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Investigation of effects of face rotation on race processing: An ERPs study

Benoit Montalan, Mathieu Veujoz, Alexis Boitout, Arnaud Leleu, Odile Camus, Robert Lalonde, Mohamed Rebaï

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N170

Abstract

Recent ERP research has indicated that the processing of faces of other races (OR) and same race (SR) as the perceiver differs at the perceptual level, more precisely for the N170 component. The purpose of the present study was to continue the investigation of the race-of-face processing across multiple orientations. Event-related brain potentials (ERPs) and performance were recorded when Caucasian participants were required to categorize by race Caucasian and African faces presented in eight different angles of orientation. Three main observations were made: (1) the face-sensitive N170 is modulated by the race of faces, being larger in response to OR compared to SR faces; (2) face rotation affected this component in the same pattern for both racial groups; (3) the N170-ORE progressively disappeared as the faces moved away from their canonical orientation at the right hemisphere only. Thus, the current findings suggest that configural/holistic information is extracted from faces of both racial groups, but that upright OR faces require increased demands.

1. Introduction

As a central source of information in social interactions, faces are considered "special" among visual categories (Farah, Wilson, Drain, & Tanaka, 1998). A large body of evidence of face specificity in visual processing initially comes from studies based on the "face inversion effect" (FIE) (Yin, 1969). Stimulus rotation by 180° in the picture plane has been observed to impair the processing of faces to a larger extent than other non-facial stimuli (e.g., Bartlett & Searcy, 1993; Farah, Tanaka, & Drain, 1995; Leder & Bruce, 2000; Rhodes, Brake, & Atkinson, 1993; Searcy & Bartlett, 1996; Sergent, 1984; Valentine, 1988; Yin, 1969), suggesting that face perception is based on a particular processing mode (Farah et al., 1998; Marzi & Viggiano, 2010). While non-facial object perception typically involves feature-based analytic processing, face perception mainly depends on configural and holistic processing strongly affected by picture-plane inversion (for reviews see Rossion, 2008, 2009; Valentine, 1988). Analytic processing focuses on the constituent parts of a face, such as individual facial features and their properties and configural/holistic processing on relations between the constituent elements of a face (e.g., Maurer, Le Grand, & Mondloch, 2002; McKone & Yovel, 2009). It is argued that configural/holistic face perception relies on several levels of processing (Diamond & Carey, 1986; Maurer et al., 2002; Rossion & Gauthier, 2002; Tanaka & Farah, 1993): first-order configural processing, i.e. the detection

of internal features in a specific face-like spatial configuration (two eyes above nose, nose above mouth), holistic processing, i.e. combining the facial features into a gestalt-like representation, and second-order configural processing, i.e. perceiving the relative distances between facial features.

A more refined approach has also been undertaken to study the influence of inversion on perceptual processing in face perception by presenting faces at multiple orientations rather than only two (upright and inverted). However, the results from behavioral studies manipulating face rotation across multiple angles have been mixed. Some research workers have found a strict linear relationship (i.e. a quantitative shift) between performance and the degree of disorientation (Valentine & Bruce, 1986). For others, this pattern revealed an early linear normalization mechanism (e.g., mental rotation). In contrast, other studies showed that performances deviated from linearity (i.e. a qualitative shift) as a function of face orientation at orientations around 90–120° (e.g., Mondloch & Maurer, 2008; Murray, Yong, & Rhodes, 2000; Rossion & Boremanse, 2008; Sturzel & Spillmann, 2000), confirming qualitatively distinct modes used to process upright versus inverted faces (Rossion, 2008, 2009).

Electrophysiological studies have also contributed to understanding face processing by means of temporal dynamics of brain activity during face and non-face object processing (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier & Taylor, 2002, 2004; Rebaï, Poiroux, Bernard, & Lalonde, 2001). Most ERPs studies focused on the N170, a negative deflection peaking between 140 and 180 ms after stimulus onset distributed over occipito-temporal areas. This

component is thought to represent neural activity involved in the perceptual encoding stage of faces (Bentin & Deouell, 2000; Eimer, 2000; for a review see Rossion & Jacques, 2008). The N170 appeared to be particularly relevant in this case because evidence has been accumulating that this component is sensitive to configural/holistic processing (Eimer, Gosling, Nicholas, & Kiss, 2011; Latinus & Taylor, 2006). It has been largely demonstrated that face inversion modulates the N170 by increasing latency and/or amplitude for inverted faces (Bentin et al., 1996; Caharel, Bernard, Lalonde, Fiori, & Rebaï, 2006; Rossion, Delvenne, Debatisse, Goffaux, Bruyer, Crommelinck, & Guérit, 1999; Itier & Taylor, 2002, 2004; Rossion, Gauthier, Tarr, Despland, Linotte, Bruyer, & Crommelinck, 2000). Therefore, N170 modulation in response to face inversion indicates that the underlying neural processes are not just involved in the feature-based analytic processing, but also in configural/holistic processing (Eimer et al., 2011; Latinus & Taylor, 2006).

Whereas configural/holistic processing is considered a hallmark of face perception, it has been shown that such processing is not applied to faces of other races (OR) faces in the same way as to faces of the same race (SR) than the perceiver (Michel, Caldara, & Rossion, 2006; Michel, Rossion, Han, Chung, & Caldara, 2006; Rhodes, Tan, Brake, & Taylor, 1989; Tanaka, Kiefer, & Bukach, 2004). More precisely, it has been suggested that configural/holistic processing is reduced for faces of other racial groups (Michel, Caldara, et al., 2006; Michel, Rossion, et al., 2006; Rhodes, Tan, Brake, & Taylor, 1989; Tanaka et al., 2004). According to the contact hypothesis, this likely stems from reduced experience or contact with other-race faces and may be the cause of the "other-race" effect (ORE) (for a review on the different theoretical accounts, see Meissner & Brigham, 2001).

Recent ERP research also addressed the question of whether processing of SR and OR faces differ at the perceptual level by focusing on the N170 component. It is worth pointing out, however, that the N170 sensitivity to the race of faces is currently equivocal given that no consistent effects on either amplitude or latency of the N170 have been reported (Ito & Bartholow, 2009). Several studies found that both amplitude and latency of the N170 were insensitive to race (Caldara, Rossion, Bovet, & Hauert, 2004; Caldara et al., 2003). In contrast, some studies reported race effects only on N170 latencies (Wiese, Stahl, & Schweinberger, 2009), with delayed N170 in response to OR compared to SR faces. But most researchers (Herrmann et al., 2007; Stahl, Wiese, & Schweinberger, 2008, 2010; Walker, Silvert, Hewstone, & Nobre, 2007; Wiese, 2012) observed an increased amplitude in the face-sensitive N170 to OR faces compared to SR faces (but for the opposite pattern, see Ito & Urland, 2005), in concordance with an enhancement of the N170 amplitude in response to facial manipulation disrupting configural/holistic processing typically applied to faces, such as face inversion (Jacques & Rossion, 2009, 2010).

It is interesting to examine recent ERP studies simultaneously investigating the FIE and the ORE. Some authors showed that inversion affects latencies (Gajewski, Schlegel, & Stoerig, 2008) or amplitudes (Caharel et al., 2011; Vizioli, Foreman, Rousset, & Caldara, 2010) of the N170 predominantly for faces from the same race of the participants, while others did not find an interaction between race and inversion effects on N170 amplitude (Wiese et al., 2009). Such a discrepancy is probably due to methodological differences. Indeed, some authors (Wiese et al., 2009) used facial and non-facial stimuli, while others (Caharel et al., 2011; Vizioli, Foreman, et al., 2010; Vizioli, Rousset, and Caldara, 2010) used only facial stimuli. Nevertheless, it has been shown that the N170 is more likely to be modulated by race when faces are perceived in a homogenous context consisting only of faces (Ito & Urland, 2005), demonstrating that the context in which we look at a face may dictate the priority of initial information extraction during perceptual encoding. Moreover, the task used by Wiese et al.

(2009) required answering whether the stimuli were upright or inverted. In the study of Vizioli, Foreman, et al., 2010; Vizioli, Rousset, et al. (2010), participants were instructed to perform an orthogonal task requiring pressing keys on the keyboard every time a "colored face" appeared on the screen. So, race was task-irrelevant in both studies, contrary to the race-categorization task used by Caharel et al. (2011), assumed to be more susceptible to affect face processing in a more configural/holistic mode for faces categorized as SR rather than OR (Michel, Corneille, & Rossion, 2010).

As a follow-up to this line of endeavor, the aim of the present study was to collect more empirical evidence on the differential processing of SR and OR faces at the perceptual level. To achieve this objective, behavioral and electrophysiological data were recorded in Caucasian participants performing a race-categorization task with Caucasian and African faces. We considered the race-categorization task as particularly relevant because race modulation of the N170 seems to be highly task-dependent (Ito & Urland, 2005) and most previous workers investigated the N170 sensitivity to race by using tasks in which race information was irrelevant (Gajewski et al., 2008; Vizioli, Foreman, et al., 2010; Vizioli, Rousset, et al., 2010; Wiese et al., 2009; but see Caharel et al., 2011; Caldara et al., 2003). Most importantly, ERPs were recorded in response to faces presented at eight different orientations from 0° to 360° in 45° steps rather than contrasting only upright and inverted faces as in previous studies (Gajewski et al., 2008; Vizioli, Foreman, et al., 2010; Vizioli, Rousset, et al., 2010; Caharel et al., 2011). Presenting face stimuli at multiple orientations should allow us to specify with a more refined approach whether perceptual encoding of faces, reflected by the N170 component, is impaired by face rotation in the same/different manner for OR and SR faces (Jacques & Rossion, 2007; Jemel, Coutya, Langer, & Roy, 2009). Secondly, it should allow us to determine at which angle of rotation effects of race of faces on N170 amplitude and/or latency disappear.

2. Method

2.1. Participants

Fifteen volunteers (10 female, mean age 22 years) from the University of Rouen participated in the study. All subjects were right-handed (Oldfield, 1971), reported normal or corrected-to-normal visual acuity, and had no history of brain injury or trauma. Informed consent was obtained from each participant. None of the participants reported having extensive social contact with African individuals. One subject (one female) was excluded due to excessively noisy EEG.

2.2. Stimuli

Eight Caucasian (Western Europeans: four males and four females) and eight African (Sub-Saharan Africans: four males and four females) unfamiliar faces were used in frontal view with neutral expression. An oval mask was used to isolate each face (see Fig. 1) and to discourage the use of a non-face feature. Resulting cropped faces were converted to a 256 gray-level format, rescaled proportionally to a size of 5.32° × 53° (6.5 × 9.2 cm), and equated for mean pixel luminance with Adobe® Photoshop® 7.0 software.

2.3. Procedure

After electrode-cap placement, subjects were comfortably seated in a light-attenuated room at a viewing distance of 70 cm

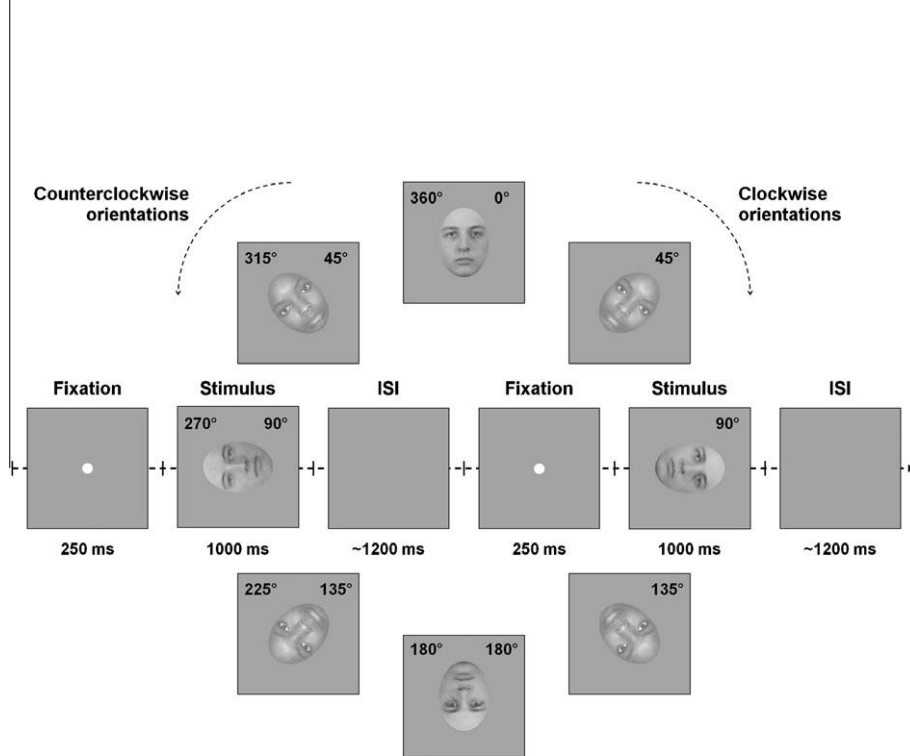


Fig. 1. Timeline of stimulus sequence and examples of face stimuli as a function of the eight different angles of orientation.

from a computer monitor. Stimuli were displayed on a light grey background. A trial started with a fixation point displayed at the center of the screen for 250 ms. After the offset of the fixation point, a face appeared for 1000 ms in one of eight orientations (0°, 45°, 90°, 135°, 180°, 225°, 270°, or 315°, Fig. 1). The offset of each stimulus was followed by a blank-screen during a random inter-stimulus interval (ISI) ranging from 1000 to 1400 ms (mean ISI: 1200 ms). Participants performed 64 trials for each of the 16 experimental conditions (eight face stimuli repeated eight times in eight orientations for both racial groups). Trials were presented in a pseudo-random order (to avoid the immediate repetition of the same stimulus) in two experimental blocks with a self-timed break in-between. Participants indicated as fast and correctly as possible whether face stimuli were Caucasian or African by pressing with the right hand one of two computer keys as soon as the stimulus appeared, with key assignment counterbalanced across participants.

2.4. EEG recording

Electroencephalographic activity was recorded from 32 surface electrodes according to the 10–20 classification system with a reference electrode placed in the fronto-central position (AFz). Electrode impedance was kept below 5 K Ω . The EEG was continuously recorded along with codes synchronized to stimulus delivery for averaging sample epochs offline. The EEG was amplified, digitized at a rate of 256 Hz, filtered (band-pass 0.1–100 Hz), and stored with Deltamed™ software. A common average reference was recalculated off-line. Only trials with correct responses were included in the averages and trials contaminated with ocular movements or artifacts (>100 μ V) were rejected. In the final phase, the data were digitally low-pass filtered with a cut-off of 48 Hz. Artifact-free data were then segmented into epochs ranging from 250 ms before to 750 ms after stimulus onset for each electrode in each condition.

2.5. Statistical analyses

Percentages of correct responses and reaction times (RTs) ranging between 150 and 1500 ms were separately submitted to a repeated-measure analysis of variance (ANOVA) with Race

(Caucasian vs. African) and Orientation (eight levels) as within-subject factors (see Table 1). Trials on which errors were made (1.3% of trials) were omitted from the statistical analysis.

Two ERP components time-locked to the onset of the facial stimulus were analyzed: the P1 and the N170. Peak amplitude and latency of the P1 and the N170 were extracted at the maximum amplitude value between 70 and 130 ms for the P1, and at the minimum amplitude value between 130 and 190 ms for the N170, at two occipito-temporal electrode sites in the left and right hemisphere (PO7 and PO8) where both components peaked maximally in all conditions (see Tables 2 and 3). These electrodes and the corresponding signals depending on the orientation and the race of faces are displayed in Fig. 2.

Given that eyes' region plays a critical role in face perception (Nemrodov & Itier, 2011), only orientations for which this region had a contralateral visual field position relative to the electrode position were included in the P1 and N170 analyses (for similar analyses, see Jacques & Rossion, 2007). Thus, the analyses on the right hemisphere electrode (PO8) were performed on orientations going counter-clockwise from 0° to 180° (eyes in left visual field), whereas those on the left hemisphere electrode (PO7) included clockwise orientations from 0° to 180° (eyes in right visual field).¹ The P1 and N170 parameters were therefore analyzed by using repeated-measures ANOVA with Race (Caucasian vs. African), Orientation (five levels), and Hemisphere (right vs. left) as within-subject factors. For all these analyses, Greenhouse–Geisser corrections with adjusted degrees of freedom were applied for controlling type I errors, corresponding to the epsilon (ϵ) value (Keselman & Rogan, 1980). Post-hoc *t*-tests (Bonferroni corrected for multiple comparisons) were also performed whenever necessary. In addition, it was particularly interesting to study the shape of orientation function associated with perceptual encoding. Therefore, we examined the effects of orientation with polynomial contrasts. Linear–quadratic relationship was used to describe effects of orientation on amplitude and latency

¹ A likely problem with the approach of Jacques and Rossion (2007) is that any differential effects in the two hemispheres are not easy to interpret because the Hemisphere factor is confounded with the particular stimuli used. To clarify this issue, the latency and amplitude values of the N170 were also submitted to a repeated-measure ANOVA with Race (Caucasian vs. African), Orientation (eight levels), and Hemisphere (left vs. right) as within-subject factors. Results are available in the "Supplementary Results" file.

Table 1

Accuracy (% of correct responses) and RTs (ms) elicited by Caucasian faces and African faces as a function of the eight different angles of orientation.

Angles (°)	Caucasian faces				Angles (°)	African faces			
	RTs (ms)		Accuracy (%)			RTs (ms)		Accuracy (%)	
	M	SE _M	M	SE _M		M	SE _M	M	SE _M
0	462	22	98.77	0.49	0	465	27	98.77	0.59
45	460	26	99.11	0.44	45	460	23	98.44	0.64
90	464	25	98.99	0.50	90	463	28	98.88	0.43
135	466	25	98.77	0.42	135	469	29	98.88	0.49
180	462	24	98.66	0.44	180	468	27	98.32	0.67
225	468	25	98.44	0.78	225	465	27	98.60	0.62
270	463	27	98.54	0.67	270	470	26	99.33	0.33
315	468	26	98.66	0.44	315	454	25	98.43	0.45
360	462	22	98.77	0.49	360	465	27	98.77	0.59

Table 2

ERP measures for the P1 elicited by Caucasian faces and African faces as a function of the eight different angles of orientation at PO7 and PO8 electrodes.

Angles	Caucasian faces				Angles	African faces			
	P1 amplitude (µV)		P1 latency (ms)			P1 amplitude (µV)		P1 latency (ms)	
	M	SE _M	M	SE _M		M	SE _M	M	SE _M
<i>PO7</i>									
0	4.89	0.48	113.84	2.27	0	5.19	0.74	114.40	2.37
45	5.87	0.70	114.68	2.11	45	5.85	0.91	114.68	2.19
90	5.19	0.74	114.40	2.37	90	5.54	0.62	116.91	2.44
135	5.85	0.91	114.68	2.19	135	6.43	0.90	111.89	2.51
180	5.54	0.62	116.91	2.44	180	5.61	0.56	115.23	2.38
225	6.43	0.90	111.89	2.51	225	6.37	0.95	116.35	1.79
270	5.61	0.56	115.23	2.38	270	6.20	0.54	117.75	2.42
315	6.37	0.95	116.35	1.79	315	7.03	0.94	121.09	1.92
360	4.89	0.48	113.84	2.27	360	5.19	0.74	114.40	2.37
<i>PO8</i>									
0	5.87	0.70	114.68	2.11	0	5.85	0.91	114.68	2.19
45	5.19	0.74	114.40	2.37	45	5.54	0.62	116.91	2.44
90	5.85	0.91	114.68	2.19	90	6.43	0.90	111.89	2.51
135	5.54	0.62	116.91	2.44	135	5.61	0.56	115.23	2.38
180	6.43	0.90	111.89	2.51	180	6.37	0.95	116.35	1.79
225	5.61	0.56	115.23	2.38	225	6.20	0.54	117.75	2.42
270	6.37	0.95	116.35	1.79	270	7.03	0.94	121.09	1.92
315	6.20	0.54	117.75	2.42	315	5.71	0.54	115.79	2.97
360	5.87	0.70	121.09	1.92	360	5.85	0.91	119.42	1.99

Table 3

ERP measures for the N170 elicited by Caucasian faces and African faces as a function of the eight different angles of orientation at PO7 and PO8 electrodes.

Angles	Caucasian faces				Angles	African faces			
	N170 amplitude (µV)		N170 latency (ms)			N170 amplitude (µV)		N170 latency (ms)	
	M	SE _M	M	SE _M		M	SE _M	M	SE _M
<i>PO7</i>									
0	-4.77	0.56	166.57	3.00	0	-6.38	0.62	164.34	3.46
45	-6.10	0.63	169.64	2.61	45	-6.78	0.67	171.04	3.15
90	-6.47	0.67	171.04	2.01	90	-7.84	0.76	171.60	3.05
135	-7.23	0.74	171.32	2.65	135	-8.33	0.81	169.92	2.45
180	-6.78	0.74	170.76	1.94	180	-7.34	0.82	170.76	2.51
225	-7.38	0.69	171.04	2.72	225	-7.04	0.80	172.16	2.51
270	-7.79	0.80	171.88	2.17	270	-7.03	0.92	174.39	2.27
315	-6.73	0.76	166.57	3.16	315	-7.75	0.78	169.09	2.67
360	-4.77	0.56	166.57	3.00	360	-6.38	0.62	164.34	3.46
<i>PO8</i>									
0	-3.62	0.86	165.74	3.14	0	-5.66	1.02	163.50	2.08
45	-6.48	0.99	168.81	3.15	45	-7.98	1.07	169.36	2.88
90	-7.12	1.04	173.55	2.31	90	-7.67	1.24	171.60	2.67
135	-7.40	1.08	172.71	2.72	135	-7.81	1.15	169.92	2.45
180	-8.05	1.19	170.48	2.30	180	-7.81	1.22	169.64	2.12
225	-8.65	1.34	170.48	1.90	225	-8.73	1.27	169.92	2.52
270	-7.77	1.26	171.88	2.81	270	-7.97	1.07	169.92	2.68
315	-6.03	1.01	169.09	3.39	315	-6.95	1.07	168.53	3.52
360	-3.62	0.86	165.74	3.14	360	-5.66	1.02	163.50	2.08

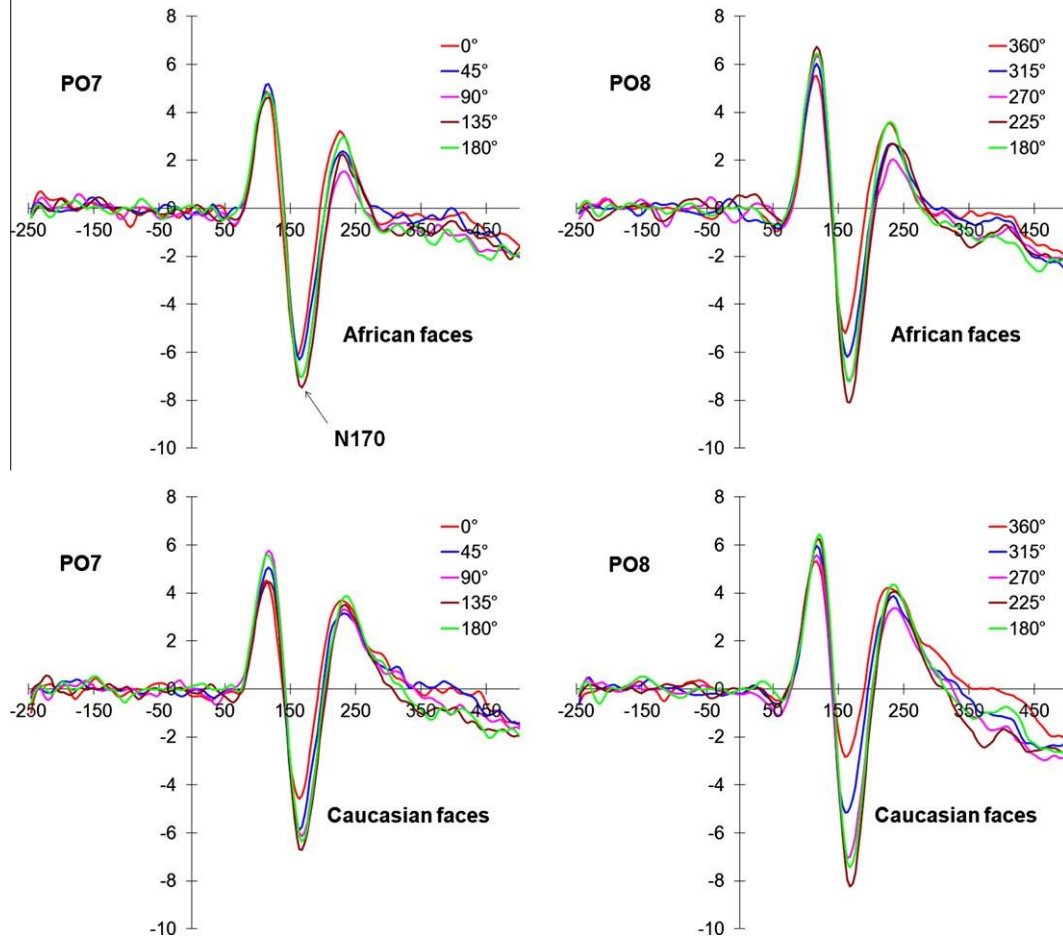


Fig. 2. Grand average ERP waveforms for Caucasian faces and African faces as a function of the eight different angles of orientation at two occipito-temporal electrodes (PO7 and PO8).

of the N170 component to determine whether perceptual processing decreases gradually with orientation (quantitative hypothesis) or by an abrupt shift (qualitative hypothesis) (Jacques & Rossion, 2007). A significance level of $p < 0.05$ was used for all reported results. (see Fig. 3).

3. Results

3.1. Behavioral data

Participants performed the race categorization task successfully, with a global average percentage of correct responses of 98.7%. No significant results were found with this dependent variable. Likewise, no significant main effects or interactions were found with RTs.

3.2. Electrophysiological data

3.2.1. P1 component

The three-factor ANOVA revealed no significant main effects or interactions on P1 amplitude. In contrast, the orientation effect on P1 latency reached significance ($F(4, 52) = 3.78, \eta^2 = 0.81, p < 0.05$), due to earlier P1 for the canonical orientation of faces than for all other orientations ($p < 0.05$).

3.2.2. N170 component

The three-factor repeated measure ANOVA on N170 latency showed a main effect for Orientation ($F(4, 52) = 12.50, \eta^2 = .67,$

$p < 0.001$), due to earlier N170 at 0° than 90° ($p < 0.05$). The trend of this relationship between face orientation and N170 latency was assessed by applying polynomial contrasts. These analyses revealed that N170 latency functions included both a significant linear ($F(1, 13) = 25.19, p < 0.001$) and quadratic ($F(1, 13) = 9.80, p < 0.01$) components that accounted respectively for 56.0% and 38.1% of the total variance in the data.

For N170 amplitude, a main effect for Race was revealed ($F(1, 13) = 23.70, p < 0.001$), due to larger amplitudes for OR faces than SR faces. The interaction between Race and Hemisphere reached also significance ($F(1, 13) = 7.27, p < 0.05$). Post-hoc *t*-tests (Bonferroni corrected) revealed a significant effect of the race of faces on N170 amplitude at the left hemisphere electrode (PO7) ($p < 0.05$). N170 amplitude was affected by face rotation as revealed by a significant Orientation effect ($F(4, 52) = 21.70, \eta^2 = .48, p < 0.001$). Bonferroni corrected post-hoc *t*-tests showed that the N170 amplitude was more negative in the $90^\circ/270^\circ$ – 180° range in comparison to the canonical orientation ($p < 0.005$) on both occipito-temporal electrodes (PO7/PO8). However, this FIE on N170 amplitude differed between left and right hemisphere sites, as revealed by a significant Orientation-by-Hemisphere interaction ($F(4, 52) = 5.70, \eta^2 = .45, p < 0.05$). Post-hoc comparisons indicated that the N170 was larger in response to faces presented at 135° compared to upright faces ($p < 0.001$) over the left electrode. On the right, the N170 was larger in the 315° – 180° range in comparison to the canonical orientation, and at 225° more than 315° ($p < 0.01$). This was reflected by polynomial contrasts showing that variations in N170 amplitude included a linear ($F(1, 13) = 15.37,$

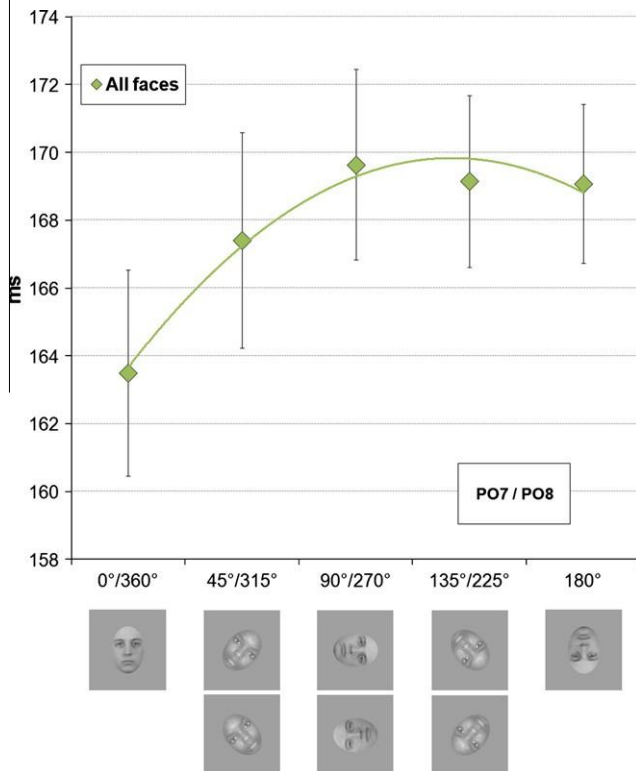


Fig. 3. Peak latencies of the N170 as a function of the eight different angles of orientation. Latency values are shown for orientations in which the eyes are in the contralateral visual field relative to the electrode position, i.e. for orientations going clockwise from 0° to 180° at PO7 and for orientations counter-clockwise from 360° to 180° at PO8. The curve represents second-order regression which provides the best fit to the data. Error bars represent standard errors of the mean.

$p < 0.001$) and a quadratic ($F(1, 13) = 9.45, p < 0.005$) component for the left electrode (PO7), accounting respectively for 67.0% and 27.0% of the total variance in the data. A significant trend for linear ($F(1, 13) = 32.04, p < 0.001, 75.0\%$ variance explained) and quadratic ($F(1, 13) = 13.29, p < 0.005, 23.3\%$ variance explained) components was also observed for the right electrode (PO8). However, modulations of the N170 amplitude by facial rotation were more marked at the right than at the left hemisphere electrode. Comparisons between the slopes of the linear trend effects obtained in the two hemispheres revealed a greater slope for PO8 than for PO7 ($F(1, 13) = 8.75, p < 0.05$). The Race \times Orientation interaction effect reached significance ($F(4, 52) = 4.71, \eta^2 = .80, p < 0.005$). Post-hoc t -tests revealed that the N170 was larger in response to OR in comparison to SR faces only when presented at 0° ($p < 0.005$). Finally, and more importantly, the ANOVA showed a significant second-order interaction between Race, Orientation, and Hemisphere ($F(4, 52) = 2.91, \eta^2 = .80, p < 0.05$). A significant interaction between Race and Orientation ($F(4, 52) = 6.17, \eta^2 = .79, p < 0.005$) was discovered at the right hemisphere site (PO8) only. Post-hoc comparisons (Bonferroni corrected) showed that the N170 amplitude was more important for OR faces than for SR faces only at 0° ($p < 0.001$). Moreover, SR faces presented in the 270–180° range elicited a larger N170 than those presented at 0° and 315° ($p < 0.001$). For the same faces, N170 amplitude increased at 315° compared to 0° ($p < 0.001$). For OR faces, post-hoc t -tests (Bonferroni corrected) showed increased N170 in response to orientations from 45° to 180° in comparison to the canonical orientation ($p < 0.001$). Additionally, OR faces rotated by 135° elicited larger N170 than those rotated by 45° ($p < 0.001$). Polynomial contrasts revealed that the relationship between face orientation and

N170 amplitude was a combination of linear ($F(1, 13) = 44.36, p < 0.001, 79.2\%$ variance explained) and quadratic ($F(1, 13) = 13.42, p < 0.005, 20.4\%$ variance explained) components for SR faces (see Fig. 4). Similarly, N170 amplitude modulations with orientation included a linear ($F(1, 13) = 16.39, p < 0.001$) and a quadratic ($F(1, 13) = 8.65, p < 0.05$) component for OR faces (see Fig. 4), accounting respectively for 67.3% and 28.5% of the total variance in the data. However, the slope of the linear trend for SR faces was more important than for OR faces ($F(1, 13) = 35.39, p < 0.001$). Additional polynomial contrasts performed on N170 differences between OR and SR faces only revealed a significant trend for a linear component ($F(1, 13) = 35.39, p < 0.001, 87.9\%$ variance explained), indicating that the N170-ORE decreased linearly with face rotation. Finally, at the left hemisphere site (PO7), the race effect reached significance ($F(1, 13) = 33.81, p < 0.001$) regardless of face orientation, OR faces eliciting larger N170 than SR faces.

4. Discussion

The general goal of the present study was to investigate the race-of-face processing across multiple orientations. To that end, ERPs and performance were simultaneously recorded when Caucasian participants were required to categorize by race Caucasian and African faces presented in eight different angles of orientation (0°, 45°, 90°, 135°, 180°, 225°, 270°, or 315°).

Contrary to previous studies (Caharel et al., 2011; Caldara et al., 2004; Levin, 1996, 2000; Valentine & Endo, 1992; Zhao & Bentin, 2008), no ORE was found at the behavioral level (i.e. percentages of correct responses and RTs for correct responses). This absence of an other-race categorization advantage could be due to methodological factors, such as the small number of faces of each racial group used. Indeed, it is possible that stimuli repetitions made facial identity highly overlearned during the experiment, the categorization task being therefore performed on the basis of the idiosyncratic properties of individual stimuli, even if participants were explicitly attending to racial information. In addition, performances were unaltered by face rotation, indicating that racial information was efficiently extracted from faces regardless of their orientation (Cloutier & Macrae, 2007). This lack of face rotation effects on performances can also be explained by the fact that the race-categorization task does not emphasize the processing of facial identity (Rossion & Boremanse, 2008), contrary to face recognition, assumed to be most sensitive to inversion (Jacques & Rossion, 2007; Rossion & Gauthier, 2002).

Our ERP findings showed that multiple face orientations affected the N170 component by modulating its latency and amplitude in a non-linear fashion. N170 amplitude and latency increased almost linearly between 0° and 90°, or slightly beyond 90°, and then slightly decreased up to 180°. The latency delay of the face-sensitive N170 is found whatever the stimulus manipulations made. It is generally ascribed to the longer time required by populations of neurons in the visual cortex to detect a transformed face in the visual environment (Perrett, Oram, & Ashbridge, 1998), as seen initially in the monkey infero-temporal cortex (Perrett, Mistlin, Chitty, Smith, Potter, Broenimann, & Harries, 1988). More specifically, some authors (Maurer et al., 2002) suggested that face inversion delays the N170 component because of an increased difficulty in detecting first-order relations, i.e. the common configuration shared by all faces. This last assertion could explain why our ERP data did not report a race effect on N170 latency, the two types of stimuli sharing the same basic facial configuration. Although this result is inconsistent with previous findings which reported delayed (Gajewski et al., 2008) or early (Stahl et al., 2008, 2010; Wiese et al., 2009) N170 peaks to SR compared to OR faces, it tallies with the observation that the neural ORE is independent of the

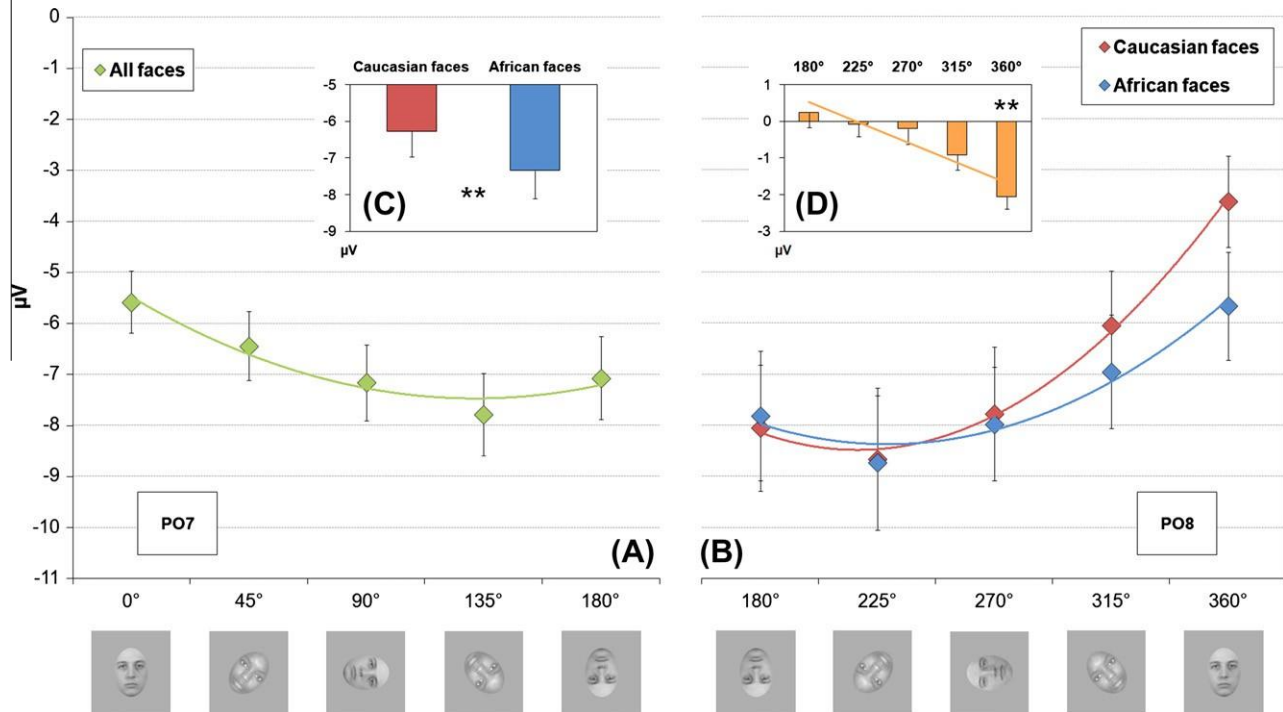


Fig. 4. Peak amplitudes of the N170 component as a function of the eight different angles of orientation. (A and B) Amplitude values are shown for orientations in which the eyes are in the contralateral visual field relative to the electrode position, i.e. for orientations going clockwise from 0° to 180° at PO7 and for orientations going counter-clockwise from 360° to 180° at PO8. The curves represent second-order regressions which provide the best fit to the data. (C) Histograms represent the differences between African and Caucasian faces at PO7. (D) Histograms represent the differences between African and Caucasian faces at PO8 as a function of orientations going counter-clockwise from 0° to 180°. The curve represents the linear regression which provides the best fit to the data. Error bars represent standard errors of the mean. ^m*p* < 0.05, ^{mm}*p* < 0.005.

well-known N170 latency delay caused by inversion (Wiese et al., 2009). In addition, since face rotation delayed N170 latency in the same pattern for Caucasian and African faces, this suggests that the relevant processing (e.g., first-order relations processing) was disrupted by stimulus manipulation to a similar extent.

Contrary to N170 latency, orientation and race of faces affected N170 amplitude. The impact of the FIE on N170 amplitude is still controversial (Rossion et al., 1999; Sadeh & Yovel, 2010). According to a “quantitative hypothesis”, inverted faces lead to an enhancement of activity of the same neural populations used for the processing of upright faces due to the increased difficulty to extract configural/holistic and/or featural information (e.g., Marzi & Viggiانو, 2007; Sekuler, Gaspar, Gold, & Bennett, 2004). According to a “qualitative hypothesis”, the increase in amplitude of the N170 component with face rotation comes mainly from the response of neurons sensitive to non-facial object stimuli (Jacques & Rossion, 2010; Rossion & Gauthier, 2002) and/or the eyes region (Nemrodov & Itier, 2011) in addition to the response of face-sensitive neurons. Our study did not allow us to clarify whether face inversion reflects a quantitative or a qualitative change in processing mode. Indeed, the present data appears to be consistent with the latter point of view, i.e. with the qualitative predictions of a curvilinear shape of the N170 amplitude modulation by face rotation (Jacques & Rossion, 2007; Jemel et al., 2009; Rossion, 2008; Rossion & Boremanse, 2008). However, we cannot assert that orientation effects on this component are curvilinear in nature given that linear trends also fit our data very well. Besides, some authors have recently provided support for both the quantitative and qualitative accounts for face rotation effects (Jemel et al., 2009). Thus, in order to clarify this issue, the N170 amplitude modulation as a function of face rotation should be tested in tasks which allow us to isolate more closely configural/holistic and feature-based processing (Mondloch & Maurer, 2008; Rossion & Boremanse, 2008).

Nevertheless, this orientation effect was more important in the right (PO8) relative to the left hemisphere site (PO7). The N170 is larger in response to faces than objects in both hemispheres, with usually (but not always) a larger N170 amplitude difference between faces and objects in the right than the left hemisphere (Bentin et al., 1996; Itier & Taylor, 2004; Rossion et al., 2003). Moreover, the face-sensitive N170 is generally found to be larger in the right than the left hemisphere, although some studies indicate the reverse (e.g., Balas & Nelson, 2010). Despite the absence of a classical right hemisphere lateralization, our finding is consistent with numerous studies that previously identified an inter-hemispheric difference for face processing; that is, the right hemisphere is more specialized in configural/holistic processing of faces, while feature-based processing would rather involve the left hemisphere (e.g., Rhodes et al., 1993; Scott & Nelson, 2006).

Particularly interesting with regard to our objective, the effect of race on N170 amplitude depended on face rotation at the right hemisphere electrode, whereas the effects of race and orientation did not interact at the left hemisphere electrode. Over the right hemisphere, OR faces elicited larger N170 than SR faces at 0°, and this neural ORE then disappeared for further orientations up to 180°.

As indicated in the introduction, it has been proposed that the reduced configural/holistic processing mode observed for OR faces is the cause of the ORE (Rossion & Michel, 2011). Given the absence of an OR advantage in race categorization at the behavioral level, our ERPs findings cannot support this theoretical account. However, they replicate previous findings showing that upright OR faces are processed differentially at the perceptual level in comparison to upright SR faces, the former eliciting a larger N170 than the latter. This observation is in line with an enhancement of the N170 amplitude in response to facial manipulation impairing the configural/holistic processing typically applied to faces. Nevertheless,

this is not to say that upright OR faces are processed as inverted faces (Balas & Nelson, 2010). Indeed, face rotation affected the right-lateralized N170 amplitude in the same pattern for both racial groups. This could rather suggest that configural/holistic information is extracted from OR faces while requiring a greater amount of resources. Thus, the enhancement of the right-lateralized N170 elicited by upright OR faces might reflect the increased demands placed on processing configural/holistic information (see also Caharel et al., 2011; Walker et al., 2007). Besides, we found that this difference in processing upright OR and SR faces at the perceptual level decreased linearly as function of face rotation. It is worth noticing, however, that some authors did not observe such differences on the N170 for upright faces, but, critically, found that inverted SR faces lead to greater recognition impairment and elicit larger N170 amplitudes compared to inverted OR faces (Vizioli, Foreman, et al., 2010; but for the reverse pattern, see Caharel et al., 2011). Therefore, future studies using tasks that tap into various aspects of face perception (from feature-based to configural/holistic processing) are necessary to clarify such a discrepancy, probably due to methodological differences.

One might also claim that such effects on the N170 amplitude are not genuinely related to race, but merely due to uncontrolled low-level parameters. One way to control low-level effects would have been to use participants and stimuli of different racial groups in order to obtain a perfect cross-over interaction. But this was not the case in the present study and we cannot consequently be sure that the effects on the ERP signal are actually related to race. Indeed, recent findings highlighted the critical role played by skin color on the ORE (Balas & Nelson, 2010; Brebner, Krigolson, Handy, Quadflieg, & Turk, 2011). For example, Brebner and collaborators (2011) found that the perceptual encoding of faces was selectively sensitive to skin color, showing an increase in N170 negativity to faces with OR skin color (see also Balas & Nelson, 2010). For these authors, skin color would be used as a race-diagnostic cue leading to a more feature-based processing of OR faces (Fallshore & Schooler, 1995), thus affecting configural/holistic processes associated with the N170 component. However, in an attempt to control for the effects of low-level parameters on the processing of OR and SR faces, we used as in numerous ERP studies grayscale images (e.g., Caldara et al., 2003, 2004; Vizioli, Foreman, et al., 2010; Wiese et al., 2009). In addition, picture-plane rotation is a transformation known for offering important control for low-level visual information (Balas & Nelson, 2010; Rossion, 2008). Consequently, neural activity modulations by race as early as at the N170 time-window is unlikely to be due to uncontrolled low-level parameters, such as color, since no N170 amplitude differences between OR and SR faces were found for orientations from 90° to 180°. Instead, according to the contact hypothesis, the difference between OR and SR faces in perceptual processing observed in the neighborhood of canonical orientation is probably due to the lesser visual experience of participants with OR relative to SR faces (Rhodes et al., 1989; Slone, Brigham, & Meissner, 2000; Valentine & Endo, 1992; Walker & Hewstone, 2006, 2008).

Finally, contrary to the right hemisphere findings, OR faces elicited larger N170 amplitudes than SR faces irrespective of orientation at the left hemisphere electrode. This observation is quite surprising relative to previous results. For example, Correll, Lemoine, and Ma (2011) found a more pronounced ORE as faces were presented to the left (rather than the right) visual field. In the same way, Turk, Handy, and Gazzaniga (2005) previously reported that a split-brain patient showed a behavioral ORE only when his right hemisphere was performing a face recognition task (i.e., when faces were presented in his left visual-field), whereas race did not affect recognition performance when the patient's left hemisphere was performing the task (i.e., when faces were presented in his right visual-field). Thus, the left hemisphere does not seem

to be able to process racial information. Again, Vizioli, Rousellet, et al. (2010) examined repetition suppression (RS), i.e. a pattern of adaptation when a stimulus is presented repeatedly, in the N170 component and found a RS for SR faces but not for OR faces. Of present interest, this pattern was most pronounced over right occipital/parietal regions. Finally, as suggested by Goldby, Gabrieli, Chiao, and Eberhardt (2001), the right hemisphere may be involved in individuating faces and the left hemisphere may be more important for categorizing OR faces with the use of race-specific information rather than individuating information. Moreover, recent findings mentioned that the ORE is not exclusively caused by configural/holistic but also by featural processing facilitation for SR compared to OR faces (Hayward, Rhodes, & Schwaninger, 2008; Rhodes, Hayward, & Winkler, 2006). In this vein, increased N170 amplitudes to OR faces observed over the left hemisphere might reflect greater effort to extract task-relevant information such as race-specific features. Besides, corroborating the present data, Stahl et al. (2008) found race effects on N170 amplitude at the left hemisphere electrode specifically, in line with the hypothesis that the left-lateralized N170 is particularly sensitive to featural changes in faces as opposed to configural/holistic changes (Scott & Nelson, 2006).

5. Conclusion

The general goal of the present study was to investigate the race-of-face processing across multiple orientations. We replicated previous findings showing that the face-sensitive N170 is modulated by the race of faces, being larger in response to OR compared to SR faces for both hemispheres. In addition, face rotation affected this component in the same pattern for both racial groups. However, only the effect of the race of faces on the right-lateralized N170 relied on face rotation, the N170-ORE progressively disappeared as the faces moved away from their typical upright orientation. In sum, the current findings indicate that configural/holistic information is extracted from faces of both racial groups, but that upright OR faces require more demands for processing.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.bandc.2012.12.004>.

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