23) = 18.95$, $MSE = 23.23$, $p < .001$, that were qualified by a condition by half interaction, $F(2,23) = 6.44$, $MSE = 10.66$, $p < .01$ (see Figure 3). Follow-up contrasts ($p < .01$, Bonferroni corrected for multiple comparisons) revealed that in the first half of the experiment, the N250 was more negative for Own ($M = .89 \mu V$, $SE = .42$) than Other ($M = 2.08 \mu V$, $SE = .42$) or Joe ($M = 2.42 \mu V$, $SE = .41$), but in the second half of the experiment, Own ($M = 1.11 \mu V$, $SE = .42$) and Joe ($M = 1.17 \mu V$, $SE = .39$) were both more negative than Other ($M = 2.89 \mu V$, $SE = .36$). The topographies of these face familiarity effects are shown in Figure 4, which displays ERP differences between the Own/Other and Joe/Other conditions at the time of the N250.

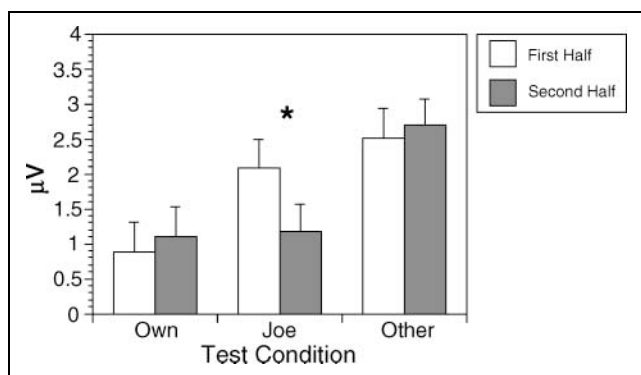


Figure 3. Bar graph showing the N250 (230- to 320-msec time window) at posterior channels (left hemisphere, 57, 58, 63, 64, 65, 69, 70; right hemisphere, 90, 91, 95, 96, 97, 100, 101) for the Own, Joe, and Other face conditions in the first versus second half of the experiment. The asterisk indicates a reliable difference between the first and second half for the Joe condition.

P300 Results

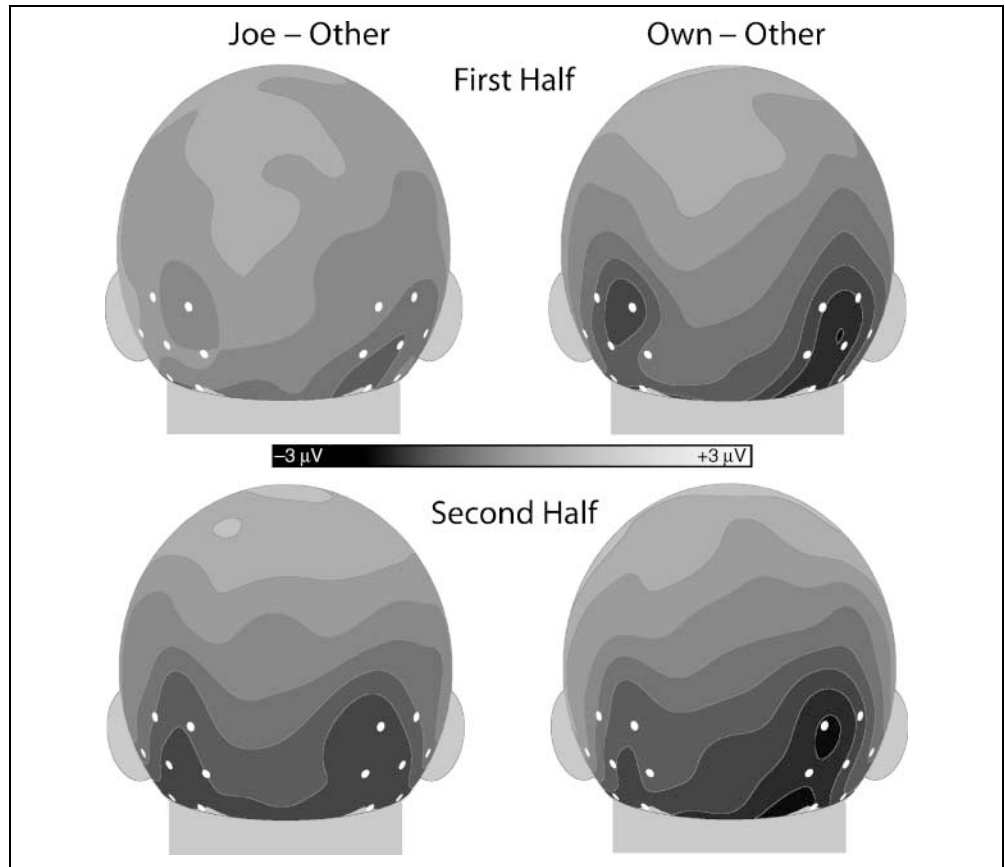
P300 latency was assessed at channel 62 (Pz). As readily seen in Figures 5 and 6, well-defined P300 components were observed only for the Own and Joe conditions, so only these conditions were included in the latency analyses. P300 latency was earlier in the Own ($M = 468$ msec) than Joe ($M = 532$ msec) conditions, $F(1,23) = 29.57$, $MSE = 3368$, $p < .001$. No effects involving experiment half were significant. Peak amplitude measures revealed no differences between these two conditions. A more reliable amplitude measure was obtained by calculating mean amplitude within separate windows around each peak ($M \pm 2SD$, SD computed across both conditions to equate window sizes): Joe = 452–612 msec, Own = 388–548 msec. Mean amplitude was greater for the Joe ($M = 6.15 \mu V$) than Own ($M = 4.13 \mu V$) conditions, $F(1,23) = 10.56$, $MSE = 9.23$, $p < .01$. Condition interacted marginally with experiment half, such that the difference between conditions tended to be larger in the second half of the experiment, $F(1,23) = 3.67$, $MSE = 4.68$, $p = .07$. As shown in Figures 5 and 6, both the Own and Joe condition have higher mean amplitude than the Other condition, $F_s > 68$, $p_s < .001$, when Joe/Own was compared to Other within their respective temporal windows.

As would be expected from the results showing that P300 latency increases with stimulus categorization/evaluation time (Kutas, McCarthy, & Donchin, 1977), latency was faster for the subject's own face than Joe's face. Presumably, subjects are quicker to identify their own face than Joe's face. It is likely that this difference was not reflected in RTs because of the delayed response paradigm used in this experiment. With regard to amplitude, we interpret the much larger P300 to Own and Joe than Other as consistent with previous research suggesting that P300 amplitude is increased by low stimulus probability (Joe = Own = 8.33%; other, including fillers that are equivalent from subjects' perspective = 83.33%) and attention (Duncan-Johnson & Donchin, 1977). The greater P300 amplitude to Joe than Own, a difference that tended to increase over the course of the experiment, probably reflects the fact that Joe was more task relevant, so subjects were more likely to attend to Joe throughout. It is also possible to interpret these P300 differences in terms of memory, because P300 amplitude is larger for remembered than nonremembered stimuli (reviewed by Curran, Tepe, & Piatt, 2006) and subjects would remember little about the other faces.

DISCUSSION

In the current experiment, we monitored ERPs while subjects viewed faces that included their own face, a target face (Joe or Jane), and other nontarget faces. With respect to the amplitude and latency of the N170

Figure 4. Topographic maps showing the mean N250 differences between conditions, 230–320 msec. The contours lines are displayed in 0.5- μ V steps. The back of the head is displayed, with dots marking the sensor locations included in the N250 analyses.



component, there were no differences between the familiar Own condition and the unfamiliar Joe/Jane and Other conditions. Consistent with previous studies (Jemel et al., 2003; Bentin & Deouell, 2000; Eimer, 2000; Bentin et al., 1996), these results demonstrated that the N170 was insensitive to differences in the familiarity of

the face stimuli. It was particularly striking that the subject's own face produced an N170 of similar amplitude and latency as that generated by completely novel faces (Joe and the nontarget faces). These results support the claim that the N170 component indexes a general category rather than the representation of a particular

Figure 5. Grand-average ERPs from selected 10-10 locations from the first half of the experiment.

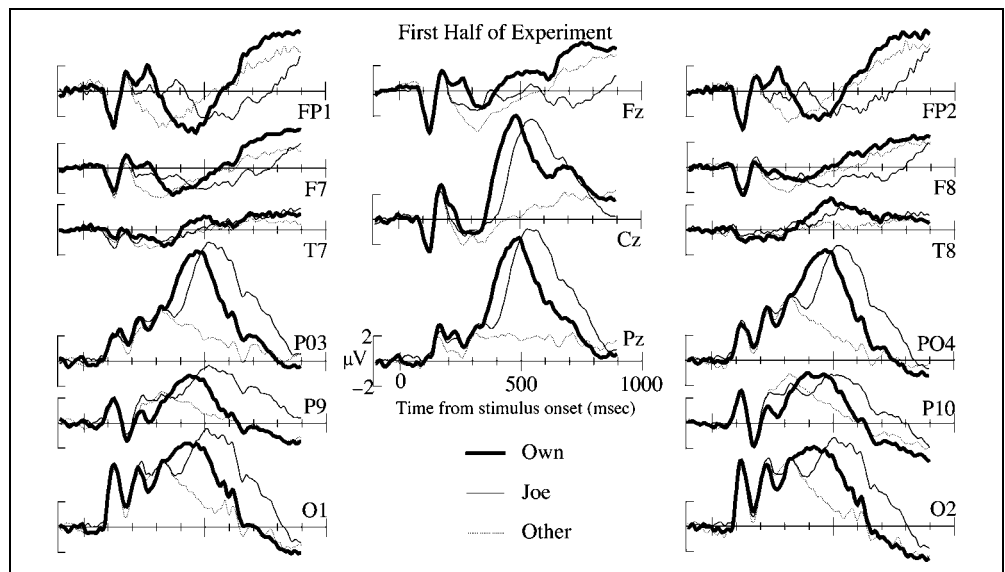
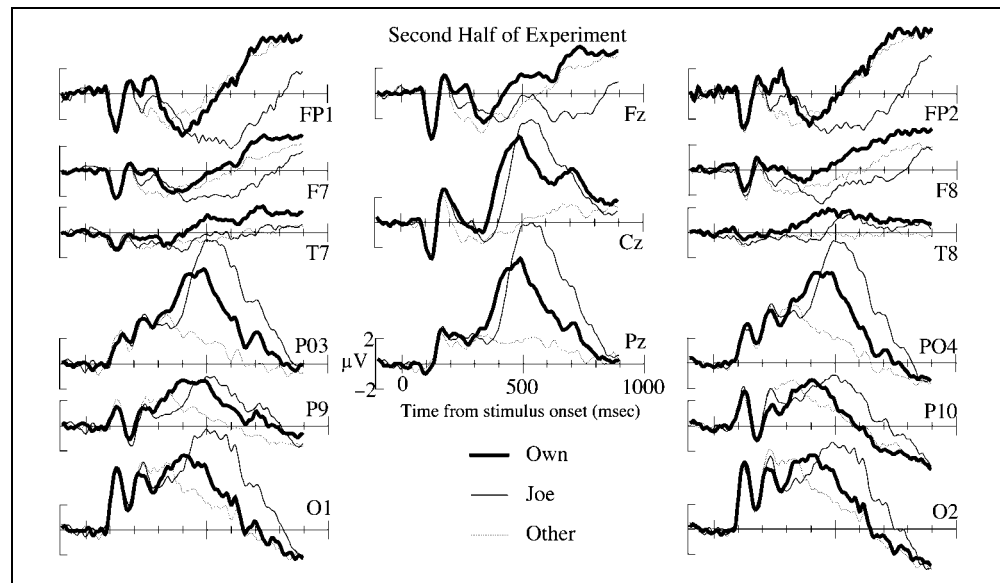


Figure 6. Grand-average ERPs from selected 10-10 locations from the second half of the experiment.



face (Bentin & Deouell, 2000; Eimer, 2000). This interpretation is consistent with other research suggesting that the N170 is sensitive to expert object domains (e.g., fingerprints, cars, birds) to which a person has extensive perceptual experience (Busey & Vanderkolk, 2005; Rossion, Kung, & Tarr, 2004; Gauthier, Curran, Curby, & Collins, 2003; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002; Tanaka & Curran, 2001).

Because of its preexperimental familiarity, the subject's own face produced a greater N250 compared to the unfamiliar Other faces and the Joe face in the first half of the experiment. The Own face response was stable across the first and second halves of the experiment. The current results are consistent with findings from repetition priming studies demonstrating that the N250 component is sensitive to different types of familiar faces, including famous faces (Schweinberger et al., 2002; Begleiter et al., 1995; Schweinberger et al., 1995), personally known faces (Herzmann et al., 2004), and experimentally learned faces (Itier & Taylor, 2004). Although subjects were ostensibly monitoring for the Joe/Jane face, their familiar, own face nevertheless elicited an enhanced N250 component.

Whereas the N250 component was responsive to the preexisting face representation of one's own face, it also was sensitive to the generation of a new representation of the target Joe face. In the first half of the experiment, the N250 to the Joe face was not differentiated from other nontarget faces. However, in the second half, the target Joe face produced a negative deflection that was similar in magnitude to the own face stimulus. This amplification of the N250 component suggests that a face representation of Joe was being formed and solidified over the course of the experiment. These results are similar to findings reported by Itier and Taylor (2004) who found in a repetition priming paradigm that the

N250 builds in response to repeated presentations of an upright, inverted, or contrast-reversed target face. In our Joe/no Joe paradigm, all faces were presented an equal number of times so the enhanced N250 to Joe, but not to Other faces, cannot be attributed strictly to the repeated exposure of a face stimulus. Nor was the Joe N250 exclusively a task-related effect because this component only emerged in the second half of the experiment (in contrast to P300 effects that differentiated Joe from others in the first and second half of the experiment). Instead, the acquired N250 demanded multiple exposures of the face stimulus and that the individuated face had to be task relevant. In future research, it would be important to know whether the N250 was specific to a particular face image (as shown in the current study) or robust across multiple images of the same person.

The observation that more learning trials were required for the N250 than P300 to discriminate Joe from Other may reflect the operation of distinct memory mechanisms. For instance, it has been hypothesized that the hippocampus learns rapidly from single trials, but the cortex learns slowly from multiple repetitions (McClelland, McNaughton, & O'Reilly, 1995). Previous research has suggested that explicit memory effects involving the P300 may be dependent upon the hippocampus (Curran, DeBuse, Woroch, & Hirshman, 2006; Duzel, Vargha-Khadem, Heinze, & Mishkin, 2001), so the hippocampus may similarly contribute to the present P300 effects. Source localization indicates that the N250 may have cortical origins in inferior temporal regions including the fusiform gyrus (Schweinberger et al., 2004; Schweinberger et al., 2002). The fact that the present N250 learning effects were observed for only Joe, but not for Other, is consistent with the perspective that error-driven cortical learning mechanisms are particularly suited for acquiring task-relevant

information (e.g., Joe) rather than merely learning from repetition (e.g., O'Reilly & Rudy, 2001).

Face familiarity effects have been investigated in functional magnetic resonance imaging (fMRI) studies where it has been shown that repeated exposures of well known, famous faces produce an attenuated response in the fusiform gyrus (Henson, Shallice, Gorno-Tempini, & Dolan, 2002; Henson, Shallice, & Dolan, 2000; Kanwisher, McDermott, & Chun, 1997). Repetition suppression effects have been attributed to the lowered thresholds required for activation of previously existing perceptual representations in contrast to repetition enhancement in response to the repeated presentations of unfamiliar faces (Henson et al., 2002). Although suppression effects are strongest for repetitions of identical face images, it is also found for repetitions of the same familiar person shown across multiple orientations, suggesting that this effect taps into a general representation of person identity (Eger, Schweinberger, Dolan, & Henson, 2005). The amount of suppression is also influenced by task demands where greater suppression effects are found when subjects are making decisions related to face identity (i.e., famous vs. nonfamous) rather than frequency (Henson et al., 2002). Repetition suppression effects in fMRI and N250 effects in ERPs are similar to the extent that both phenomena require the individuation of a previously known face or a recently familiarized face.

A much debated issue in the vision literature is whether the neural mechanisms mediating face perception are "special" to faces (Kanwisher, 2000) or whether they constitute a general form of perceptual expertise (Tarr & Gauthier, 2000). In ERPs, the component that has been most closely associated with face-specific processes is the N170 where a greater negative deflection is found to human faces compared to animal faces, hands, and furniture (Bentin & Deouell, 2000; Bentin et al., 1996). However, other studies have shown that the N170 is influenced by expertise; specifically, car, bird, and dog experts show a greater N170 to objects in their domain of expertise relative to novices (Gauthier et al., 2003; Tanaka & Curran, 2001). This raises the issue regarding whether the N250 is face specific. Evidence for the face selectivity of the N250 is provided by experiments showing that repetition of human faces elicited a larger negative response relative to faces of nonhuman monkeys and facelike stimuli, such as car grills (Schweinberger et al., 2004). However, a recent study by Scott, Tanaka, Sheinberg, and Curran (2006) suggests that the N250 is not face specific, but a general marker of perceptual expertise. In the Scott et al. study, subjects learned to classify birds at either the basic (owls, wading birds) or species (screech owl, green heron) level. Like the face N170, an increased N170 was found to both owl and wading bird stimuli regardless of basic or subordinate level learning. In contrast, an enhanced N250 was found only to those birds that were differentiated as individual

species (e.g., screech owl, green heron). It is possible that the N170 indexes basic-level category representations (faces, owls, wading birds), whereas the N250 taps into individual exemplars within a basic-level category (own face, Joe's face, screech owls, or green herons). However, because the Scott et al. study included only bird stimuli and not faces, the equivalence of the face N250 and the object N250 remains unclear.

To summarize, this study demonstrates that the N250 component is sensitive to two types of familiarity effects in face processing. The first type involves the robust activation of previously stored face representations (e.g., own face, famous faces) and is characterized by a stable N250 response. The second type reflects the plasticity of an acquired familiarity that accrues gradually over time and is marked by enhancement of the N250 component. We presume that it is the latter learning processes that contribute to the long-term memory representations of familiar faces. These results provide new insights into the neurophysiological mechanisms mediating the activation of preexisting face memories and formation of new face representations.

Acknowledgments

This research was supported by grants from the James S. McDonnell Foundation (Perceptual Expertise Network), the National Institutes of Health (MH64812-01) and the National Science and Engineering Research Council of Canada. We thank Gabriel Matthews, Trang Phan, Robby Siegel, Sarah Sutherland, Brion Woroch, and Brent Young for research assistance.

Reprint requests should be sent to either James Tanaka, Department of Psychology, University of Victoria, PO Box 3050, STN CSC, Victoria, BC, V8W 3P5, Canada or Tim Curran, Department of Psychology, University of Colorado, Campus Box 345, Boulder, CO 80309-0345, USA, or via e-mail: jtanaka@uvic.ca (J. Tanaka), tcurran@buffmail.colorado.edu (T. Curran).

REFERENCES

- Begleiter, H., Porjesz, B., & Wang, W. Y. (1995). Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces. *Electroencephalography and Clinical Neurophysiology*, *94*, 41–49.
- 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.
- Bentin, S., & Deouell, L. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanism. *Cognitive Neuropsychology*, *17*, 35–54.
- Bruce, V., & Valentine, T. (1985). Identity priming in the recognition of familiar faces. *British Journal of Psychology*, *76*, 373–383.
- Busey, T. A., & Vanderkolk, J. R. (2005). Behavioral and electrophysiological evidence for configural processing in fingerprint experts. *Vision Research*, *45*, 431–448.
- Caharel, S., Poiroux, S., & Bernard, C. (2002). ERPs associated with familiarity and degree of familiarity during face recognition. *International Journal of Neuroscience*, *112*, 1531–1544.

- Curran, T., DeBuse, C., Woroch, B., & Hirshman, E. (2006). Combined pharmacological and electrophysiological dissociation of familiarity and recollection. *Journal of Neuroscience*, *26*, 1979–1985.
- Curran, T., Tepe, K. L., & Piatt, C. (2006). ERP explorations of dual processes in recognition memory. In H. D. Zimmer, A. Mecklinger, & U. Lindenberger (Eds.), *Binding in human memory: A neurocognitive approach* (pp. 467–492). Oxford: Oxford University Press.
- Dien, J. (1998). Issues in the application of the average reference: Review, critiques, and recommendations. *Behavior Research Methods, Instruments and Computers*, *30*, 34–43.
- Duncan-Johnson, C. C., & Donchin, E. (1977). On quantifying surprise: The variation of event-related potentials with subjective probability. *Psychophysiology*, *14*, 456–467.
- Duzel, E., Vargha-Khadem, F., Heinze, H. J., & Mishkin, M. (2001). Brain activity evidence for recognition without recollection after early hippocampal damage. *Proceedings of the National Academy of Sciences, U.S.A.*, *98*, 8101–8106.
- Eger, E., Schweinberger, S. R., Dolan, R. J., & Henson, R. N. (2005). Familiarity enhances invariance of face representations in human ventral visual cortex: fMRI evidence. *Neuroimage*, *26*, 1128–1139.
- Eimer, M. (2000). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, *111*, 694–705.
- Gauthier, I., Curran, T., Curby, K. M., & Collins, D. (2003). Perceptual interference supports a non-modular account of face processing. *Nature Neuroscience*, *6*, 428–432.
- 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.
- Goffaux, V., Jemel, B., Jacques, C., Rossion, B., & Schyns, P. G. (2003). ERP evidence for task modulations on face perceptual processing at different spatial scales. *Cognitive Science*, *27*, 313–325.
- Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, *287*, 1269–1272.
- Henson, R., Shallice, T., Gorno-Tempini, M. L., & Dolan, R. J. (2002). Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cerebral Cortex*, *12*, 178–186.
- Herzmann, G., Schweinberger, S. R., Sommer, W., & Jentsch, I. (2004). What's special about personally familiar faces? A multimodal approach. *Psychophysiology*, *41*, 688–701.
- Itier, R. J., & Taylor, M. J. (2002). Inversion and contrast polarity reversal effect both encoding and recognition processes of unfamiliar faces: A repetition study using ERPs. *Neuroimage*, *15*, 353–372.
- Itier, R. J., & Taylor, M. J. (2004). Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs. *Neuroimage*, *21*, 1518–1532.
- Jemel, B., Pisani, M., Calabria, M., Crommelinck, M., & Bruyer, R. (2003). Is the N170 for faces cognitively penetrable? Evidence from repetition priming of Mooney faces of familiar and unfamiliar persons. *Cognitive Brain Research*, *17*, 431–446.
- Junghöfer, M., Elber, T., Tucker, D. M., & Braun, C. (1999). The polar average reference effect: A bias in estimating the head surface integral in EEG recording. *Clinical Neurophysiology*, *110*, 1149–1155.
- Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, *3*, 759–763.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Keenan, J. P., Wheeler, M., Platek, S. M., Lardi, G., & Lassonde, M. (2003). Self-face processing in a callosotomy patient. *European Journal of Neuroscience*, *18*, 2391–2395.
- Kircher, T. J., Senior, C., Phillips, M. L., Rabe-Hesketh, S., Benson, P. J., Bullmore, E. T., Brammer, M., Simmons, A., Bartels, M., & David, A. S. (2001). Recognizing one's own face. *Cognition*, *78*, B1–B15.
- Kutas, M., McCarthy, G., & Donchin, E. (1977). Augmenting mental chronometry: The P300 as a measure of stimulus evaluation time. *Science*, *197*, 792–795.
- McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, *102*, 419–457.
- O'Reilly, R. C., & Rudy, J. W. (2001). Conjunctive representations in learning and memory: Principles of cortical and hippocampal function. *Psychological Review*, *108*, 311–345.
- Paller, K. A., Gonsalves, B., Grabowecky, M., Bozic, V. S., & Yamada, S. (2000). Electrophysiological correlates of recollecting faces of known and unknown individuals. *Neuroimage*, *11*, 98–100.
- Pfütze, E. M., Sommer, W., & Schweinberger, S. R. (2002). Age-related showing in face and name recognition: Evidence from event-related brain potentials. *Psychology and Aging*, *17*, 140–160.
- Picton, T. W., Lins, O. G., & Scherg, M. (1995). The recording and analysis of event-related potentials. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (vol. 10, pp. 3–73). Amsterdam: Elsevier.
- Rossion, B., Gauthier, I., Goffaux, V., Tarr, M. J., & Crommelinck, M. (2002). Expertise training with novel objects leads to left-lateralized facelike electrophysiological responses. *Psychological Science*, *13*, 250–257.
- Rossion, B., Gauthier, I., Tarr, M. J., Depland, 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., Kung, C. C., & Tarr, M. J. (2004). Visual expertise with nonface objects leads to competition with the early perceptual processing of faces in the human occipitotemporal cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *101*, 14521–14526.
- Schweinberger, S. R., Huddy, V., & Burton, A. M. (2004). N250r: A face-selective brain response to stimulus repetitions. *NeuroReport*, *15*, 1501–1505.
- Schweinberger, S. R., Pfütze, E. M., & Sommer, W. (1995). Repetition priming and associative priming of face recognition: Evidence from event-related potentials. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 722–736.
- Schweinberger, S. R., Pickering, E. C., Jentsch, I., Burton, A. M., & Kaufmann, J. M. (2002). Event-related brain potential evidence for a response of inferior temporal

- cortex to familiar face repetitions. *Cognitive Brain Research*, *14*, 398–409.
- Scott, L. S., Tanaka, J. W., Sheinberg, D. L., & Curran, T. (2006). A reevaluation of the electrophysiological correlates of expert object processing. *Journal of Cognitive Neuroscience*, *18*, 1453–1465.
- Srinivasan, R., Nunez, P. L., Tucker, D. M., Silberstein, R. B., & Cadusch, P. J. (1996). Spatial sampling and filtering of EEG with spline Laplacians to estimate cortical potentials. *Brain Topography*, *8*, 355–366.
- Tanaka, J. W., & Curran, T. (2001). The neural basis of expert object recognition. *Psychological Science*, *16*, 145–151.
- Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience*, *3*, 764–769.
- Tong, F., & Nakayama, K. (1999). Robust representations for faces: Evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 1016–1035.
- Tucker, D. (1993). Spatial sampling at head electrical fields: The geodesic sensor net. *Electroencephalography & Clinical Neurophysiology*, *87*, 154–163.
- Winer, B. J. (1971). *Statistical principles in experimental design* (2nd ed.). New York: McGraw-Hill.