

Recognizing an individual face: 3D shape contributes earlier than 2D surface reflectance information

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ARTICLE INFO

Article history:

Received 13 February 2009

Revised 21 April 2009

Accepted 19 May 2009

Available online 1 June 2009

Keywords:

Face recognition

N170

ERP Adaptation

2D surface reflectance

3D shape

ABSTRACT

The human brain recognizes faces by means of two main diagnostic sources of information: three-dimensional (3D) shape and two-dimensional (2D) surface reflectance. Here we used event-related potentials (ERPs) in a face adaptation paradigm to examine the time-course of processing for these two types of information. With a 3D morphable model, we generated pairs of faces that were either identical, varied in 3D shape only, in 2D surface reflectance only, or in both. Sixteen human observers discriminated individual faces in these 4 types of pairs, in which a first (adapting) face was followed shortly by a second (test) face. Behaviorally, observers were as accurate and as fast for discriminating individual faces based on either 3D shape or 2D surface reflectance alone, but were faster when both sources of information were present. As early as the face-sensitive N170 component (~160 ms following the test face), there was larger amplitude for changes in 3D shape relative to the repetition of the same face, especially over the right occipito-temporal electrodes. However, changes in 2D reflectance between the adapter and target face did not increase the N170 amplitude. At about 250 ms, both 3D shape and 2D reflectance contributed equally, and the largest difference in amplitude compared to the repetition of the same face was found when both 3D shape and 2D reflectance were combined, in line with observers' behavior. These observations indicate that evidence to recognize individual faces accumulate faster in the right hemisphere human visual cortex from diagnostic 3D shape information than from 2D surface reflectance information.

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Introduction

The recognition of others from their face is a fundamental biological and social function. A human face consists of two intrinsic properties: three-dimensional (3D) shape and two-dimensional (2D) surface reflectance. Surface reflectance has also been termed as 'color', 'texture', 'albedo', or 'pigmentation' in the past.² Recent studies have shown that in addition to face shape, surface reflectance properties are important for the perception of facial identity (e.g. Troje and Bühlhoff, 1996; Lee and Perrett, 1997; O'Toole et al., 1999; Yip and Sinha, 2002; Vuong et al., 2005; Russell et al., 2006, 2007; Jiang et al., 2007; Russell and Sinha, 2007). For example, exaggerating color information of a face relative to its veridical version enhances recognition performance (Lee and Perrett, 1997). The inclusion of texture map induces better view general-

ization, even when the main skin color is kept identical across faces (Troje and Bühlhoff, 1996). Besides their diagnostic contribution, color cues can also play a supplementary rule, allowing a better segmentation of facial features, especially when shape cues are degraded (Yip and Sinha, 2002). The role of reflectance information also seems to be more crucial in recognizing familiar faces (Russell and Sinha, 2007), supporting the hypothesis that the degree to which we rely on surface properties in general might well be dependent on our prior experience (Vuong et al., 2005).

Given that recognizing individual faces is a challenging task for the visual system, it is not surprising that shape and reflectance information both contribute. It has been shown that they can be about equally useful in face recognition (O'Toole et al., 1999; Jiang et al., 2007; Russell et al., 2007). Using computer graphics, O'Toole et al. (1999) manipulated 3D shape and 2D surface reflectance independently of each other, creating faces that varied selectively in shape or reflectance. They found roughly equal performance in an old/new recognition task for these two types of faces, highlighting again the importance of both shape and surface reflectance for the recognition of unfamiliar faces. Russell et al. (2007) reported similar results in a matching task, in which participants matched the target and distractor faces on the base of shape or reflectance properties. In a recent study, Jiang et al. (2007) explicitly assessed the role of shape

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² Here, we use the term 'surface reflectance' to refer to the efficiency of facial surface in reflecting light, as defined in (O'Toole et al., 1999).

and reflectance information in face identity adaptation, where prolonged exposure to a face alters the perception of a subsequently presented face with opposite features (Leopold et al., 2001). Significant after-effects were found after adaptation to face morphs that varied selectively in reflectance or shape. Moreover, identity after-effects induced by shape-varying or reflectance-varying faces both survived a substantial viewpoint change between the adapting and test faces. These results indicated that shape and reflectance information in faces may be equally important not only for the identity adaptation but also for its transfer across changes in 3D viewpoint.

Although it is evident that both 3D shape and 2D reflectance information are exploited, their relative contribution over the time-course of face recognition in the human brain remains unknown. At an early neural level, shape and surface reflectance information are processed in partially segregated visual areas and pathways (e.g., Tovee, 1996; Grill-Spector and Malach, 2004). An important question to answer is how do these sources of information combine to perform individual face recognition. Are they initially segregated, with each of these cues providing independent evidence to recognize an individual face, and then merged into a single face representation? Or, do they combine as early as the processing stages at which the perceptual system has accumulated enough evidence to identify an individual's face? According to a coarse-to-fine view of the processing of visual information (Flavell and Draguns, 1957; Navon, 1977; Nowak and Bullier, 1997; Hochstein and Ahissar, 2002), in particular for faces (Sergent, 1986; Sugase et al., 1999; Goffaux and Rossion, 2006), sensitivity to the individual face may emerge faster from a first wave of low spatial frequency achromatic information, carried by the global 3D shape, while information provided by color and high spatial frequencies would accumulate later. Alternatively, there is evidence from monkey physiology and ERP recordings in humans that early brain responses to faces (Edward et al., 2003) and visual scenes (Goffaux et al., 2005) are sensitive to color diagnosticity, suggesting that the contribution of 2D reflectance information in coding for individual faces may emerge as early as 3D shape information.

In the present study we aimed at clarifying this issue of the time-course of individual face recognition based on 3D shape versus 2D surface reflectance. An individual's face is recognized in a few hundreds of milliseconds, from the onset of the visual stimulus to an observer's behavioral response. However, the perceptual system is able to tell apart different individual faces well before that latency, as suggested by the response properties of face-selective neurons in the monkey infero-temporal cortex, which accumulate information about individual faces within the first tens of milliseconds following their initial response (about 100 ms mean onset latency, e.g., Tovee and Rolls, 1995; Matsumoto et al., 2005). In humans, evidence for fast discrimination of individual exemplars is provided by event-related potentials (ERPs) recorded on the scalp in response to faces. The first consistent individual face repetition effect across studies has been observed as early as 160 ms following stimulus onset, during the time-window of the N170 face-sensitive component (Bentin et al., 1996; Jeffreys, 1996; for a review see Rossion and Jacques, 2008; for the corresponding component in Magnetoencephalography, M170, see Halgren et al., 2000; Liu et al., 2000). Several studies have found that repeating the same face photograph leads to a smaller N170 amplitude than a different face (Campanella et al., 2000; Ewbank et al., 2008; Guillaume and Tiberghien, 2001; Itier and Taylor, 2002; Jemel et al., 2003; Heisz et al., 2006; Jacques et al., 2007). The most compelling evidence for this early sensitivity to the individual face is found when using a long adaptation paradigm (several seconds duration for the first face) with a short interstimulus interval (100–300 ms) between the adapting face and the test face (Jacques et al., 2007). This early effect generalizes at least partially across different face views

(Caharel et al., 2009), but not when the face is presented upside-down (Jacques et al., 2007), indicating that it reflects an encoding of high-level visual information that allows the representation of an individual face. The N170 is followed by an additional individual face repetition effect usually observed starting at around 220–250 ms after stimulus onset, in the form of a more negative ERP for repeated compared to unrepeated faces around 250 ms over temporal scalp regions (the “N250” or “N250r”; e.g. Begleiter et al., 1995; Schweinberger et al., 1995; Tanaka et al., 2006).

In order to clarify the time-course of unfamiliar individual face discrimination based on 3D shape versus 2D surface reflectance, we used an ERP adaptation paradigm, in which we selectively manipulated the shape or reflectance property of the test face relative to the adapting face. Specifically, we included four experimental conditions: (1) repetition of the exact same face stimulus (same); (2) variation in 3D shape only (shape-different); (3) variation in 2D surface reflectance only (reflectance-different); (4) variation in both 3D shape and 2D surface reflectance (different) (Fig. 1). Observers performed a same/different matching task on 4 kinds of pairs of faces while the ERP response to the second face of the pair was measured. Behaviorally, we expected our participants to perform roughly equally well with reflectance-different and shape-different conditions (O'Toole et al., 1999; Jiang et al., 2007; Russell et al., 2007). The superior performance would occur in the different condition, in which the differences in both shape and reflectance properties were present. Neurally, we expected to disclose differences in the onset of sensitivity to different sources of information diagnostic for individual faces.

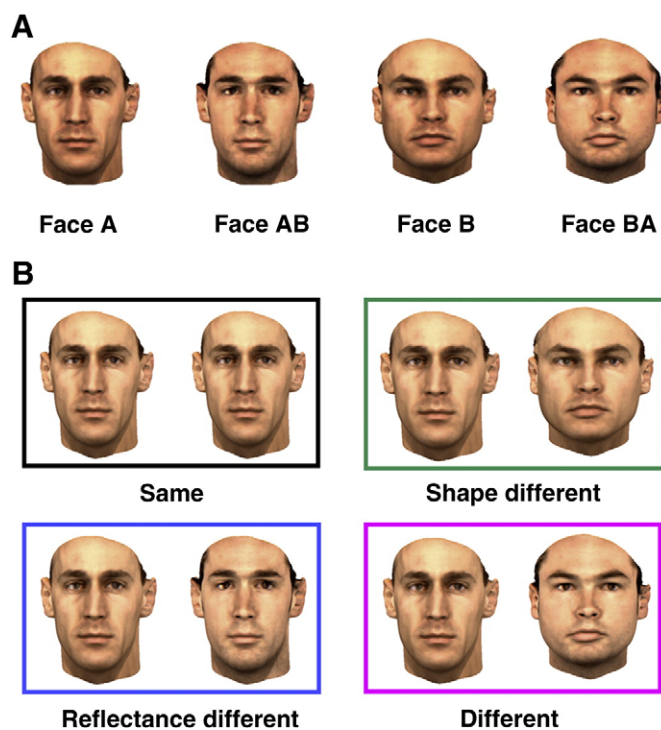


Fig. 1. Example stimuli and experimental conditions. (A) Illustration of an example pair of original faces (A and B) and corresponding faces (AB and BA) created with a 3D morphable model (Blaiz and Vetter, 1999) by swapping the 3D shape/surface reflectance between two original faces. Face AB was created by mapping the reflectance of face B onto face A's shape, while face BA was created by mapping the reflectance of face A onto face B's shape. (B) Illustration of experimental conditions. Conditions were defined by the shape and surface reflectance properties of the test stimulus with respect to the adapting stimulus. Four conditions were included: repetition of the same adapting face (same); variation in 3D shape only (shape-different); variation in 2D surface reflectance only (reflectance-different); and variation in both 3D shape and 2D surface reflectance (different).

Materials and methods

Participants

Sixteen right-handed participants (10 females; mean age = 21.4 ± 2.25) were included in the study. All participants were right-handed and had normal or corrected vision. Written informed consent was obtained from all participants prior to the experiment.

Stimuli

Stimuli used in this experiment were generated with a three-dimensional (3D) morphable model (Blanz and Vetter, 1999) that implemented a multidimensional face space based on 200 3D face scans. This model transforms the 3D shape (x, y, z) and surface reflectance (r, g, b) of a face into separate vectors constructed from 75,000 surface points in correspondence with a reference face. With this correspondence established, the reflectance of one face can be mapped on to the shape of another face, resulting a realistically looking new face with both physical and perceptual differences.

Using this model, we created *shape-different* and *reflectance-different* faces by exchanging the shape and reflectance properties between a pair of faces. Specifically, we picked 40 original faces (20 females) from the face space and split them into 20 gender-matched pairs. Each pair consisted of two original faces, for example, A and B. From these two original faces, we created two additional faces – AB and BA. We used two letters to describe faces created from their original parents, with the first letter indicating the origin of their shape and the second indicating the origin of their reflectance. Face AB was created by mapping the reflectance of face B onto the shape of A, and face BA was created by mapping the reflectance of face A onto the shape of B. Therefore, face AB differed from face A in reflectance and from face B in 3D shape, while face BA differed from face A in 3D shape and from face B in reflectance. Also note face AB and BA were different in both 3D shape and surface reflectance map. An example pair of original faces and their AB and BA version are shown in Fig. 1A.

Procedure

The experiment consisted of an ERP adaptation paradigm on individual faces with identical parameters as used in our previous studies (Jacques et al., 2007; Caharel et al., 2009). Participants were asked to judge whether a test face was the same individual as an adapting face or different. The shape and surface reflectance properties of the test face were manipulated with respect to the adapting face. As shown in Fig. 1B, four test conditions were included: (1) repetition of the same adapting face (*same*); (2)

variation in 3D shape only (*shape-different*); (3) variation in 2D surface reflectance only (*reflectance-different*); (4) variation in both 3D shape and 2D surface reflectance (*different*). Participants were informed that the difference between two faces, if there was any, could be in the shape, but also in the texture/color of a face.

After electrode-cap placement, participants were seated in light- and sound-attenuated room, at viewing distance of 100 cm from a computer monitor. Stimuli were displayed using E-prime 1.1 (PST Inc), on a light grey background. In each trial, two faces (adapting and test faces) were presented sequentially. A trial started with a fixation point displayed at the center of the screen for 200 ms. Approximately 200 ms (randomized between 100 and 300 ms) after the offset of the fixation point, the first face (adapting face) appeared for a duration of ~3000 ms (2800 to 3200 ms). After a short interval of about 250 ms (150 to 350 ms), a second face (test face) appeared for 200 ms. The offset of the second face was followed by an inter-trial interval of about 1600 ms (1500 to 1700 ms) (Fig. 2). These parameters of a long duration for the adaptor face (Kovacs et al., 2006) and a short ISI (Jeffreys, 1996; Harris and Nakayama, 2007; Ganis and Schendan, 2008) have been used successfully in prior ERP or MEG studies that measured adaptation effects on the N170 (or M170) both at the category level (i.e., face-face versus object-face), and at the individual level (i.e., faceA-faceA versus faceB-faceA, Jacques et al., 2007; Caharel et al., 2009).

To further avoid any possible pixel-based adaptation effect, the test face of each trial was 10% larger than the adapting face. The adapting face was presented 216×256 pixels in size and the test face was presented 238×282 pixels in size, sustaining a visual angle of $4.35^\circ \times 5.16^\circ$ and $4.79^\circ \times 5.68^\circ$ respectively. The average pixel intensity based difference between the adapting face image and the 10% larger test face image was 45.42 ± 3.73 in the same condition, 45.51 ± 6.38 in the shape-different condition, 50.56 ± 4.82 in the reflectance-different condition, and 53.10 ± 5.83 in the different condition. Note that the smaller adapting face images were padded with light grey (the background color used during trial presentation) in the calculation.

Participants performed a delayed matching task between the adapting and test faces, and gave their response by pressing one of two keys with their right hand. They were instructed to maintain eye gaze fixation to the center of the screen during the whole trial and to respond as accurately and as fast as possible. Each participant performed a total of 320 trials in eight blocks (80 trials per condition) separated by a self-paced pause. Trials were presented randomly for each participant. Note that each face was used equally as an adaptor or as a test stimulus both within and across experimental conditions (see Table 1 for 16 trials formed from a pair of original faces). In trials in which the faces were different, two faces of the same gender were always presented.

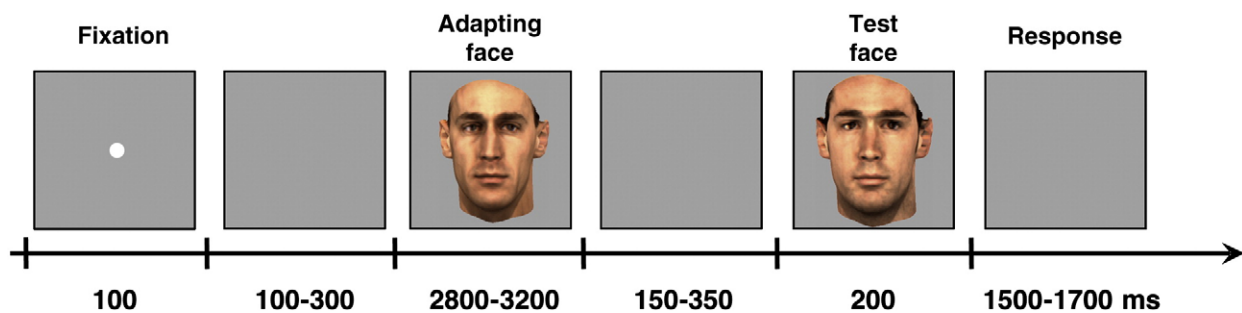


Fig. 2. Timeline of stimulus presentation. Following the presentation of the first stimulus (adapting face), there were 4 possible manipulations to the second face stimulus (test face) relative to the first stimulus, including no change, 3D shape change, 2D reflectance change, or both (here 2D reflectance change). The presentation of the adapting face did not allow participants to predict the nature of the change in the test face. Electrophysiological brain responses are analyzed and displayed with respect to the onset of the test face. To avoid pixel-based adaptation effect, the test face of each trial was 10% larger than the adapting face.

Table 1

Illustration of 16 trials (4 trials per condition) generated from one pair of original faces (A and B) and their shape/reflectance-different versions (AB and BA).

Conditions	Adapting face	Test face
Same	A	A
	B	B
	AB	AB
	BA	BA
Shape-different	A	BA
	B	AB
	AB	B
	BA	A
Reflectance-different	A	AB
	B	BA
	AB	A
	BA	B
Different	A	B
	B	A
	AB	BA
	BA	AB

Each face was used equally as an adaptor or as a test face both within and across conditions. Note: for face AB and BA, the first letter refers to the origin of face shape, and the second letter refers to the origin of face reflectance.

EEG recording

EEG was recorded from 128 Ag/AgCl electrodes mounted in an electrode cap (Waveguard, ANT). Electrode positions included the standard 10–20 system locations and additional intermediate positions. Vertical and horizontal eye movements were monitored using four additional electrodes placed on the outer canthus of each eye and in the inferior and superior areas of the right orbit. During EEG recording, all electrodes were referenced to the left mastoid reference, and electrode impedances were kept below 10 k Ω . EEG was digitalized at a 1000 Hz sampling rate and a digital anti-aliasing filter of .27*sampling rate was applied at recording (at 1000 Hz sampling rate, the usable bandwidth is 0 to ~270 Hz). After a .1 Hz high-pass and 30 Hz low-pass filtering of the EEG, trials contaminated with eye movements or other artifacts ($\geq \pm 80$ μ V) were marked and rejected. When there were many eye-blink artifacts (3 participants), a correction was applied using a principal component analyses method (Ille et al., 2002). Incorrect trials and trials containing EEG artifacts were removed, and the number of trials was equated between

conditions. Participants' averages were baseline corrected using the 200 ms pre-stimulus epoch and then re-referenced to a common average reference.

Statistical analyses

Behavior

Accuracy and mean correct response time at the individual face matching task were computed for each of the four conditions and were submitted to a repeated-measures analysis of variances (ANOVA) with *Condition* (same, shape-different, reflectance-different, and different) as a within-subject factor.

Electrophysiology

Two clear visual components elicited by the second (test) face were analyzed: the P1 (maximal at approximately 106 ms), and the N170 (maximal at approximately 165 ms). Amplitude values of these components were measured at different pairs of occipito-temporal electrodes in the left and right hemisphere where they were the most prominent (for the P1: P7/8, O1/2, PO5/6, PO7/8, PPO5/6h, PO9/10, PPO9/10h, POO9/10h, and for the N170: P7/8, TP7/8, PO7/8, PO9/10, P9/10, TPP7/8h, PPO9/10h, POO9/10h, TPP9/10h) (Fig. 3). Amplitudes were quantified for each condition as the mean voltage measured within 40 ms windows centered on the grand average peak latencies of the components' maximum. The mean amplitude of the N250r was also measured in the interval from 270 to 310 ms after stimulus onset at 6 pairs of occipito-temporal electrodes (P7/8, TP7/8, TPP9/10h, PO9/10, P9/10, PPO9/10h) where this component was the most prominent (Fig. 3). The amplitude values of each component were then submitted to separate repeated-measures analysis of variance with *Condition*, *Hemisphere*, and *Electrode* as within-subject factors.

All effects with two or more degrees of freedom were adjusted for violations of sphericity according to the Greenhouse–Geisser correction. Polynomial contrasts were performed for post-hoc comparisons.

To statistically identify the onset latency of the differential ERP responses between the conditions compared, a permutation test (Blair and Karniski, 1993; Nichols and Holmes, 2002) was performed on each scalp electrode and each time sample. This method was used previously to assess the time-course of individual face adaptation effects in ERPs (Jacques et al., 2007; Jacques and Rossion, 2009). In a

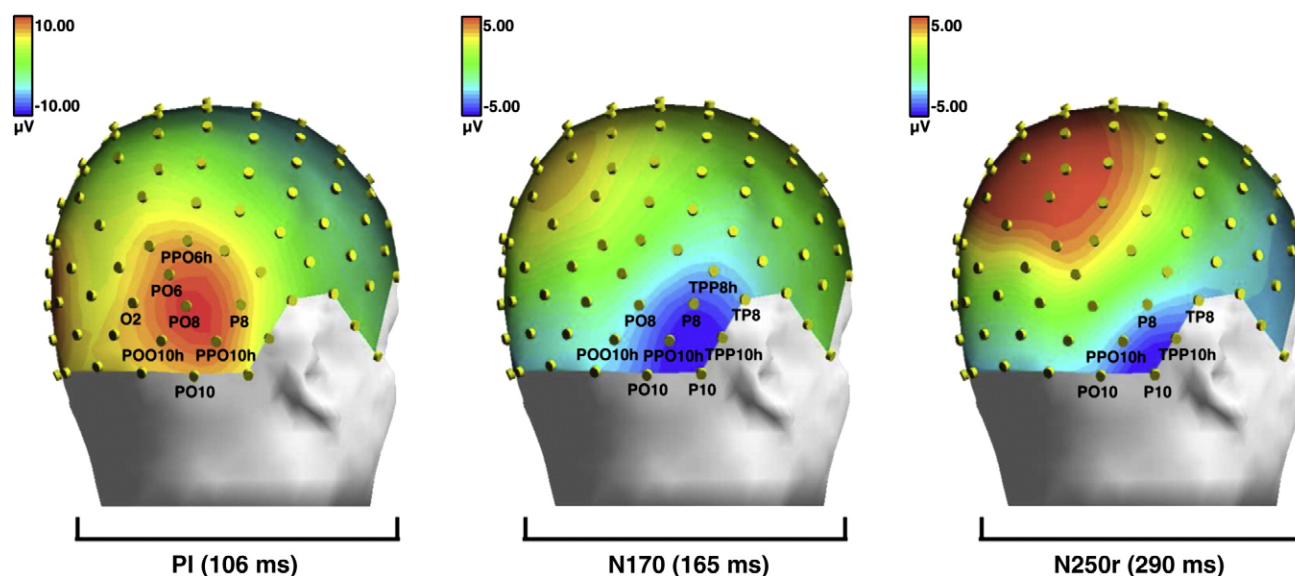


Fig. 3. Topographical display from grand-averaged data of all participants ($n = 16$) of the sequence of evoked visual potentials of interest in the right hemisphere and their mean peak latency. The electrode sites labeled here were defined based on the topographical maps and those used in analyzing the P1, N170, and N250r visual components.

given permutation sample the ERP data (consisting of the whole electrode \times time-point matrix) for the two conditions compared are randomly permuted within each subject (i.e. paired comparisons) to obtain two new bins of size N . Because permutation shuffles the assignment of the conditions, the difference between the means of the two new bins reflects the difference between conditions under the null hypothesis. We performed 10,000 of all 2^{16} possible permutations to generate a distribution of ERP differences under the null hypothesis. Comparing the observed ERP difference between the two conditions with the permutation distribution allowed estimating the probability that this observed ERP difference was due to chance (i.e. a p -value). The results of this analysis are displayed in time by electrode statistical plots in which significant differences between conditions are color-coded as a function of the amplitude of ERP difference. To minimize the probability of type I errors (false positives) due to the large number of comparisons performed, only significant differences at the $p < .01$ (two-tailed), that lasted for more than 20 consecutive time-samples (Rugg et al., 1995) and included a cluster of at least two neighbor electrodes were considered.

Results

Behavioral results

Observers performed the face delayed face matching task successfully, with an average performance of 95% across conditions (Table 2). There was a significant difference between the 4 conditions on accuracy rates ($F(3,45) = 5.91$, $p = .002$). Participants were less accurate when matching identical faces than in the conditions requiring discrimination (shape-different, reflectance-different, different, $p < .01$). There was no difference between these three different conditions ($p > .05$). This was particularly true for the shape-different and reflectance-different conditions, which led to equal performance ($p = .738$). This observation is consistent with previous studies showing that in addition to face shape, surface reflectance properties contribute to face recognition (Troje and Bülthoff, 1996; Lee and Perrett, 1997; O'Toole et al., 1999; Yip and Sinha, 2002; Vuong et al., 2005; Russell et al., 2006, 2007; Jiang et al., 2007; Russell and Sinha, 2007). Similar effects were found for correct response times (RTs; Table 2), with a significant main effect of condition ($F(3,45) = 9.45$, $p < .0001$). Participants were faster in the different condition than all other conditions ($p < .01$), and were slower in the same condition than all other conditions ($p < .05$).³

Most importantly for our purpose, as for accuracy rates, there was no hint of a difference between the shape-different and reflectance-different conditions ($p = .97$) in terms of the speed of behavioral response.

Event-related components: amplitude analysis

Electrophysiological data time-locked to the presentation of the test face stimulus showed the classical succession of visual event-related potential (ERP) waveforms in response to complex visual events (Fig. 3).

First, a bilateral occipital positivity (P1) was observed, which was slightly larger in the right than in the left hemisphere ($F(1,14) = 4.97$,

Table 2
Behavioral results.

	Conditions			
	Same	Shape-different	Reflectance-different	Different
Response times (ms)	733.9 \pm 31.7	693.5 \pm 42.3	694.2 \pm 43.7	639.7 \pm 39.2
Accuracy (%)	90.8 \pm 2.2	95.7 \pm .9	96.3 \pm .9	98.3 \pm .6

Mean correct response times and accuracy (\pm standard error) data for four experimental conditions.

$p = .043$) but did not differ in amplitude between the 4 conditions ($F(3,42) = .48$, $\epsilon = .81$, $p = .659$) (Fig. 4A). Aside from differences in amplitude recorded between the local electrode sites irrespective of the conditions ($F(7,98) = 6.56$, $\epsilon = .33$, $p = .003$), there were no other significant effects on the P1 amplitude. Even though face-sensitivity due to low-level parameters may be observed at that early latency in some studies (Halgren et al., 2000; Tanskanen et al., 2005; Rossion and Jacques, 2008), the absence of adaptation to individual faces on the P1, an early visual potential originating from striate and extrastriate visual areas (Clark et al., 1995; Di Russo et al., 2002), is in line with previous observations (Jacques et al., 2007).

Second, the face-sensitive N170 potential was larger on the lateral compared to the more medial electrodes ($F(8,120) = 19.71$, $\epsilon = .39$, $p < .0001$) (Fig. 3) and showed an effect of condition on the most posterior channels only (Condition \times Electrode interaction ($F(24,360) = 3.72$, $\epsilon = .22$, $p = .0037$; effect of Condition on posterior channels: ($F(3,45) = 8.29$, $\epsilon = .91$, $p = .0003$). Compared to the repetition of the same face, the N170 amplitude was largely increased when a different face was presented ($p < .0001$, Fig. 4A). Whether this individual face repetition effect is taken as an adaptation effect to the same individual face or a release from adaptation to different faces (e.g., Jacques et al., 2007; Ewbank et al., 2008), it is generally taken as evidence that the perceptual system has accumulated enough evidence from neuronal populations' responses to discriminate between individual exemplars of faces at that latency (see also Jacques and Rossion, 2006). Most importantly, when compared to the repetition of the same face, the EEG amplitude at that latency was larger when the difference between the two faces was defined by 3D shape alone, but not by 2D reflectance alone ($p > .05$) (Fig. 4A). Thus, individual faces that differed in shape alone were discriminated at the N170 level, whereas the reflectance change alone was insufficient for such discrimination. In addition, the shape-different condition did not differ from the different condition ($p = .54$), further indicating that the surface reflectance information did not contribute substantially to face individualization at that early stage. The N170 amplitude observed in the two critical conditions (shape-different and different conditions) was significantly larger than that in the reflectance-different condition (respectively, $p = .046$ and $p = .011$).

Third, the statistical analysis on amplitude revealed a second wide time-window, between 250 ms and 350 ms following stimulus onset (Fig. 4A), in which the three conditions of interest differed from the same condition. The differences were highly significant ($p < .01$) for all three conditions on a large subset of occipito-temporal channels. This time-window corresponds to the so-called N250r, the relative negative ERP for repeated compared to unrepeated faces around 250 ms over temporal electrodes (Fig. 3, e.g. Begleiter et al., 1995; Kovacs et al., 2006; Caharel et al., 2009), which has been shown to be sensitive to immediate (e.g. Schweinberger et al., 2002; Caharel et al., 2009) and short lag individual face repetitions (Pfütz et al., 2002). Here the N250r was larger in amplitude on the most lateral electrodes compared to other channels ($F(5,75) = 10.41$, $\epsilon = .39$, $p = .0004$). Most importantly, the N250r amplitude differed across conditions ($F(3,45) = 31.9$, $\epsilon = .67$, $p < .0001$) (see Fig. 4A), being more negative for the same condition than for the shape-different, reflectance-different

³ This slower response time when participants have to match as compared to discriminate individual faces in a delayed presentation task is not unusual when the two stimuli must be compared, and when there are several ways according to which the faces can differ (shape versus reflectance; relative distances between features versus local features, etc.) (e.g., Sergent, 1984). Indeed, as soon as a difference is found between the target and adapter face, whether it is in terms of shape, reflectance or both, the participant can respond. However, for "same" trials, he/she has to make sure that there is no difference, in any of the property of the face. This requires processing both the shape and the reflectance in the present experiment when the adapter and the target face are identical.

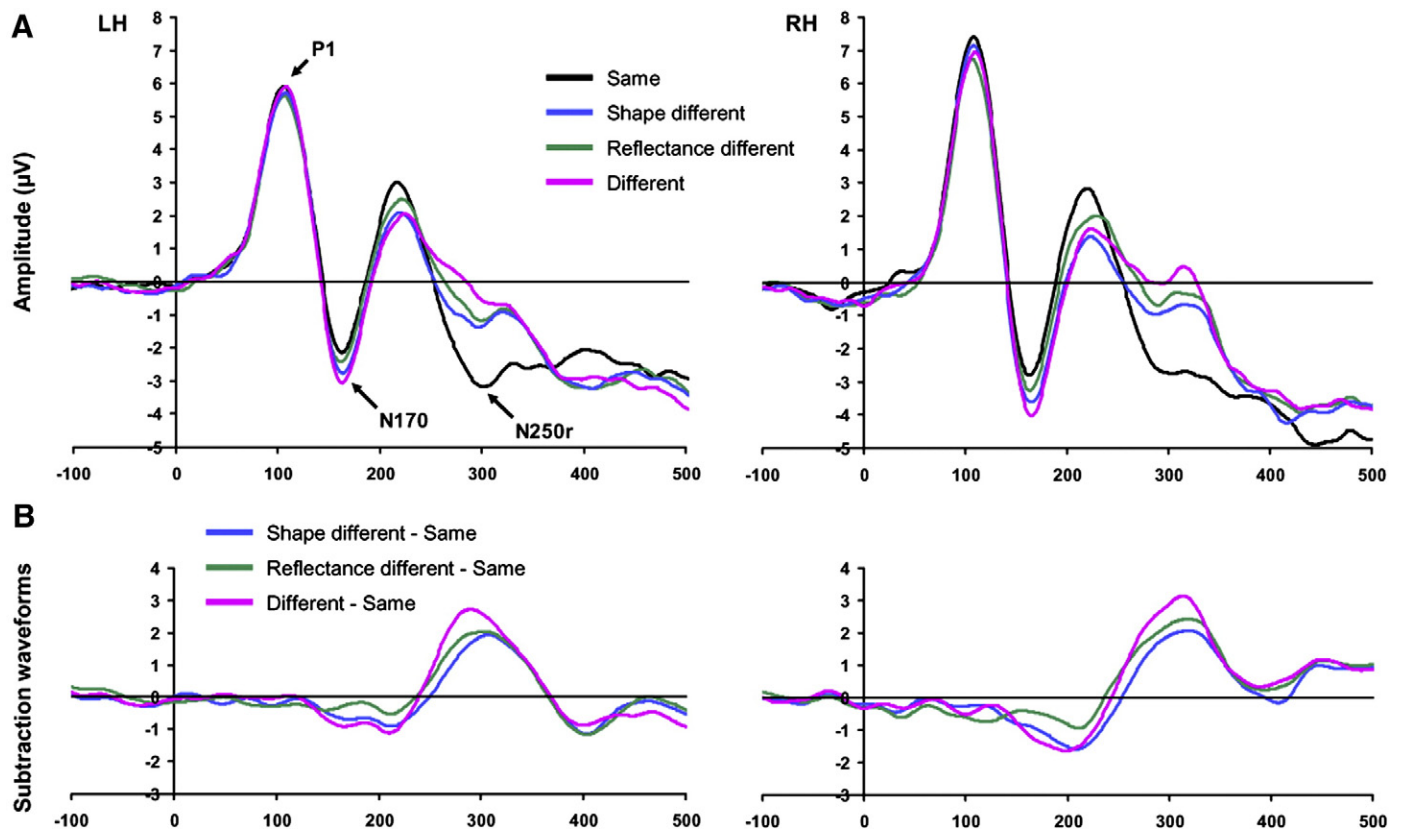


Fig. 4. Grand average ERP waveforms elicited by the second (test) face at left and right pooled occipito-temporal electrode sites (waveforms averaged for electrodes P9/10, PPO9/10h, PO7/8, POO9/10h, P7/8, PO9/10). (A) ERP components for all four conditions (same, shape-different, reflectance-different and different). (B) Subtraction ERP waveforms (ERP waveforms elicited in the same condition were subtracted out from ERPs elicited in the shape-different, reflectance-different and different conditions, respectively).

and different conditions ($p < .0001$). There was no significant difference between the shape-different and reflectance-different conditions ($p = .55$), but both conditions produced a more negative amplitude than the different condition (respectively, $p = .01$ and $p = .044$). Hence, the different condition produced the largest adaptation effects at that latency.

Finally, we also observed a clear dissociation from about 350 ms between the condition “same” and the other three conditions, at centro-parietal electrode sites, which was identified as a P3b (Supplementary Fig. S1), in agreement with the view that this component reflects the association of the perceptual representation with the decision that has to be taken about the stimulus (Verleger et al., 2005).

Differential waveforms: N170 and N250r

In order to take into account the inter-subject variance in the raw EEG amplitude data, ERP waveforms obtained in the same condition was subtracted point-by-point from each of the waveforms obtained in the 3 conditions of interest (shape-different, reflectance-different, different). The differential waveforms resulted from subtraction enabled us to identify the exact time-course of individual face discrimination based on face properties manipulated in this study (Fig. 4B).

The amplitudes of the differential waveforms during N170 window were submitted to a repeated-measures analysis with factors of conditions (3 levels), hemisphere, and electrode. A significant main effect of condition was observed ($F(2,30) = 4.50$, $\epsilon = .91$, $p = .023$). Shape-different (difference = $-.86 \pm .24 \mu V$ (SE)) and different (difference = $-.99 \pm .23 \mu V$) conditions led to equally large voltage differences ($p = .52$), which were in turn significantly larger than the reflectance-different condition (respectively,

$p = .034$ and $p = .007$) (see Figs. 4B and 5). There was also a marginally significant effect of hemisphere ($F(1,15) = 4.14$, $p = .059$), but the interaction between condition and hemisphere did not reach significance ($F(2,30) = 4.45$, $\epsilon = .88$, $p = .61$). This marginal Hemisphere effect, therefore, indicates that only the overall differences had a tendency to be larger in the right than in the left hemisphere. This tendency, however, is more evident in the shape-different and different conditions (Fig. 4B), as confirmed by the point-by-point permutation test (Fig. 6).

The analysis on the differential waveforms during N250r window confirmed these results. The differential amplitude for the different condition (difference = $+2.95 \pm .42 \mu V$) was larger than for the shape-different (difference = $+2.09 \pm .33 \mu V$; $p = .001$) and reflectance-different conditions (difference = $+2.28 \pm .39 \mu V$, $p = .009$). There was no significant difference between the shape-different and reflectance-different conditions ($p = .42$) (Figs. 4B and 5).

Point by point permutation tests

Finally, to identify precisely the time-point at which individualization based on shape or reflectance information of the faces emerged on occipito-temporal channels, we applied permutation tests on differential waveforms at each time-point at relevant electrodes (see methods). This analysis showed again that as early as 160 ms following stimulus onset, shape change alone led to significant amplitude differences with respect to the repetition of the same face on a large cluster of occipito-temporal electrodes (Fig. 6, starting significance level at channel POO10h). Most importantly, the contribution from shape alone at this early stage was only evident in the right hemisphere. The analysis also shows that reflectance change alone does not lead to a significant amplitude difference until 250 ms after the onset of the test

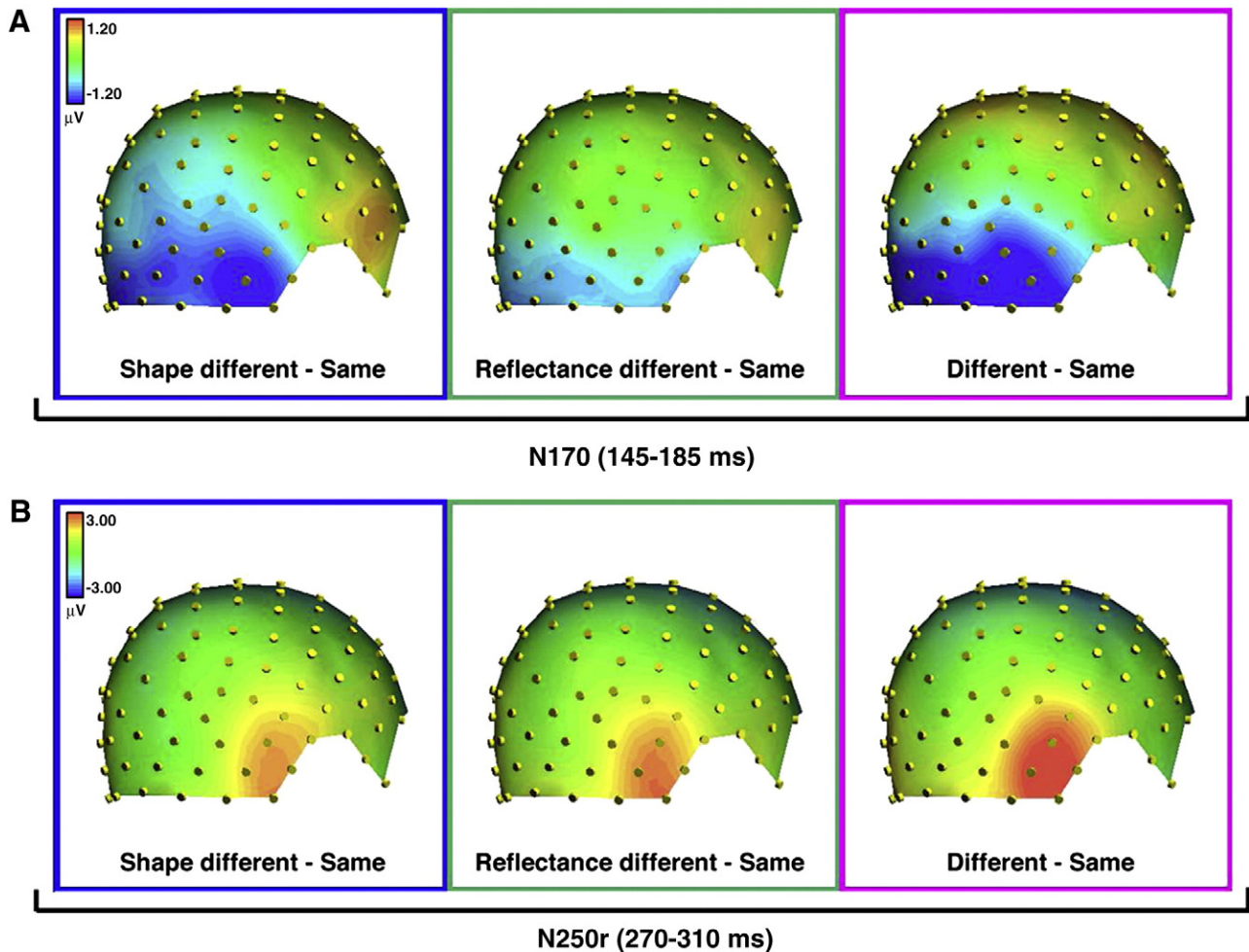


Fig. 5. Topographical maps of grand-averaged data during the N170 (between 145 and 185 ms) and N250r (between 270 and 310 ms) time-windows, representing differences comparing the shape-different, reflectance-different, and different conditions, respectively compared to the repeated face ("same") condition.

stimulus. At this level (~250–350 ms), the effect is found bilaterally in all three conditions, and is the strongest when both shape and reflectance information is diagnostic.

Discussion

Using an ERP face adaptation paradigm, we examined the time-course of individual face perception based on 3D shape versus 2D surface reflectance information. We found that early sensitivity to individual faces (~160–230 ms) was due predominantly or even exclusively to diagnostic 3D shape information, an observation that has not been reported before and cannot be derived from behavioral data. The observations made on the later N250r time-window (~250–350 ms) indicate a contribution of both 3D shape and 2D surface reflectance information, equally strongly. The combined changes in both face shape and surface reflectance induced larger effects than any one of the changes did alone. This integration advantage is entirely compatible with the behavioral responses that occurred several hundreds of milliseconds later: participants were faster when 3D shape and 2D reflectance were simultaneously diagnostic, than when only one of the sources of information was diagnostic (Table 2). Thus, both our behavioral and electrophysiological observations are consistent with studies demonstrating an important role of 3D shape and 2D surface information in the perception of face identity (Troje and Bühlhoff, 1996; Lee and Perrett, 1997; O'Toole et al., 1999; Yip and Sinha, 2002; Vuong et al., 2005; Russell et al., 2006, 2007; Jiang et al., 2007; Russell and Sinha, 2007).

However, and most importantly, our findings reveal a processing difference at an early encoding stage of individual faces between the two main forms of diagnostic cues that are used by our perceptual system: 3D shape and 2D surface reflectance. That is, early sensitivity to individual faces, during the N170 window, is predominantly based on 3D shape diagnostic cues, while 2D surface reflectance does not contribute significantly at this latency. The N170, or the M170 as recorded with Magnetoencephalography, is a well documented visual potential observed at the occipito-temporal surface whose onset time (~130 ms) generally marks the earliest reliable sensitivity to the category of faces (i.e., difference in amplitude on the scalp between faces and non-face objects, e.g. Bentin et al., 1996) which cannot be accounted for by low-level parameters (Rousselet et al., 2008; Rossion and Jacques, 2008). Here the contribution of 3D shape (alone or combined with reflectance) to face individualization took place at about 160 ms, i.e. 30 ms after the initial categorization of the stimulus as a face marked by the N170 onset time. This is in line with previous observations of N170 repetition effects to an individual face made with the same parameters of stimulation as here (Jacques et al., 2007; Caharel et al., 2009), or different parameters (Campanella et al., 2000; Ewbank et al., 2008; Guillaume and Tiberghien, 2001; Itier and Taylor, 2002; Jemel et al., 2003; Heisz et al., 2006), although none of these studies could disentangle the contribution of 3D shape versus 2D reflectance in accounting for these early effects.

Our observations indicate that as early as 160 ms following the onset of the face, the visual system has accumulated enough information from 3D shape alone to discriminate two individual

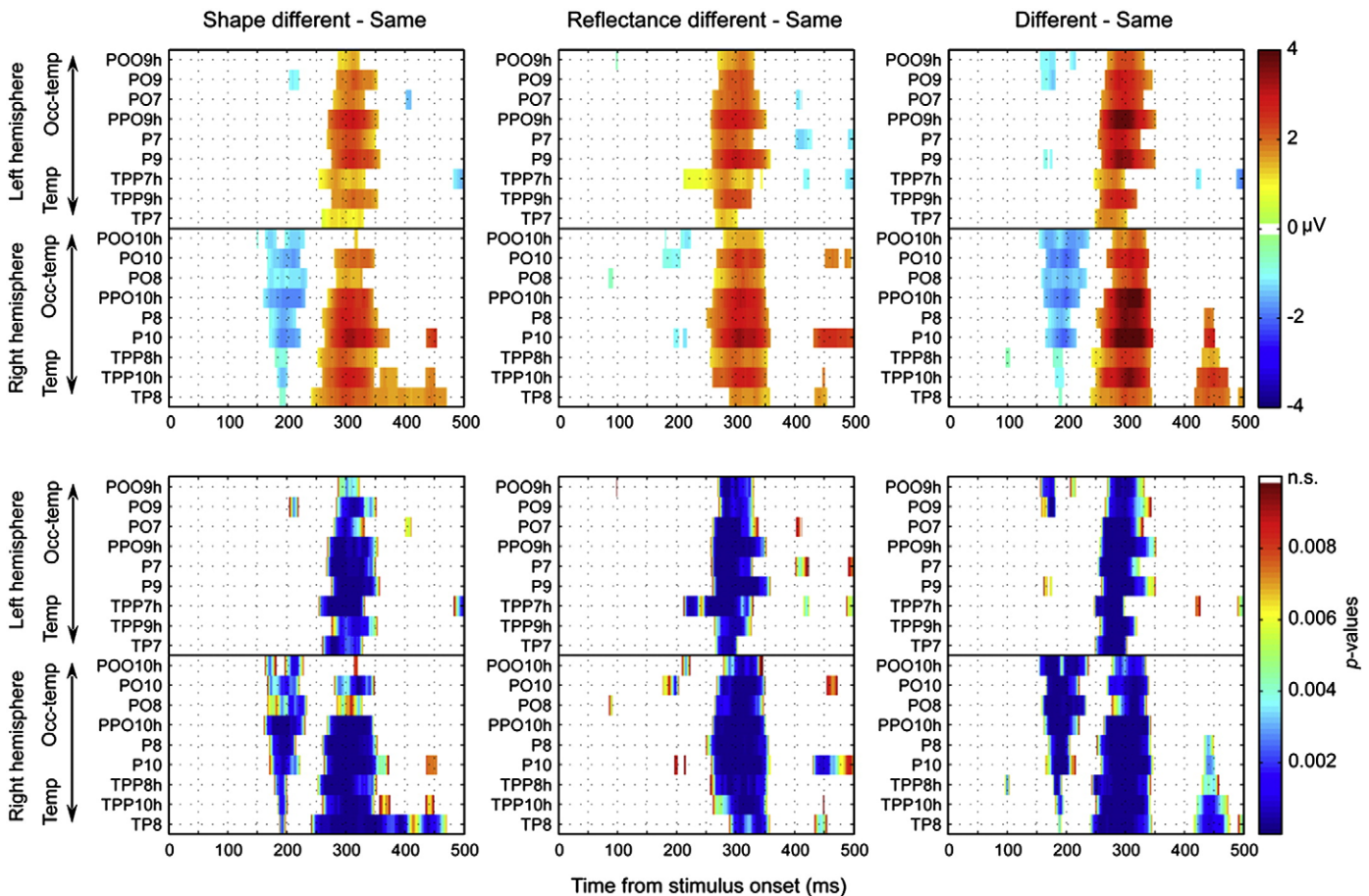


Fig. 6. Permutation statistical tests comparing the shape-different, reflectance-different, and different conditions, respectively, to the repeated face (same) condition. Each column shows the time-course of the significant differences ($p < 0.01$; two-tailed) between two conditions. Analyses were performed on each time sample for 9 occipito-temporal electrodes and significant differences are color-coded as a function of the amplitude of the ERP difference (upper row) and the p -value (lower row). The first area of significance (in blue in the upper row) takes place between 150 ms and 200 ms in the right occipito-temporal cortex for the conditions shape-different (left) and different (right). The second significance area (in red) was centered around 300 ms, bilaterally, and with the strongest effect occurring in the Different condition, where both the 3D shape and 2D surface reflectance were combined (rightmost column).

exemplars of a category (faces) that has been activated a few tens of milliseconds earlier. Thus, while observers' behavior indicated a strong contribution of 2D reflectance, and an equal performance as when shape alone was diagnostic, the contribution of reflectance was not significantly found in this early sensitivity to individual faces. This observation underlies the power and interest of recording global signal processing in the human brain at the millisecond range in order to reveal differences in sensitivity to different kinds of visual information that can be absent from behavioral outputs. Note that even though a change in 2D surface reflectance between the adaptor and target face did not give rise to significant increase at the level of the N170, there was a small variation in amplitude with respect to the repetition of the same face (Fig. 4A), suggesting that some information has accumulated from reflectance cues, but that it is insufficient at this stage to distinguish individual faces. However, with information derived from highly realistic surface-reflections, perhaps on familiar faces (see below), we cannot exclude that stronger and earlier effects of sensitivity to the individual face would be observed.

Notwithstanding the contribution of 2D surface reflectance during the recognition of an individual face, the present observations indicate that this contribution takes place significantly only *after* the early extraction of 3D shape diagnostic information, particularly in the right hemisphere. One major factor underlying this temporal advantage of diagnostic shape information could be that 3D shape can be extracted from a very coarse representation of the stimulus, because shape defines the global contour of the face (e.g., round versus elongated

head shape, see Fig. 1) in addition to local cues (mouth or eyebrows shape, etc), while 2D surface reflectance concerns essentially the fine details of the stimulus (eye color, skin pigmentation, etc). Several sources of evidence in the behavioral literature indicate that faces are processed along a coarse-to-fine hierarchy (Sergent, 1986), coarse information about a global individual face stimulus becoming available before the fine details (Coin et al., 1992; Parker et al., 1997; Morrison and Schyns, 2001; Goffaux and Rossion, 2006). This view has also received support from single-cell recording studies, reporting that the same populations of face-selective cells may carry information for coarse categorization early in their response, and then for finer-grained analysis of the stimulus (Sugase et al., 1999). The dominance of the right hemisphere in the early (but not later) sensitivity to 3D shape changes also supports this interpretation, since the global or holistic mode of processing an individual face is largely dependent on the right hemisphere (Hillger and Koenig, 1991; Schiltz and Rossion, 2006). If this interpretation is correct, our results may perhaps explain at least partly why there is still a discrepancy between studies observing early (N170) sensitivity to individual face repetition (e.g., Guillaume and Tiberghien, 2001; Jemel et al., 2003; Heisz et al., 2006; Jacques et al., 2007; Ewbank et al., 2008) and other studies reporting only later (>250 ms) effects (e.g., Begleiter et al., 1995; Henson et al., 2003; Schweinberger et al., 1995; Tanaka et al., 2006). In addition to other methodological factors (adaptor and ISI duration, presence or absence of intervening stimuli), the lack of an early N170 effect could be due to the fact that the natural 3D shape variations,

which largely accounted for early individual face repetition effects reported in the current study, is often minimized in some experiments (e.g. through “cropping” or normalization of the face contour).

Here, to make this point clear, our results do not imply that the first wave of information reaching face representations in the ventral visual stream would be essentially low spatial frequency and achromatic (Delorme et al., 2000). Indeed, early face-sensitivity as recorded by the N170 onset may well be boosted by appropriate color and texture of the face at the category level, just like what is observed for populations of face-selective neurons in monkeys' infero-temporal cortex (e.g., Edwards et al., 2003), and what is found for colored versus achromatic visual scenes (Goffaux et al., 2005). Rather, the present observations indicate that diagnostic information about a particular individual's face accumulates faster in the visual face processing system from 3D shape than from 2D surface reflectance, presumably because of an earlier availability of global cues conveyed by 3D shape information alone.

Finally, we note that the respective contribution of these two sources of information, and their differential time-course at the level of the early access to face representations (N170), might be dependent on face familiarity. Several studies have reported that the later part of the N170 response is enhanced in amplitude for familiar faces (e.g., Caharel et al., 2006; but see Bentin and Deouell, 2000). Interestingly, electrophysiological activity in response to familiar faces is unaffected by shape caricaturing, whereas effects are observed for unfamiliar faces, for which caricaturing increases occipito-temporal N170 and N250 components (Kaufmann and Schweinberger, 2008). In addition, using an image-averaging technique, it has been shown that recognition of familiar (averaged) faces is high even when shape information is normalized (Burton et al., 2005). The role of reflectance information also seems to be more crucial for the recognition of personally familiar (friends) faces (Russell and Sinha, 2007). The faces used in the present study were unfamiliar to the participants. Thus, it would be interesting to determine, using the same face adaptation paradigm in ERPs, the time-course of processing for shape and reflectance information for familiar faces. Given the evidence described above, it may be that surface reflectance properties modulate the time-course of face processing earlier for familiar than unfamiliar faces, perhaps as early as for diagnostic 3D shape information.

In conclusion, while confirming their complementary contribution, the present observations disentangle in time the contribution of the two main sources of diagnostic information for face recognition, revealing an earlier sensitivity to 3D shape than 2D surface reflectance in the human brain.

Acknowledgments

We thank Corentin Jacques for his help in data analysis and illustration. This work was supported by a grant from Communauté Française de Belgique – Actions de Recherche Concertées [07/12-007] and a Human Frontier Science Program (HFSP) postdoctoral award to Fang Jiang. Bruno Rossion and Stéphanie Caharel are supported by the Belgian National Fund for Scientific Research (Fonds de la Recherche Scientifique – FNRS).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.05.065.

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