

The timing of individual face recognition in the brain

Xin Zheng, Catherine J. Mondloch^{**}, Sidney J. Segalowitz^{*}

Department of Psychology, Brock University, 500 Glenridge Avenue, St. Catharines, Ontario L2S 3A1, Canada

ARTICLE INFO

Article history:

Received 30 March 2011
Received in revised form 29 October 2011
Accepted 23 February 2012
Available online 5 March 2012

Keywords:

Electroencephalography
ERPs
Face perception
Face space
N170
P2
N250

ABSTRACT

Previous neural research on face perception has mainly focused on the distinction between faces and non-face stimuli. However, the brain mechanisms for differentiating one face from another are not well understood. In the present study, using scalp-recorded event-related potentials (ERPs), we investigated the brain responses to faces that varied in identity strength as a result of morphing individual faces to an “average” face in steps of 10%. Participants performed a face identification task. Behavioral results showed categorical boundaries of face identification at 30% and 70%. Face identity strength related to initial brain responses occurring shortly after 200 ms in the ventral P2 and the N250 components: stronger identity strength was associated with a smaller P2 and a larger N250. In contrast, the brain responses within 200 ms, as reflected by the P1, the N170, and the dorsal P2 component, were not affected by face identity strength. Consistent with recent imaging studies and animal research, our results provide the ERP evidence for brain responses to variations in face identity strength relative to an “average” face. Furthermore, with the high temporal resolution of ERPs, our results help to clarify the timing of neural events that are associated with the different stages involved in recognizing individual faces, thus providing a timeline for the classical face recognition model in the brain.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Numerous behavioral and neuropsychological studies have provided evidence that adults' perception of faces is different from their processing of other visual stimuli. Adults rapidly detect that a stimulus is a face even when realistic features are not physically present, so long as the face-like configuration of two eyes above a nose above a mouth can be inferred. For example, they can see a face in paintings by Archimbaldo consisting of only fruits and vegetables and in two-tone Mooney stimuli in which black and white shadows lead to the perception of a face. Adults process faces holistically (Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987) and are sensitive to small differences among faces in the shape of individual features and the spacing among them (Freire, Lee, & Symon, 2000; Mondloch, Le Grand, & Maurer, 2002; reviewed in Maurer, Le Grand, & Mondloch, 2002). Collectively, these behavioral skills allow adults to extract a wealth of information each time they encounter a human face (e.g., age, race, gender, emotional expression). Most notably, adults are able to recognize the identity of hundreds of faces at a glance and they can do so under poor lighting conditions, from numerous viewpoints, and after a

face has aged by several years, at least for the kinds of faces they encounter on a daily basis (e.g., upright same-race faces).

Although behavioral researchers have investigated each aspect of face perception quite thoroughly, neural research on face processing with both humans and non-human primates has primarily investigated the neural markers that distinguish faces from non-face objects (Allison et al., 1994; Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bötzel, Schulze, & Stodieck, 1995; Desimone, Albright, Gross, & Bruce, 1984; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Perrett, Rolls, & Caan, 1982; Puce, Allison, Gore, & McCarthy, 1995; Rolls & Baylis, 1986; Tsao, Freiwald, Tootell, & Livingstone, 2006). As a result, several brain regions (e.g., middle fusiform gyrus, inferior occipital gyrus, and superior temporal sulcus) and electrophysiological signals (e.g., the intracortical N200 and the scalp-recorded N170) have been found to respond more strongly to faces than to non-face objects. In contrast to the face versus non-face distinction, however, much less is known about the neural mechanisms underlying the perception and recognition of individual faces within the face category.

To account for adults' expertise in face recognition, Valentine (1991) proposed a norm-based coding mechanism, a process by which individual faces are compared to a norm (prototype) that represents the average of all faces previously encountered. In his model, each face is represented as a point in a multi-dimensional face space; the origin of the face space corresponds to the prototypical face and the location of each face represents how and how much that face deviates from the average. Faces near the norm are

^{*} Corresponding author. Tel.: +1 905 688 5550x3465; fax: +1 905 688 6922.

^{**} Corresponding author. Tel.: +1 905 688 5550x5111; fax: +1 905 688 6922.

E-mail addresses: cmondloch@brocku.ca (C.J. Mondloch),
sid.segalowitz@brocku.ca (S.J. Segalowitz).

rated as more typical/attractive than faces that are far from the norm and they are categorized more quickly in a face/nonface task. In contrast, faces far from the norm are recognized more quickly than typical faces, perhaps because they reside in a less populated area of face space (Valentine & Bruce, 1986; but see Burton & Vokey, 1998, for evidence suggesting that distance from the norm and local density may be sufficient to produce differences in the recognition of typical versus distinctive faces).

Recently, two studies have tested Valentine's norm-based model at a neural level. Their results indicate that neural activity increases as a function of face identity strength, i.e., as a function of how much individual faces differ from an average face (Leopold, Bondar, & Giese, 2006; Löffler, Yourganov, Wilkinson, & Wilson, 2005). In each study, identity strength was manipulated by varying the relative weighting of an individual face versus the average face. Using synthetic faces of different identities, Löffler et al. (2005) reported greater BOLD responses from fusiform face area (FFA) as identity strength increased. Löffler et al. concluded that the BOLD response elicited by a face reflects the distance of the face from the average face because (a) the BOLD response did not increase as a function of the distance from a non-average face and (b) adaptation to a single facial identity reduced the BOLD response to other faces along the same identity trajectory, but not to faces along different trajectories. Similarly, in a single-cell recording study with monkeys, Leopold et al. (2006) found that neural responses from anterior inferotemporal cortex became stronger as face identity strength increased. Although these studies indicate that the magnitude of neural activity may code for identity strength, which is consistent with Valentine's norm-based coding model, the temporal parameters of individual face perception remain unclear. The goal of the current study was to examine the timing of brain responses to face identity strength using scalp-recorded ERPs.

There is some evidence that the face-sensitive N170 component, traditionally interpreted as a neural marker for structural encoding of faces (Eimer, 2000b), may also be sensitive to visual face identities. When the same identity is presented on consecutive trials, the amplitude of the N170 is reduced relative to when two different identities are presented (Caharel, Jiang, Blanz, & Rossion, 2009; Campanella et al., 2000; Jacques & Rossion, 2006; Jacques, d'Arripe, & Rossion, 2007; but see Schweinberger, Huddy, & Burton, 2004; Schweinberger, Pickering, Burton, & Kaufmann, 2002), even when the viewpoints are different across presentations (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009). This adaptation effect on N170 may occur as early as 160 ms post face onset (Caharel, d'Arripe, et al., 2009; Caharel, Jiang, et al., 2009; Jacques et al., 2007). In addition, when a face discrimination task was made more difficult by rotating the faces away from their canonical upright orientation, N170 amplitude increased along with error rates and reaction times (Jacques & Rossion, 2007).

However, these immediate repetition effects on the N170 may not indicate that the N170 reflects individual face recognition; rather, the N170 may reflect the processing of individual facial characteristics (Eimer, 2000b; Zheng, Mondloch, Nishimura, Vida, & Segalowitz, 2011), and adaptation to the face category (Eimer, Kiss, & Nicholas, 2010). First, although N170 adaptation for upright faces is larger when the adaptor is a face than when the adaptor is a house, N170 adaptation occurs when the test face is preceded by an adaptor stimulus of a different facial identity and the magnitude of this effect is independent of whether the adaptor is an upright face, an inverted face, a face without eyes, or eyes only (Eimer et al., 2010; see Harris & Nakayama, 2007, 2008, for similar results using MEG technology). Second, N170 is not influenced by face identity when faces are presented in a random order; under these conditions only later ERP components are influenced by identity (Bentin & Deouell, 2000; Eimer, 2000a; Gosling & Eimer, 2011; Kaufmann, Schweinberger, & Burton, 2008; Rossion et al., 1999;

Tanaka, Curran, Porterfield, & Collins, 2006). Given that the priming effects on later ERP components are robust even when the prime (e.g., a picture of Nancy Reagan) shares no facial characteristics with the target (e.g., Ronald Reagan) (Schweinberger, Pfütze, & Sommer, 1995), it is thus possible that modulation of the N170 reflects brain processes related to the encoding of facial characteristics (Eimer, 2000b; Zheng et al., 2011) and that modulation of later components (e.g., N250) reflects brain processes related to the visual recognition of a face.

To further explore the temporal parameters of visual face recognition we adopted a method previously used to study the influence of face identity on the BOLD signal (Löffler et al., 2005) and single-cell activity (Leopold et al., 2006). Specifically, we investigated the influence of variation in identity strength relative to an average face on the magnitude of early ERP components (P1, N170, P2, N250). We manipulated face identity strength by first constructing an "average" face based on 32 individual female faces; each individual face was then morphed with this "average" face to produce continua of face identity (Fig. 1a and b). The relative weighting of an original face in these morphed faces ranged from 100% to 0% in 10% decrements. Participants performed a face identification task, in which they were instructed to press a button whenever they felt that they had detected a target face or a face that looked like a target face (see Fig. 1c). We predicted that the amplitude of one or more ERP components would increase with identity strength. Our primary question was whether this effect would be observed as early as in the N170 or only in later components.

2. Materials and methods

2.1. Participants

Seventeen Caucasian female undergraduate students (mean age = 20.4 ± 1.5 years) at Brock University participated in the current ERP study for either a research credit or a \$15 honorarium. All participants were right-handed native English speakers with normal or corrected-to-normal vision. No participants reported any neurological disorders, psychiatric history, or attentional problems. The experimental procedures were approved by Brock University Research Ethics Board, and written informed consent was obtained from all participants.

2.2. Stimuli

The experimental stimuli included 36 individual female faces (original) unknown to participants (see Supplementary Fig. 1 for the complete set of face stimuli) and their morphed versions that were created by gradually morphing each original face with an "average" of the 32 individual faces in steps of 10% using Norrkross MorphX software. Four faces and their morphed versions served as targets in a face identification task, and the other 32 faces and their morphed versions served as non-targets. The "average" face was constructed using non-target original faces (see Supplementary Text 1 for details). For each original-average face pair, over 140 reference points were placed at various regions (e.g., eyes, eye brows, nose, mouth, cheeks, and face contour) on both faces (see Fig. 1a for the placement of reference points for an original-average face pair). Based on these reference points, the original faces (including both target and non-target faces) were morphed with the "average" face in steps of 10% to generate continua of morphed faces that vary in the amount of identity strength they carry, ranging from 100% (i.e., an original face) to 0% (i.e., the "average" face in this study) (see Fig. 1b for an example).

A black background with a diamond-shape cut out in the middle was placed on top of each face stimulus to exclude non-facial information (e.g., hair); the position of a face stimulus within the outline was vertically adjusted so that the eye region was at approximately the same level and did not differ systematically across faces that varied in face identity strength. In addition, because the overall average face was based on the averaging of 32 original faces, it appeared to be smooth and slightly blurry. As a result, the "smoothness" and "blurriness" of the morphed faces increased as facial identity decreased. To address this issue, we applied a Gaussian filter to each face stimulus using Adobe® Photoshop® software. The radius of filtering ranged from 0.1 to 1.0. The original faces were filtered to the maximum degree with less filtering applied as identity strength decreased. All face stimuli were approximately equal in size (7.4–8.1 cm for width; 9.2–10.8 cm for height) and viewed at a distance of 100 cm, subtending a visual angle of 2.4° – 2.6° (horizontally) by 2.9° – 3.4° (vertically); the faces along the same identity trajectory are equal in size.

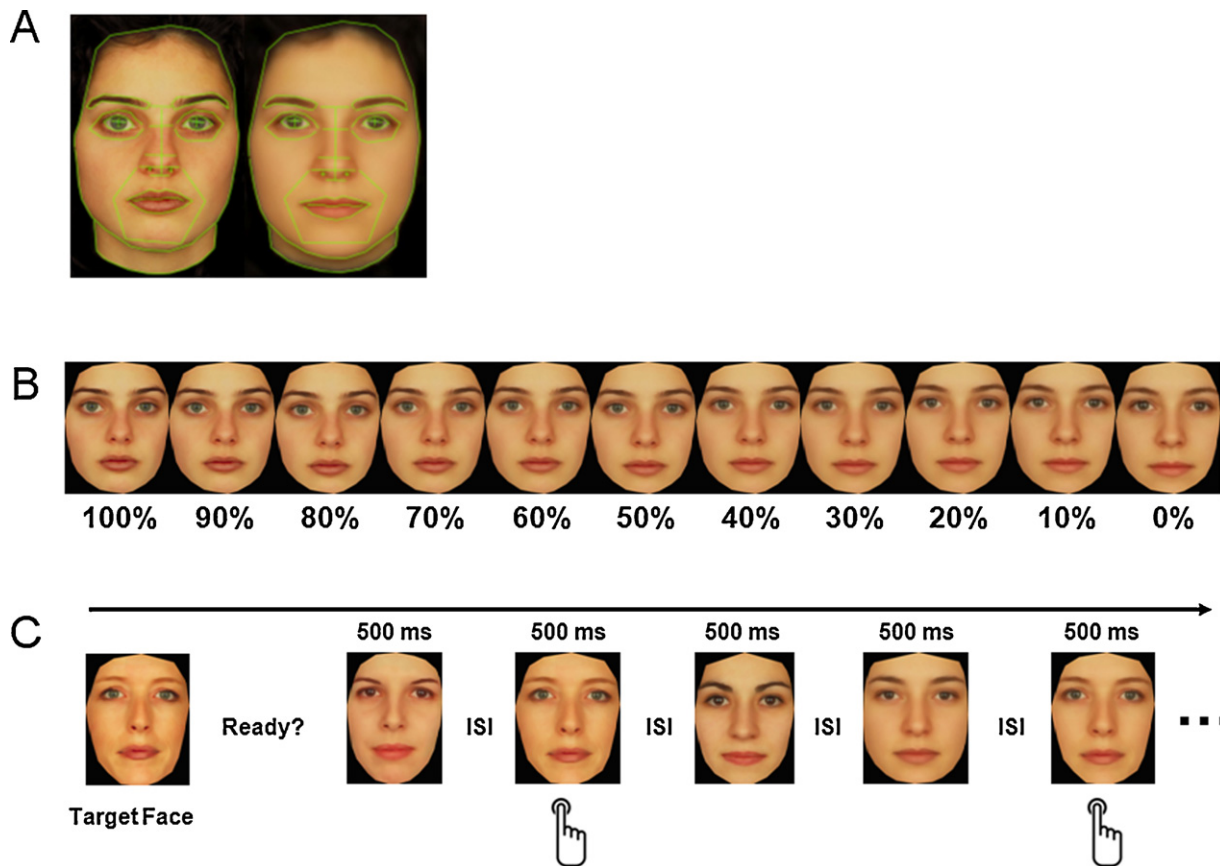


Fig. 1. Examples of face stimuli and the trial procedure for face identification task. (a) Based on over 140 reference points, an original face (left) were morphed with the “average” face (right) to produce a continua of faces varying in identity strength; the “average” face was constructed with 32 faces of different identities. (b) Examples of the morphed faces along one identity trajectory, decreasing in identity strength in steps of 10%. (c) At the beginning of each block, a target face was shown for visual inspection; during the task, the face stimuli were presented sequentially, and participants were instructed to press a button whenever they felt that they had detected a target face or a face that looked like the target; both response time and accuracy were emphasized.

2.3. Face identification task

Participants performed four blocks of a face identification task. At the beginning of each block, a target face (original) was presented, and participants were given as much time as needed to visually inspect and memorize the target face. On the following trials, a face stimulus was presented in the center of a computer screen for 500 ms, followed by a randomly selected interstimulus interval (ISI) of 600, 700, or 800 ms. Participants were instructed to press either a left or a right button, counter-balanced across participants, whenever they felt that they had detected a target face or a face that looked like the target (i.e., another face on that same identity trajectory). Responses could be made either during the presentation of a face stimulus or during the ISI. Both response speed and accuracy were emphasized (see Fig. 1c for the trial procedure).

Each block consisted of 220 trials, including one target face and its morphed versions (including the “average” face) each presented four times, and 16 non-target faces and their morphed versions (including the “average” face) each presented only once. The order of presentation within each block was randomized. A different target face was used in each of four blocks. Each of the 32 non-target faces and their morphed versions appeared in two blocks (e.g., blocks 1 and 3 or blocks 2 and 4); the blocks in which a stimulus (including both target and non-target faces) appeared was counter-balanced across participants.

2.4. EEG recording and data analyses

The EEG was recorded from an elastic net (Electrical Geodesics, Inc.) containing 128 silver chloride-plated electrodes embedded in sponges. Recorded EEG was referenced to the vertex (Cz) and amplified by Net Amps 200 (band-pass filter 0.01–100 Hz; digitized sampling rate 500 Hz; impedance below 50 k Ω). Eye movements and blinks were monitored by electrodes placed below and beside each eye. Raw EEG data were segmented into epochs starting 200 ms before and ending 800 ms after stimulus onset. Trials were visually inspected for contamination by movements and were manually rejected. The number of trials rejected did not differ across conditions ($F(10, 160) < 1.0$, $p = .454$), and there were approximately 58 trials (i.e., 91.2% of the 64 non-target faces at each identity strength level, with a range of 89.7–92.2%) in each averaged ERP for each morphing condition. Trials

containing eye artifacts were corrected using the artifact correction method provided by BESA 5.1 software (MEGIS Software GmbH). The 128-channel data were subsequently transformed through spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989) to the standard 81 electrode montage according to the expanded 10–10 system (Nuwer et al., 1998).

The amplitudes of ERP components were measured as the positive or negative deflections relative to the prestimulus baseline of 200 ms. Specifically, the P100 was measured as the maximum peak positivity between 80 and 130 ms at occipital sites (PO3, O1, O9 for the left and PO4, O2, O10 for the right). The N170 component was measured as the maximum peak negativity between 140 and 190 ms at occipitotemporal sites (P7, P9, PO7, PO9 for the left sites and P8, P10, PO8, PO10 for the right sites). The P2 component was separated into an early (190–230 ms) and a late (230–270 ms) time window. The early P2 (dorsal P2) was measured as the mean amplitude between 190 and 230 ms at parietal-occipital sites (CP3, CP1, P1, P3, PO3 for the left and CP2, CP4, P2, P4, PO4 for the right); the late P2 (ventral P2) was measured as the mean amplitude between 230 and 270 ms but at more ventral sites (P5, P7, PO7, PO9 for the left and P6, P8, PO8, PO10 for the right). Following the ventral P2 component, the N250 was measured as the mean amplitude between 270 and 330 ms at occipitotemporal sites (P7, P9, TP9, PO9 for the left and P8, P10, TP10, PO10 for the right) (see Fig. 2 for the representative ERP waveforms of each component). All ERP components were first measured at individual electrode sites on both the left and the right sides; the most positive (P100, P2) and the most negative (N170, N250) values of those individual measurements for each side were then used to represent the components. Because all face stimuli elicited the P100 very close to 120 ms ($sd \approx 1$ ms) and the N170 very close to 168 ms ($sd \approx 1.5$ ms), the peak latencies of these two components were not further analyzed in relation to face identity strength. To investigate the timing of face identity strength affecting ERP responses, we correlated the amplitude of each ERP component (P100, N170, early and late P2, N250) with face identity strength (from 100% to 0% in decrements of 10%) for each participant. After Fisher transformation, the individual correlation coefficients were then analyzed with single sample t -tests to examine whether there was a significant relationship between face identity strength and ERP components across all participants as a group. For each participant, the ERPs used for these analyses were averages of 32 non-target faces and of their morphed versions. The same analyses were performed separately for the montages on the left and the right sides.

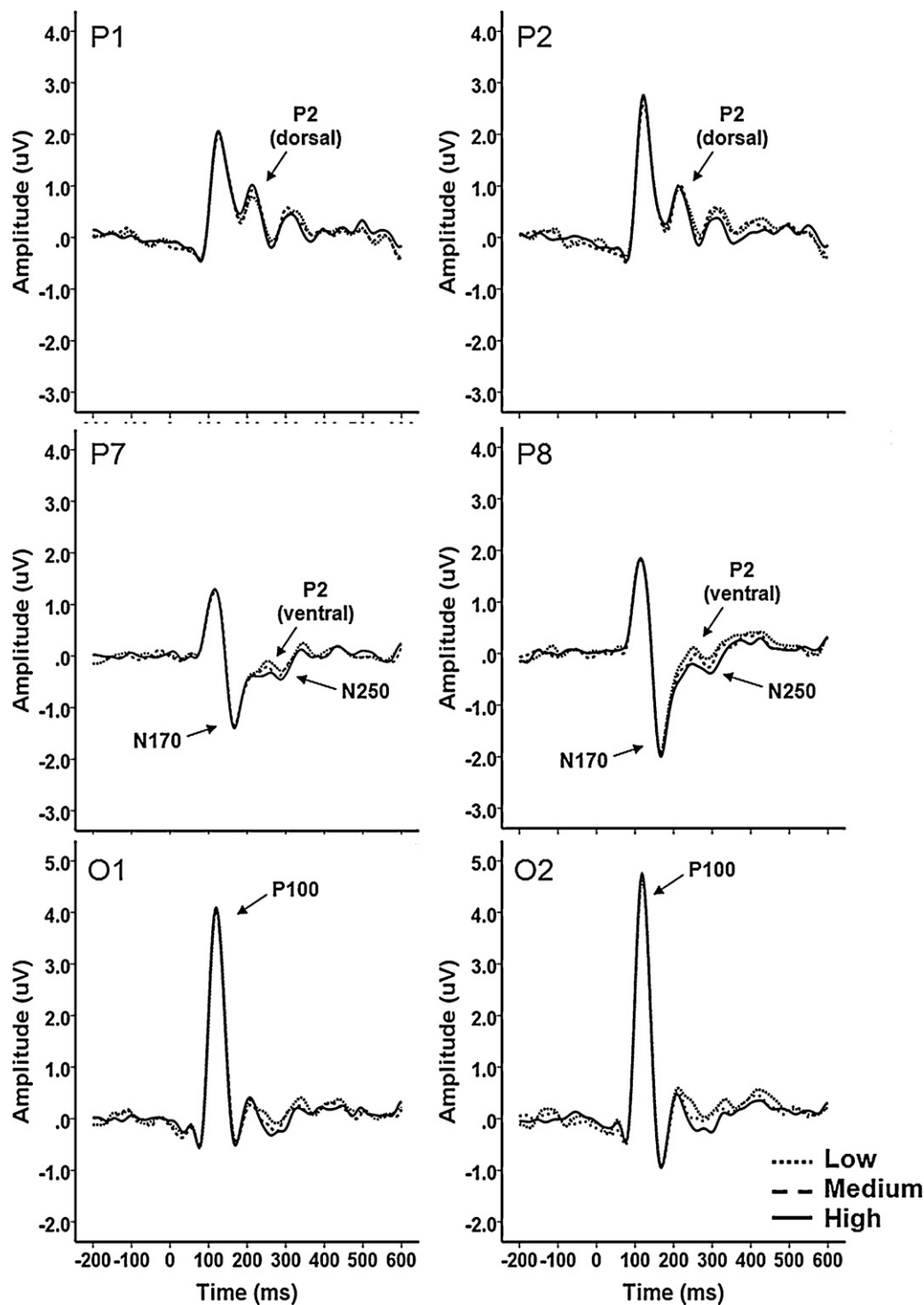


Fig. 2. The representative ERP waveforms for the P100 (80–130 ms), N170 (140–190 ms), dorsal P2 (190–230 ms), ventral P2 (230–270 ms) and N250 (270–330 ms) component, averaged for non-target faces with either high-, medium-, or low-identity strength (see Section 2).

The target faces and their morphed versions were excluded from the correlational analyses, because the number of trials for producing ERPs was rather small (16 trials at most) for each identity strength level, they were excluded from the correlational analyses.

When a significant relationship was found between face identity strength and ERP components across participants, we further assessed its consistency across individual faces. Because each non-target face stimulus and their morphed versions were presented only twice during the entire task, the number of trials for generating ERPs was small. Consequently, we randomly paired non-target faces and combined ERP responses to each pair and to their morphed versions accordingly. With single sample *t*-tests, the final face-based analyses were performed on the individual correlation coefficients (per face pair) between face identity strength and the amplitude

of ERP components (averaged over all participants) of 16 combined non-target face pairs.

3. Results

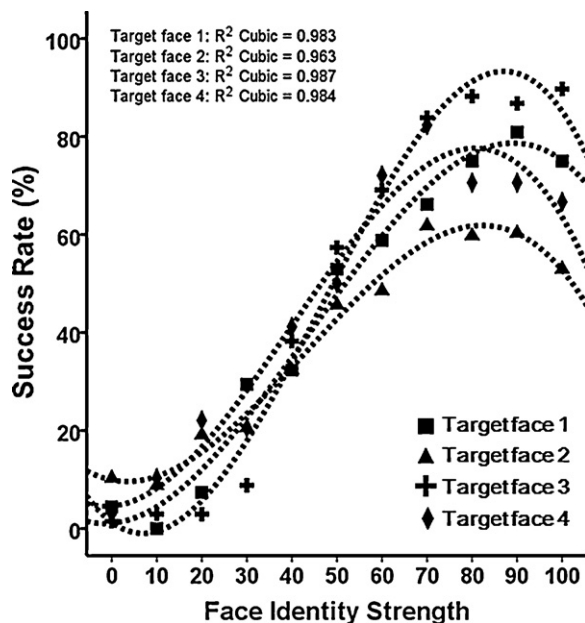
3.1. Behavioral results

Averaged across all participants, accuracy in detecting target faces followed a cubic function with face identity strength (Fig. 3) (for target face 1, $p = .010$; for target face 2, $p = .014$; for target face

Table 1

The relationship between face identity strength and the ERP amplitudes for each component further separate by the left and right hemisphere.

	Face identity strength			Face identity strength		
	Linear	Quadratic	Cubic	Linear	Quadratic	Cubic
P1						
Left	$p = .353$	$p = .136$	$p = .163$	$p = .272$	$p = .462$	$p = .270$
Right	$p = .525$	$p = .335$	$p = .971$	$p = .100$	$p = .956$	$p = .705$
N170						
Left	$p = .623$	$p = .478$	$p = .891$	$p = .291$	$p = .838$	$p = .122$
Right	$p = .554$	$p = .147$	$p = .554$	$p = .201$	$p = .613$	$p = .501$
Dorsal P2						
Left	$p = .124$	$p = .348$	$p = .574$	$p = .107$	$p = .341$	$p = .945$
Right	$p = .379$	$p = .708$	$p = .474$	$p = .954$	$p = .765$	$p = .667$
Ventral P2						
Left	$p = .016$	$p = .648$	$p = .560$	$p = .043$	$p = .334$	$p = .746$
Right	$p < .001$	$p = .683$	$p = .507$	$p < .001$	$p = .859$	$p = .531$
N250						
Left	$p = .090$	$p = .263$	$p = .956$	$p = .106$	$p = .296$	$p = .502$
Right	$p = .001$	$p = .920$	$p = .689$	$p = .002$	$p = .460$	$p = .441$
	(based on individual participants)			(based on individual faces, with target faces excluded)		

**Fig. 3.** Success rate of identifying a target face as a function of face identity strength. The categorical boundary for face identification occurred at 30% and 70% of face identity strength (see [Supplementary Text 2 for the results](#)).

3, $p = .001$; for target face 4, $p = .001$; overall, for all target faces, $p < .001$).¹ When examined individually for each participant (i.e., a cubic function was fitted for each participant to produce individual coefficients) and then tested with single sample t -tests based on individual coefficients, the relationship between accuracy and identity strength was significant for all target faces (for target face 1, $t(16) = -3.2$, $p = .006$; for target face 2, $t(16) = -3.3$, $p = .005$; for target face 3, $t(16) = -3.7$, $p = .002$; for target face 4, $t(16) = -12.6$, $p < .001$; overall for all target faces, $t(16) = -8.1$, $p < .001$). As shown in [Fig. 3](#), participants performed poorly when identity strength was lower than 30%, performance increased gradually between 30% and 70% identity strength with no further increase after that. These

observations were subsequently examined and confirmed by the ANOVA analyses with repeated measures (see [Supplementary Text 2 for the results](#)).

3.2. Electrophysiological results

3.2.1. Participant-based analyses

When the amplitude of the ERP components (averaged over 32 non-target faces) was examined in relation to face identity strength for all participants as a group, a linear relationship between ERP amplitude and face identity strength was found after 230 ms post stimulus onset in the ventral P2 and the N250 components: as face identity strength increased, the ventral P2 became smaller and the N250 became larger. The relationship between face identity strength and the ventral P2 amplitude was found from both left and right sites (for the left ventral P2, $t(16) = -2.68$, $p = .016$; for the right ventral P2, $t(16) = -5.96$, $p < .001$) with a similar magnitude on the two sides ($t(16) = 1.28$, $p = .218$). For the N250, the effect of face identity strength was found on the right ($t(16) = -4.08$, $p = .001$), and there was also a similar trend on the left ($t(16) = -1.80$, $p = .090$). In contrast to the ventral P2 and the N250 component, such a linear relationship was not found during earlier time windows (i.e., prior to 230 ms post stimulus onset) with the P100, the N170 and the dorsal P2 component on either the left or the right (for left and right P100 and N170, and the right dorsal P2, $t(16) < 1.0$; for the left dorsal P2, $t(16) = 1.62$, $p = .124$). Separated by the different ERP components, [Fig. 4](#) illustrates the individual correlation coefficients between the ERP amplitude and the face identity strength for each participant. A consistent relationship between the two was only seen after 230 ms, particularly on the right side. Unlike the behavioral data, there was no cubic relationship between ERP amplitudes and face identity strength ([Table 1](#)).

3.2.2. Face-based analyses

When the amplitude of ERP components was examined in relation to face identity strength for each face-pair stimulus (averaged over the 17 participants), the same results were found. A linear relationship between the two was found only for the ventral P2 and the N250 components: greater face identity strength was associated with a smaller ventral P2 and a larger N250. The relationship was found from both left and right sites for the ventral P2 component (for the left ventral P2, $t(15) = -2.22$, $p = .043$; for the right ventral P2, $t(15) = -4.64$, $p < .001$); it was mainly found from the right site for the N250 component (for the left N250, $t(15) = -1.72$, $p = .106$;

¹ The behavioral data similarly fitted sigmoid functions, which accounted for 94.8%, 97.0%, 97.1%, and 99.1% of the variance for the four target faces; averaging across all target faces, 99.6% of the variance was accounted for.

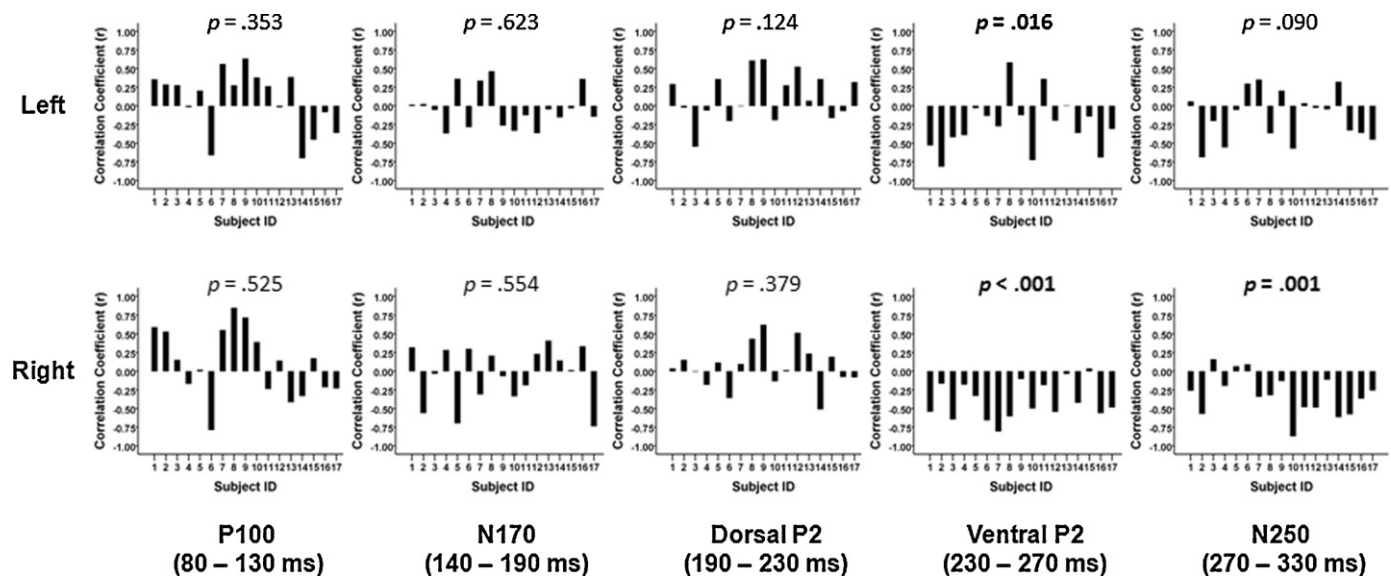


Fig. 4. The correlation coefficients between face identity strength and the amplitude of ERP components for individual participants (over all non-target faces). Consistent relationships were found across participants shortly after 200 ms in the ventral P2 and the N250 component.

for the right N250, $t(15) = -3.64$, $p = .002$). In contrast, the amplitudes of the P100, the N170 and the dorsal P2 did not relate to the face identity strength (for left P100, $t(15) = 1.14$, $p = .272$; for right P100, $t(15) = 1.76$, $p = .100$; for left N170, $t(15) = -1.10$, $p = .291$; for right N170, $t(15) = -1.34$, $p = .201$; for the left dorsal P2, $t(15) = 1.72$, $p = .107$; for the right dorsal P2, $t(15) < 1.0$, $p = .954$). The individual correlation coefficients between the ERP amplitude and the face identity strength for each pair of face stimuli are illustrated in Fig. 5. When we fitted cubic functions to predict the ERP amplitude using face identity strength, we found no significant effect for any ERP component on either left or right side, thus also consistent with findings from participant-based analyses (Table 1).

Together, these results suggested that neural responses to face identity strength did not occur within 200 ms, but rather occurred later, starting at approximately 230 ms after a face was presented. This conclusion was further supported when we divided the face stimuli into three groups based on their identity strength (0%, 10%, 20% for low strength; 40%, 50%, 60% for medium strength;

80%, 90%, 100% for high strength), and then compared their ERP amplitudes, using a 2 (left/right) $\times$ 3 (low/medium/high identity strength) ANOVA with repeated measures.

3.2.3. Group analyses comparing faces with low-, medium-, and high-identity strength

The average ERP amplitudes elicited by each face group for each component are illustrated in Fig. 6. The amplitudes of the three early ERP components were not affected by face identity strength: the P100 ($F(2,32) < 1.0$, *n.s.*), the N170 ($F(2,32) < 1.0$, *n.s.*), and the dorsal P2 component ($F(2,32) < 1.0$, *n.s.*). In contrast, significant differences in ERP amplitude were found for the ventral P2 ($F(2,32) = 17.14$, $p < .001$) and the N250 ($F(2,32) = 9.17$, $p = .001$) components. Post hoc comparisons revealed that higher identity strength was associated with a smaller ventral P2 and a larger N250, consistent with the findings from the correlational analyses. Although the effect of face identity strength on ERP amplitude appeared to be larger on the right than on the left for both the

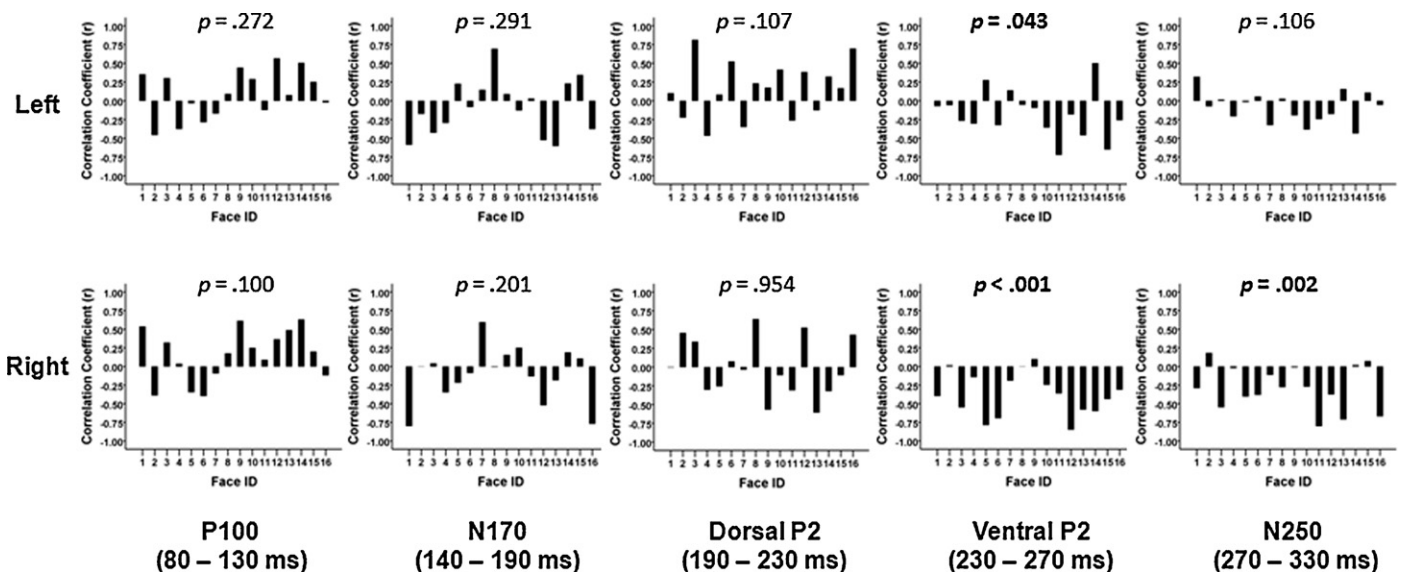


Fig. 5. The correlation coefficients between face identity strength and the amplitude of ERP components for individual non-target face-pairs (over all participants). The relationship between face identity strength and the amplitude of the ventral P2 and the N250 components was similarly found across non-target faces.

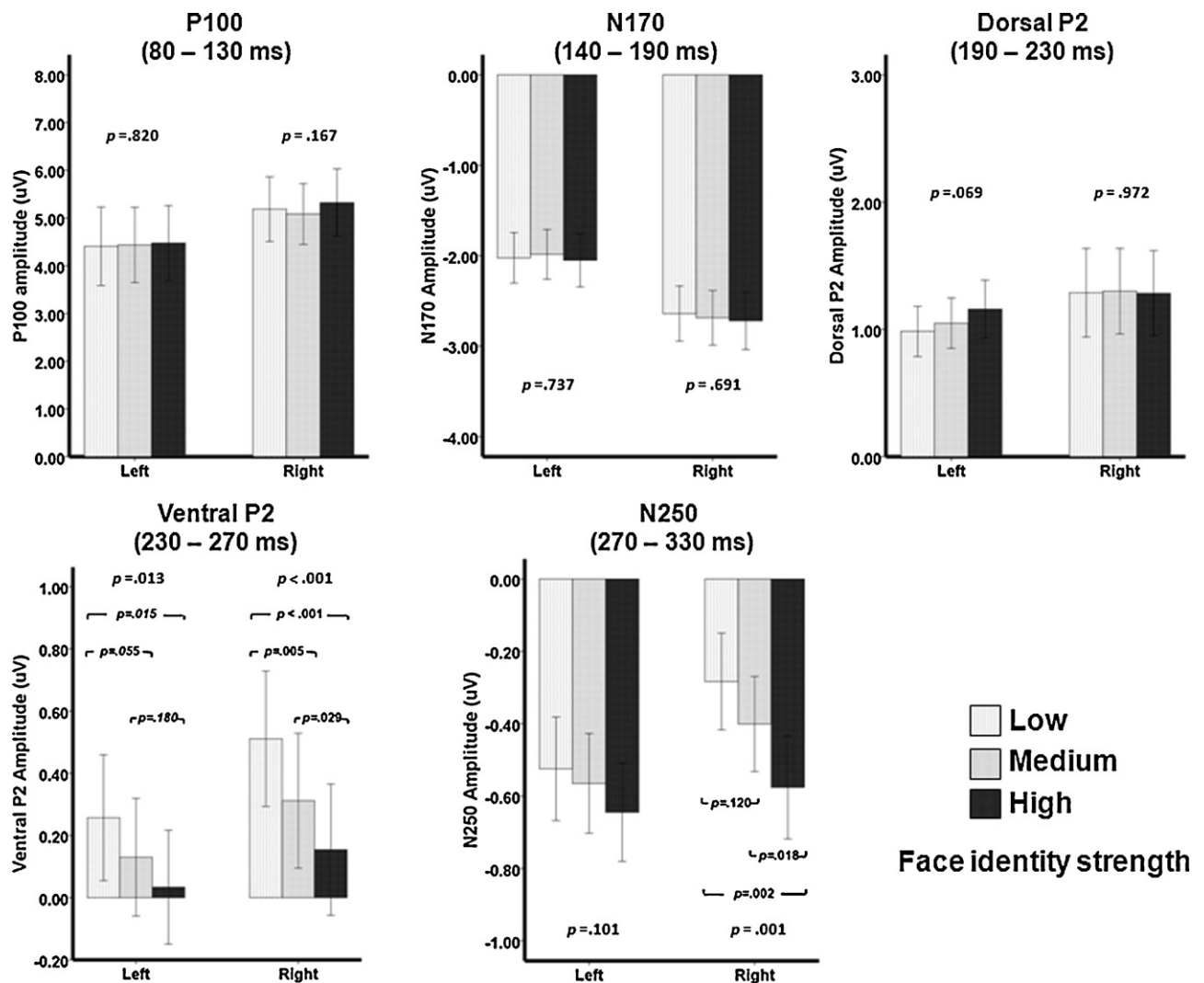


Fig. 6. Comparing non-target faces with high (100%, 90%, 80%), medium (60%, 50%, 40%), and low (20%, 10%, 0%) identity strength, differences in ERP amplitude were found for the ventral P2 and the right N250 component, but not for the earlier components (P1, N170, dorsal P2). Error bars represent the s.e.m.

ventral P2 and the N250 component, the interaction between hemisphere and face identity strength did not reach significance for either component (for the ventral P2, $F(2,32) = 1.03$, $p = .369$; for the N250, $F(2,32) = 2.16$, $p = .132$).

Grouping the target faces into low- (0%, 10%, 20%), medium- (40%, 50%, 60%) and high-identity (80%, 90%, 100%) strength conditions,² similar results were obtained: the P100, the N170, and the dorsal P2 components were not affected by face identity strength (for P100, $F(2,32) = 1.9$, $p = .171$; for N170, $F(2,32) = 1.6$, $p = .226$; for dorsal P2, $F(2,32) < 1$, *n.s.*). In contrast, a main effect of identity strength was found for the N250 ($F(2,32) = 3.5$, $p = .043$) and marginally for the ventral P2 ($F(2,32) = 3.0$, $p = .066$): greater identity strength was associated with a smaller ventral P2 and a larger N250 (Fig. 7). The effect of identity strength on the ventral P2 and on the N250 appeared to be much weaker for the target faces relative to non-targets. This however might be due to the smaller

number of ERP trials used to produce the low-, medium-, and high-identity strength conditions for the target faces (48 trials) than for the non-target faces (192 trials).

4. Discussion

Recent studies with humans and non-human primates (Leopold et al., 2006; Loffler et al., 2005) have found that neural responses from face-sensitive regions are sensitive to the strength of face identities relative to an average face. In the present study we investigated the timing of these neural events (i.e., we investigated when the effect of face identity strength occurs in the brain). Face identity strength did not affect the amplitude of the P100 (80–130 ms) or the N170 (140–190 ms) or the dorsal P2 components (190–230 ms), but affected the two later components: the ventral part of the P2 (230–270 ms) and the N250 (270–330 ms). As face identity strength increased (i.e., when faces become more distinctive relative to the “average” face), the ventral P2 became smaller and the N250 became larger. This linear relationship between face identity strength and the amplitude of the ventral P2 and the N250 was found across individual participants and across face stimuli. Similarly, when we performed the group analyses to compare the amplitude of ERP components elicited by faces of high- (100%, 90%,

² Although we did not perform correlational analyses with the target faces due to the rather small number of trials (16 trials at most) obtainable for each identity strength level, grouping the target faces into low-, medium- and high-identity strength conditions increased the number of trials for each condition (48 trials at most). This allowed us to perform the same group analyses for the target faces as we did for the non-target faces.

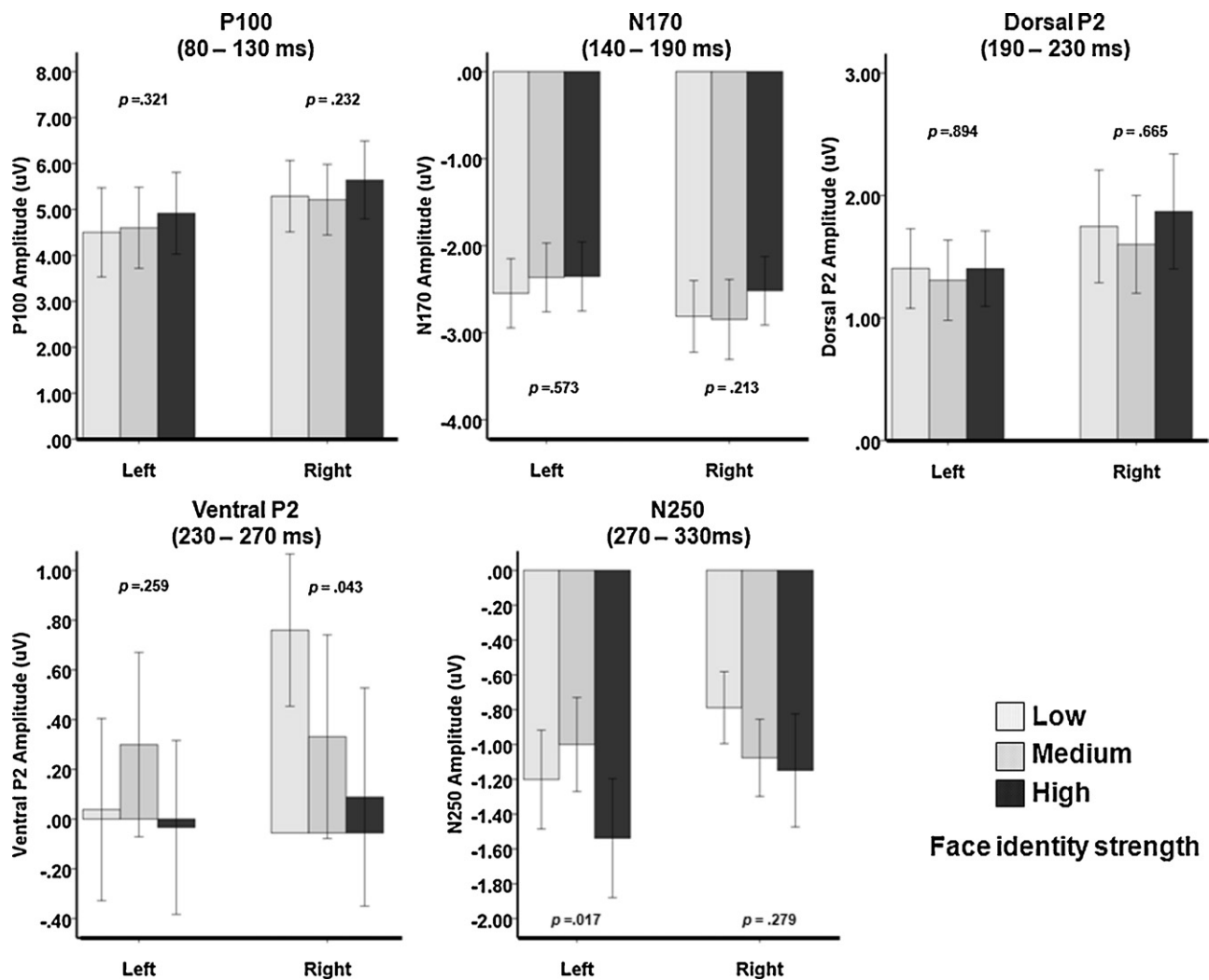


Fig. 7. Despite the much smaller number of trials (see Section 2), when the target faces were examined, similar patterns of results were found: differences in ERP amplitude among high (100%, 90%, 80%), medium (60%, 50%, 40%), and low (20%, 10%, 0%) identity strength was found for the N250 and marginally for the ventral P2 (see Section 3), but not for the earlier components (P1, N170, dorsal P2). Error bars represent the s.e.m.

80%), medium- (60%, 50%, 40%) and low-identity strength (20%, 10%, 0%), the effect of identity strength was only found in the ventral P2 and the N250 components for both non-target and target faces. Our study is one of the first to investigate ERP responses in relation to systematic variations in face identity strength relative to an average face (see Kaufmann & Schweinberger, 2008, for a study using caricatures and anti-caricatures). Collectively, our results suggest that the brain does not respond to visual face identity until 230 ms after a person sees a face.

It is generally accepted in the literature that the P100 component reflects the cortical processing of low-level visual information (e.g., spatial frequency, contrast, luminosity) (see Regan, 1989) and is not associated with the processing of high-level information, such as a particular class of visual stimuli (e.g., faces, houses) (see Rossion & Jacques, 2008, for a review); therefore, our result that the P100 amplitude was not affected by individual faces varying in identity strength is consistent with this established view.

Whether the N170 is influenced by face identity is more controversial. Our results are consistent with those of many studies suggesting that the N170 is not influenced by face identity (Bentin & Deouell, 2000; Eimer, 2000a; Gosling & Eimer, 2011; Kaufmann et al., 2008; Rossion et al., 1999; Schweinberger et al., 2002; Tanaka et al., 2006). For example, Gosling and Eimer (2011) reported that the N250, but not the N170, was modulated by whether

participants were viewing famous faces that were explicitly recognized versus famous faces that were not recognized or non-famous faces. Likewise, the N170 was not modulated by face familiarity in a task in which different exemplars of learned faces were interspersed with novel faces; in contrast, the N250 was enhanced for learned faces (Kaufmann et al., 2008).

We acknowledge that other studies have reported an influence of face identity on the N170. For example, Jacques and Rossion (2006) morphed two facial identities to create a continuum between face A and face B. The amplitude of the N170 response to a morphed face (e.g., with 65% of face A and 35% of face B) was smaller when that face was preceded by a face that was located on the same side of the perceptual identity boundary (e.g., with 95% of face A and 5% of face B) than when it was preceded by an equally distant face that was located on the other side of the boundary and thus perceived as having a different identity (e.g., with 35% of face A and 65% of face B) (see Caharel, d'Arripe, et al., 2009; Jacques et al., 2007, for other reports that the N170 adaptation is modulated by face identity).

One possible interpretation of these conflicting results is that the N170 is modulated by face characteristics rather than identity per se. The N170 is sensitive to a variety of face characteristics including the eyes, facial layout, and face outline (Bentin et al., 1996; Eimer, 2000b; Itier, Alain, Sedore, & McIntosh, 2007; Zheng et al., 2011), so

it is important for adaptation studies to control the potential influence of such facial information on the N170 component before a conclusion can be drawn on whether the perception of face identities occurs before 200 ms. Any time that the N170 is adapted when the same identity is presented on consecutive trials it is possible that adaptation is attributable to face characteristics rather than identity per se. In fact, even when it is not possible for N170 to have been modulated by identity, adaptation of this component can still be observed. For example, when the adaptor is a face of a different identity or even just a face part from a different identity (e.g., the eyes), the adaptation of N170 can still occur to the test face (Eimer et al., 2010). Therefore, the adaptation of N170 in and of itself is not enough to support the claim that the N170 is a neural index of perceiving individual face identities. Furthermore, when the potential adaptation effect caused by facial characteristics was removed with associative priming (Schweinberger et al., 1995) or reduced by using face stimuli from very different sources (Schweinberger et al., 2002), the effect of face identity on ERPs is found later, and not earlier in the N170.

In the present study, instead of using an adaptation paradigm, we presented faces in a random order, with a large number of face identities appearing within each block (i.e., 16 non-target faces and one target face plus their morphed versions). As a result, the probability of one face immediately following another face along the same identity trajectory was relatively small (.06), minimizing any immediate adaptation effect attributable to either facial characteristics or face identities. Therefore, the effects of face identity strength on ERP responses likely reflected the underlying brain dynamics for processing visual face identities. Consistent with previous ERP studies (Kaufmann et al., 2008; Schweinberger et al., 2004, 1995, 2002; Tanaka et al., 2006), we found the earliest evidence of face identity strength affecting brain responses after 230 ms (ventral P2 and N250) post stimulus onset, but not earlier (P100, N170, dorsal P2). The linear relationship between face identity strength and the amplitude of the ventral P2 and the N250 component, with the “average” face eliciting the largest ventral P2 and the smallest N250 compared to more distinctive faces, is in general consistent with the conclusion drawn from the imaging data in humans (Loffler et al., 2005) and from the single-cell recordings in monkeys (Leopold et al., 2006); it provides further support for the specific role played by an “average” face in a neural model underlying the perception of individual face identities.

Interestingly, in a recent paper, Davidenko, Remus, and Grill-Spector (in press) argued that the results of Loffler et al. (2005) and, by extension, our own results might be difficult to interpret because image variability across faces also varies as a function of the distance from the average face. In their study, the BOLD signal in FFA was measured, while participants viewed silhouettes that differed in face-likeness. When image variability was not controlled (i.e., was largest for the most distinctive, but least face-like silhouettes), the BOLD signal was largest for the least face-like stimuli. In contrast, when image variability was controlled, the pattern was reversed: the BOLD signal was largest for the most typical, face-like silhouettes. While their results seem to suggest that a larger image variability may account for the greater neural responses to distinctive silhouettes (or faces in general), a closer examination of their data suggests that their results might actually be driven by perceptual variability: while image variability was controlled in their second experiment, perceptual variability was not; it was largest for the most face-like silhouettes (see Supplementary Fig. 7b in their paper), which may explain why the BOLD signal was enhanced for these stimuli. Therefore, their results can be viewed as consistent with the findings by Loffler et al. (2005) and our own results that the ventral P2 and the N250, but not the N170, are modulated by the perception of face identities relative to an average face; a similar conclusion that had also been reached from another recent

ERP study in which participants viewed caricatures, veridical face images, and anti-caricatures (Kaufmann & Schweinberger, 2008). Indeed, perceptual variability/similarity and face identity strength are intrinsically linked in models of multi-dimensional face space (Valentine, 1991) and so the influences of these two variables are inherently confounded.

In addition to providing strong evidence that the effect of face identity strength in relation to an average face is evident only after 200 ms, our results also provide new insights about when this effect occurs. Although previous ERP studies have reported the face identity effect on the N250 component, the time-window selected for measuring the N250 component was slightly different across studies. Some studies measured the N250 component as the averaged activity approximately between 260 ms and 320 ms (Kaufmann et al., 2008; Schweinberger et al., 2004); other studies have extended the time-window by including the early portion of the 200–300 ms period (e.g., 200–300 ms in Schweinberger et al., 2002; 230–320 ms in Tanaka et al., 2006). Thus, although these studies have provided converging evidence in support of a face identity effect after approximately 260 ms post stimulus onset, it was not clear whether the perception of individual face identities might start even earlier. Dividing the 230–330 ms period into two smaller time-windows, i.e., 230–270 ms for the ventral P2 and 270–330 ms for the N250, allowed us to demonstrate that the effect is present during both time windows and even stronger between 230 and 270 ms. These results therefore help to further locate the timing of initial brain responses to individual face identities to as early as 230 ms post stimulus onset.

Although the P2 component has not been studied extensively in relation to individual face perception, there is some evidence in addition to our own results suggesting that the P2 is sensitive to face identities. For example, when faces were made more distinctive/atypical by enlarging the distance between eyes and nose and between nose and mouth, the P2 amplitude became smaller (Halit, Haan, & Johnson, 2000), although the timing of this effect is unclear because of the very large time window (188–300 ms) used; in contrast, the N170 was not affected by the face typicality through this manipulation. In another study examining the ERP correlates of the other-race effect (ORE) in face recognition, Stahl, Wiese, and Schweinberger (2008) found that P2 amplitude is smaller for other-race faces than for own-race faces. Importantly, this effect was only found in individuals with minimal other-race experience, corresponding well with the face ethnicity by expertise interaction found in behavioral studies (Rhodes et al., 2009; Walker & Hewstone, 2006).

Identity strength influenced the N250 in addition to the ventral P2, raising an interesting question about the extent to which these two ERP components reflect the same processes involved in perceiving individual faces or separable processes associated with different aspects of individual face perception. For example, the ventral P2 might reflect the integration of structural information and the formation of a perceptual representation for the incoming face stimulus. In contrast, the N250 component might reflect the process by which that representation is compared to previously seen faces, and thus might be linked to face recognition more directly. The N250 might also be sensitive to other non-visual person information. This latter explanation, positing a functional dissociation between the ventral P2 and the N250 component that occur in sequence between 230 and 330 ms also seems to fit well with the classical stage model for face recognition (Bruce & Young, 1986), and with the lack of correlation we found between the right ventral P2 and the right N250 ($r = .382$, $p = .130$), despite each being strongly affected by face identity strength. Furthermore, when we statistically examined the right ventral P2 and the right N250 together, we found that their relationships with face identity strength were indeed dissociable: adjusting for the right ventral P2

in a regression model, the linear relationship between face identity strength and the right N250 amplitude was still significant, $t(16) = -2.64$, $p = .018$; similarly, the linear relationship between face identity strength and the right ventral P2 amplitude was also significant, $t(16) = -3.40$, $p = .004$, after adjusting for the N250.

Although these results are provocative, the current study was not designed to disentangle the relationship between the ventral P2 and the N250 component. To examine whether they reflect the same or different processes for individual face perception, future research is needed. For this purpose, using faces that differ at various perceptual and semantic levels might prove very useful. For example, Herzmann, Schweinberger, Sommer, and Jentzsch (2004) studied the effect of priming on ERP responses elicited by unfamiliar, famous, and personally familiar faces. After dividing the 230–330 ms period into two smaller time-windows as ours (i.e., 230–270 ms and 270–330 ms), they found that the priming effects on ERPs from the temporal region (similar to the locations where the ventral P2 and the N250 were measured in the present study), not only differed among the three types of face stimuli, but also changed slightly between the two time windows: while personally familiar faces showed a larger priming effect than did famous faces and unfamiliar faces for both time-windows, the larger priming effect for famous faces compared to unfamiliar faces only occurred later between 270 and 330 ms, raising again the possibility of dissociable neural processes underlying individual face perception during the 230–330 ms period. Similarly, in a recent study by Gosling and Eimer (2011), it was found that the occipital-temporal N250 differed between famous and unknown faces; however, this effect appeared to be driven primarily by famous faces that were explicitly recognized; in contrast, the N250 for famous faces that were not recognized but were only rated as familiar did not differ from the N250 for unknown faces. Their results and interpretations seemed to be consistent with our own suggestion that the N250 may be related to face recognition more directly and could be affected by semantic person information. However, because the N250 was measured with a large time window (i.e., 230–400 ms) in their study, it was not clear when this difference in N250 between recognition and familiarity initially occurred. If our hypothesis was correct, we think that this difference in N250 should happen close to 300 ms post stimulus onset, but not earlier.

Finally, for both the ventral P2 and the N250 component, the effect of face identity strength we found in the present study cannot be explained as a result of the morphing procedure or low-level visual information. Measures were taken to ensure that faces with different identity strength did not differ systematically in such irrelevant visual information as face outline and blurriness. In addition, if any low-level visual information might have accounted for the ventral P2 and the N250 effect, we would expect it to affect the P100 component to at least some extent. However, we found no evidence of early effects due to face identity strength until 230 ms post stimulus onset. Therefore, the overall patterns of these results and their consistency with previous literature suggest that the effects of face identity strength on the ventral P2 and the N250 components are due to the processing of visual face identities only.

One limitation of our study is that all faces were unfamiliar to participants; it is plausible that a different pattern of results might be obtained for familiar/known faces. People have a remarkable ability to recognize familiar faces even under very challenging conditions (e.g., under poor lighting and for degraded images); in contrast, they perform quite poorly when asked to recognize or match identities for unfamiliar faces (see Hancock, Bruce, & Burton, 2000, for a review). Behavioral evidence suggests that the mechanisms for perceiving individual face identities might be different between these two types of faces (Ellis, Shepherd, & Davies, 1979; Young, Hay, McWeeny, Flude, & Ellis, 1985), and previous studies have shown different ERP effects for familiar versus unfamiliar faces

(Eimer, 2000a; Rossion et al., 1999; Schweinberger et al., 2002) and for personally familiar versus famous faces (Herzmann et al., 2004). Future studies should examine the effects of face identity strength on ERP responses for familiar faces.

A second limitation of our study is that every face along a particular identity trajectory was derived from the same original image. It would be very interesting to create new identity continua using multiple images, perhaps with some variation in head orientation and/or emotional expression. Doing so would not only enhance the ecological validity of this research by asking participants to recognize facial identities across images, but also contribute to the debate about the influence of image variability versus perceptual face distinctiveness per se on brain responses.

In summary, using scalp-recorded ERPs, we investigated the timing of brain responses to individual faces that varied in identity strength. Our results suggest that the initial brain responses to face identity information occur shortly after 200 ms, but not earlier. In light of previous ERP research and based on the classic face recognition model by Bruce and Young (1986), the results of the present study may allow us to temporally delineate the neural events that are associated with individual face recognition. Indexed by the P100 component at approximately 100 ms after a person sees a face, the brain processes low-level visual information (e.g., color, contrast, spatial frequency). At some point between 100 and 150 ms, the incoming stimulus is detected as a face; subsequently, between 150 and 200 ms, various facial information including both internal and external features are processed (i.e., structural encoding), and these processes are reflected in the N170 component. Shortly after 200 ms, following the structural encoding, the facial information is integrated to form a perceptual representation of the incoming face. This representation is then compared to face representations established previously, and the result of this comparison determines whether a face is visually recognized or not. By approximately 300 ms after a person sees a face, the neural processes involved in perceiving individual face identities should be completed. While Bruce and Young's model has provided a general account of the stages involved in face recognition, the exact timing for each stage to occur at a neural level has not been solved yet. Here, we tentatively provide such a timeline and hope it can serve as a working model for future testing.

Acknowledgements

We thank M.D. Vida (Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, ON) for data collection, and M. Nishimura (Department of Psychology, Carnegie Mellon University, Pittsburgh, PA) for providing the original face stimuli. We also thank three anonymous reviewers for their comments and suggestions in helping us clarify some important issues. The work was supported by Natural Sciences and Engineering Research Council of Canada (C.J.M. and S.J.S.) and Canada Foundation for Innovation (S.J.S.).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2012.02.030.

References

- Allison, T., Ginter, H., McCarthy, G., Nobre, A. C., Puce, A., Luby, M., et al. (1994). Face recognition in human extrastriate cortex. *Journal of Neurophysiology*, 71(2), 821–825.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8(6), 551–565.

- Bentin, S., & Deouell, L. Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology*, 17, 35–54.
- Bötzel, K., Schulze, S., & Stodieck, S. R. G. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research*, 104(1), 135–143.
- Bruce, V., & Young, A. (1986). Understanding face recognition. *British Journal of Psychology*, 77, 305–327.
- Burton, A. M., & Vokey, J. R. (1998). The face-space typicality paradox: Understanding the face-space metaphor. *The Quarterly Journal of Experimental Psychology, Series A*, 51, 475–483.
- Caharel, S., d'Arripe, O., Ramon, M., Jacques, C., & Rossion, B. (2009). Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: Evidence from the N170 ERP component. *Neuropsychologia*, 47(3), 639–643.
- Caharel, S., Jiang, F., Blanz, V., & Rossion, B. (2009). Recognizing an individual face: 3D shape contributes earlier than 2D surface reflectance information. *NeuroImage*, 47, 1809–1818.
- Campanella, S., Hanoteau, C., Dépy, D., Rossion, B., Bruyer, R., Crommelinck, M., et al. (2000). Right N170 modulation in a face discrimination task: An account for categorical perception of familiar faces. *Psychophysiology*, 37(6), 796–806.
- Davidenko, N., Remus, D. A., & Grill-Spector, K. Face-likeness and image variability drive responses in human face-selective ventral regions. *Human Brain Mapping*, in press.
- Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *The Journal of Neuroscience*, 4(8), 2051–2062.
- Eimer, M. (2000a). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, 111, 694–705.
- Eimer, M. (2000b). The face-specific N170 component reflects late stages in the structural encoding of faces. *NeuroReport*, 11(10), 2319–2324.
- Eimer, M., Kiss, M., & Nicholas, S. (2010). Response profile of the face-sensitive N170 component: A rapid adaptation study. *Cerebral Cortex*, 20(10), 2442–2452.
- Ellis, H. D., Shepherd, J. W., & Davies, G. M. (1979). Identification of familiar and unfamiliar faces from internal and external features: Some implications for theories of face recognition. *Perception*, 8, 431–439.
- Freire, A., Lee, K., & Symon, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception*, 29, 159–170.
- Gosling, A., & Eimer, M. (2011). An event-related brain potential study of explicit face recognition. *Neuropsychologia*, 49, 2736–2745.
- Halit, H., Haan, M. D., & Johnson, M. H. (2000). Modulation of event-related potentials by prototypical and atypical faces. *NeuroReport*, 11(9), 1871–1875.
- Hancock, P. J. B., Bruce, V., & Burton, A. M. (2000). Recognition of unfamiliar faces. *Trends in Cognitive Sciences*, 4(9), 330–337.
- Harris, A., & Nakayama, K. (2007). Rapid face-selective adaptation of an early extrastriate component in MEG. *Cerebral Cortex*, 17, 63–70.
- Harris, A., & Nakayama, K. (2008). Rapid adaptation of the M170 response: Importance of face parts. *Cerebral Cortex*, 18, 467–476.
- Herzmann, G., Schweinberger, S. R., Sommer, W., & Jentzsch, I. (2004). What's special about personally familiar faces? A multimodal approach. *Psychophysiology*, 41, 688–701.
- Itier, R. J., Alain, C., Sedore, K., & McIntosh, A. R. (2007). Early face processing specificity: It's in the eyes. *Journal of Cognitive Neuroscience*, 19(11), 1815–1826.
- Jacques, C., d'Arripe, O., & Rossion, B. (2007). The time course of the inversion effect during individual face discrimination. *Journal of Vision*, 7(8), 3, 1–9.
- Jacques, C., & Rossion, B. (2006). The speed of individual face categorization. *Psychological Science*, 17(6), 485–492.
- Jacques, C., & Rossion, B. (2007). Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans. *NeuroImage*, 36, 863–876.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, 17(11), 4302–4311.
- Kaufmann, J. M., & Schweinberger, S. R. (2008). Distortions in the brain? ERP effects of caricaturing familiar and unfamiliar faces. *Brain Research*, 1228, 177–188.
- Kaufmann, J. M., Schweinberger, S. R., & Burton, A. M. (2008). N250 ERP correlates of the acquisition of face representations across different images. *Journal of Cognitive Neuroscience*, 21(4), 625–641.
- Leopold, D. A., Bondar, I. V., & Giese, M. A. (2006). Norm-based face encoding by single neurons in the monkey inferotemporal cortex. *Nature*, 442, 572–575.
- Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience*, 8(10), 1386–1390.
- Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, 6(6), 255–260.
- McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, 9(5), 605–610.
- Mondloch, C. J., Le Grand, R., & Maurer, D. (2002). Configural face processing develops more slowly than featural face processing. *Perception*, 31, 553–566.
- Nuwer, M. R., Comi, G., Emerson, R., Fuglsang-Frederiksen, A., Guérit, J. M., Hinrichs, H., et al. (1998). IFCN standards for digital recording of clinical EEG. *Electroencephalography and Clinical Neurophysiology*, 106, 259–261.
- Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurons responsive to faces in the monkey temporal cortex. *Experimental Brain Research*, 47, 329–342.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, 72, 184–187.
- Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology*, 74(3), 1192–1199.
- Regan, D. (1989). *Human brain electrophysiology: Evoked potentials and evoked magnetic fields in science and medicine*. New York: Elsevier.
- Rhodes, G., Ewing, L., Hayward, W. G., Maurer, D., Mondloch, C. J., & Tanaka, J. W. (2009). Contact and other-race effects in configural and component processing of faces. *British Journal of Psychology*, 100, 717–728.
- Rolls, E. T., & Baylis, G. C. (1986). Size and contrast have only small effects on the responses to faces of neurons in the cortex of the superior temporal sulcus of the monkey. *Experimental Brain Research*, 65, 38–48.
- Rossion, B., Campanella, S., Gomez, C. M., Delinte, A., Debatisse, D., Liard, L., et al. (1999). Task modulation of brain activity related to familiar and unfamiliar face processing: An ERP study. *Clinical Neurophysiology*, 110, 449–462.
- Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *NeuroImage*, 39, 1959–1979.
- Schweinberger, S. R., Huddy, V., & Burton, A. M. (2004). N250r: a face-selective brain response to stimulus repetitions. *NeuroReport*, 15(9), 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(3), 722–736.
- Schweinberger, S. R., Pickering, E. C., 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.
- Stahl, J., Wiese, H., & Schweinberger, S. R. (2008). Expertise and own-race bias in face processing: An event-related potential study. *NeuroReport*, 19(5), 583–587.
- Tanaka, J. W., Curran, T., Porterfield, A. L., & Collins, D. (2006). Activation of preexisting and acquired face representations: The N250 event-related potential as an index of face familiarity. *Journal of Cognitive Neuroscience*, 18(9), 1488–1497.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology*, 46A, 225–245.
- Tsao, D. Y., Freiwald, W. A., Tootell, R. B. H., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science*, 311, 670–674.
- Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion, and race in face recognition. *The Quarterly Journal of Experimental Psychology, Series A*, 43, 161–204.
- Valentine, T., & Bruce, V. (1986). The effects of distinctiveness in recognising and classifying faces. *Perception*, 15(5), 525–535.
- Walker, P. M., & Hewstone, M. (2006). A perceptual discrimination investigation of the own-race effect and intergroup experience. *Applied Cognitive Psychology*, 20, 461–475.
- Young, A. W., Hay, D. C., McWeeny, K. H., Flude, B. M., & Ellis, A. W. (1985). Matching familiar and unfamiliar faces on internal and external features. *Perception*, 14, 736–737.
- Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception*, 16, 747–759.
- Zheng, X., Mondloch, C. J., Nishimura, M., Vida, M. D., & Segalowitz, S. J. (2011). Telling one face from another: Electrocortical correlates of facial characteristics among individual female faces. *Neuropsychologia*, 49, 3254–3264.