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Face versus non-face object perception and the ‘other-race’ effect: a spatio-temporal event-related potential study

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Abstract

Objective: To investigate a modulation of the N170 face-sensitive component related to the perception of other-race (OR) and same-race (SR) faces, as well as differences in face and non-face object processing, by combining different methods of event-related potential (ERP) signal analysis.

Methods: Sixty-two channel ERPs were recorded in 12 Caucasian subjects presented with Caucasian and Asian faces along with non-face objects. Surface data were submitted to classical waveforms and ERP map topography analysis. Underlying brain sources were estimated with two inverse solutions (BESA and LORETA).

Results: The N170 face component was identical for both race faces. This component and its topography revealed a face specific pattern regardless of race. However, in this time period OR faces evoked significantly stronger medial occipital activity than SR faces. Moreover, in terms of maps, at around 170 ms face-specific activity significantly preceded non-face object activity by 25 ms. These ERP maps were followed by similar activation patterns across conditions around 190–300 ms, most likely reflecting the activation of visually derived semantic information.

Conclusions: The N170 was not sensitive to the race of the faces. However, a possible pre-attentive process associated to the relatively stronger unfamiliarity for OR faces was found in medial occipital area. Moreover, our data provide further information on the time-course of face and non-face object processing.

Keywords: Face processing; Event-related potentials; Temporal segmentation; Source reconstruction

1. Introduction

Recognizing faces is an essential and effortless social process, which takes only a few hundreds of milliseconds. At the functional level, it is dissociated from non-face object recognition, as suggested by several sources of evidence. For instance, brain-damaged patients with bilateral (Damasio et al., 1982; Gauthier et al., 1999a) or unilateral right occipito-temporal lesions (De Renzi, 1986; Landis et al., 1986) have been reported to suffer from prosopagnosia, a deficit that essentially impairs perception and recognition of faces while sparing object recognition (but see Gauthier et al., 1999a). Patients with a specific deficit for non-face object recognition and preserved face recognition have also been observed (e.g. Moscovitch et al., 1997), thus providing a double dissociation between face and object recognition. The idea that faces are differently processed than non-face object stimuli has also been suggested by several behavioral studies. For instance, face recognition is disproportionately impaired by the inversion of the stimulus as compared to non-face objects (Yin, 1969; for a recent review see Rossion and Gauthier, 2002). At the neural level, several methods have provided evidence for specific brain areas devoted to face processing. Single-unit recordings in non-human primates revealed neurons within the superior temporal sulcus and the inferior temporal cortex that preferentially respond to human and primate faces (e.g. Perrett et al., 1982; Desimone, 1991). Recent neuroimaging studies in normal subjects confirmed and refined the role of the occipito-temporal regions in face and non-face object processing (e.g. Kanwisher et al., 1997; McCarthy et al., 1997; Gauthier et al., 1999b, 2000; George et al., 1999).

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These studies suggested that there is at least an area in the fusiform gyrus, the so-called fusiform face area (FFA), that is highly responsive to faces, although other areas more activated for faces than objects are usually described in the occipito-temporal cortex and the superior temporal sulcus (for a review, see Haxby et al., 2000).

Electrophysiological studies have also contributed to the understanding of the temporal dynamics of brain activity during face and non-face object processing. Studies using intracranial recording techniques in patients undergoing presurgical epilepsy evaluations reported a face-specific event-related potential (ERP) component (N200) in the lateral fusiform and inferior temporal gyrus (Allison et al., 1994). More recently, an N200 component for non-face objects was found from sites that extended from the inferior lingual gyrus medially to the middle occipital gyrus laterally (Allison et al., 1999; McCarthy et al., 1999; Puce et al., 1999). Moreover, scalp ERP studies on human face perception have shown a face-sensitive component over the lateral temporal lobes (N170) (Bentin et al., 1996; George et al., 1996). Both electrophysiological components are not affected by face familiarity (Jemel et al., 1999; McCarthy et al., 1999; Rossion et al., 1999; Bentin and Deouell, 2000), and seem to be related to the 'structural encoding stage' of face processing described in the functional architecture of the Bruce and Young (1986) model (Bentin et al., 1996; Eimer, 1998).

However, previous electrophysiological studies have largely ignored an important factor in studying the electrophysiological correlate of face processing: the 'race' of the faces. In face perception theory, it was demonstrated almost a century ago that faces of ones own race are more accurately recognized than faces of other races (Feingold, 1914). This phenomenon, related to the popular belief that other-race faces 'all look alike', has often been reported as the 'other-race' effect (for reviews, see Shepherd, 1981; Anthony et al., 1992; Meissner and Brigham, 2001). Several empirical studies have confirmed the robustness of this phenomenon in recognition tasks. Faces of the same-race (SR) are recognized better and faster than other-race (OR) faces. A greater experience with own race faces has been proposed as an explanation of the other-race effect (e.g. Brigham and Barkowitz, 1978; Valentine and Endo, 1992; Fallshore and Schooler, 1995). Nevertheless, frequent contact with OR faces, namely the amount of the encountered OR faces without any need of recognizing them at the individual level, does not improve recognition ability for these faces (e.g. Brigham et al., 1982; Brigham and Malpass, 1985; Platz and Hosch, 1988). Several experimental and ecological studies suggested that essentially the quality of the contact, namely the necessity to recognize and discriminate OR faces at individual level, has an improvement in recognition performances for OR faces (Carroo, 1986; Chiroro and Valentine, 1995). Recently an alternative explanation of the other-race effect has been proposed by authors that have emphasized the role of social categorization factors in the observation of the other-race effects (Levin, 1996, 2000). Using visual search tasks, Levin (1996, 2000) has shown that Caucasian-American people take less time to detect an African-American face (OR face) among Caucasian faces (SR faces), than a Caucasian face among African-American faces. To explain these results, this author suggested that there is a quickly detected racial marker in OR faces that influence the level of processing for OR faces. However, the face feature(s) responsible for faster detection and classification of OR faces remain unknown (Levin, 1996). Levin (2000) proposed that emphasis on general social category information specifying race as visual feature, at the expense of individuating information, change interracial group perception and might be responsible for the other-race effect.

Recently, the neural basis of the perception of other race faces has been investigated by several neuroimaging studies (Hart et al., 2000; Phelps et al., 2000; Golby et al., 2001). In the study by Phelps et al. (2000) two independent groups of European-American subjects were exposed with European-American and African-American pictures and a greater activation of the amygdala was found for OR faces, suggesting a role of this structure in the social evaluation of racial groups (see also Hart et al., 2000). Golby et al. (2001) investigated the identification and recognition of different face races by European-American and African-American subjects and showed a greater activation of the FFA for own race faces during an encoding stage of a face recognition task. Moreover, the differential level of activation in the left FFA and the medial temporal lobe for SR and OR faces was correlated with the differential performance in a memory recognition task performed outside of the scanner. These results have been interpreted in the framework of the visual expertise studies. The primary implication of these results is that they showed that the activity of the FFA can be modulated by the level of expertise for within face category stimuli. Indeed, previous studies showed a greater activation of the FFA (and other face sensitive areas) for non-face objects for which subjects have developed a specific visual artificial expertise (see Gauthier et al., 1999b, 2000). However, Golby et al. (2001) suggest that a greater attention paid for SR faces could also explain a greater activation of the FFA. The latter interpretation is in line with the Levin (1996, 2000) explanation of the other-race effect. Taken together, and independent of the result interpretations, all these studies showed that social factors can influence the perception, the evaluation and the recognition of OR faces, and this can be observed at the brain level by different patterns of activity.

Given these recent findings, the first objective of the present ERP study was to track the temporal course of brain processing differences between SR and OR faces. To our knowledge, this question has never been investigated before in the face and object ERP literature and has even gained more interest with the recent neuroimaging findings described above. Moreover, it has been shown that the face-sensitive N170 component can also be modulated by visual expertise with non-face objects (Tanaka and Curran, 2001; Rossion et al., 2002). However, the question concerning its modulation by the visual expertise for within face category stimuli remains open.

Our first goal was to test whether the large N170 obtained for any kind of face configuration can be modulated by the interaction between the race of the face and the race of the observer. Our study will explore the N170 component under the light of the face within-category expertise. In order to do that, we presented Caucasian subjects with a classical design previously used to compare (Caucasian) face and object processing (Bentin et al., 1996), in which we added a set of Asian faces matched for low level visual properties. Thus, pictures of Caucasian and Asian faces as well as non-face objects (cars and furniture) were sequentially and randomly presented to Caucasian subjects. These stimuli were randomly interspersed with butterfly pictures as visual target stimuli. Subjects had to detect and mentally count the occurrence of target stimuli.

The second aim of the present paper was both methodological and theoretical. Until now, face and object processing has been studied in electrophysiological studies by conventional methods of ERP peak identification and measurement. While this method has already provided important information about the time course of these processes, it lacks an objective – data-driven – way to define these functional stages of processing, and thus depends highly on a priori hypotheses about the spatio-temporal areas of interest. For instance, the choice of the time window to calculate mean amplitudes tends to be influenced by subjective post hoc considerations (Picton et al., 2000, p. 142). An alternative approach, the spatio-temporal segmentation analysis (Lehmann and Skrandeis, 1980) is based on multi-channel ERP recordings and analysis of surface potential configurations (taking electrodes of a whole scalp array into account) and has been successfully applied recently to the study of low-level and high-level visual processes (e.g. Morand et al., 2000) and other cognitive processes such as mental imagery (Pegna et al., 1997), motor (Thut et al., 1999, 2000) and language processing (Khateb et al., 1999).

Here we applied this approach for the first time to face and object processing. It allowed us to submit the surface potential configurations to spatio-temporal analysis procedures which give access to stable periods of functional stages of processing (e.g. Michel et al., 1999b), namely microstates (or segments), for face and non-face objects. Finally, functional microstates were also submitted to two source localization algorithms, LORETA (Pascual-Marqui et al., 1994) and BESA (Scherg and Van Crammon, 1985).

2. Methods

2.1. Subjects

Twelve healthy Caucasian volunteers (six males) aged 20–30 years (mean age 25.4) participated in this experiment. All the subjects were classified as right-handed as measured by the Edinburgh Inventory (Oldfield, 1971), had a right predominant eye and normal or corrected-to-normal vision. None of the subjects knew more than one Asian person at the individual level, namely their name and their associated semantic information (such as profession), and all were unaware of the purpose of the present study.

2.2. Stimuli

One hundred and sixty different grayscale photographs of Caucasian (40 male, 40 female) and Asian faces (40 male, 40 female) digitally scanned from a college yearbook were used. No face had particular distinctive features and male faces were clean-shaven. All images showed a frontal view, with eyes aligned on the horizontal midline of the image. The non-face object stimuli consisted of 240 different grayscale pictures; evenly distributed in 3 categories (butterflies, cars and furniture). Face stimuli occupied a visual angle of $3.75° \times 4.25°$ and non-face object stimuli a visual angle of $4.75° \times 4.75°$.

2.3. Procedure

Subjects were seated in a dimly lit, sound-attenuated room. A computer monitor was placed at a distance of 120 cm from the participants. All stimuli were delivered for 200 ms at the center of the computer screen, with an inter-stimulus interval randomly varying between 2500 and 3500 ms. Stimuli were presented in 5 experimental sessions of 80 images each. In each session an equal number of Asian and Caucasian faces was presented ($n = 16$, half male, half female), randomly alternated with all 3 types of non-face object stimuli. Participants were engaged in a target detection task in which the target stimuli were butterflies. They were required to mentally count the number of butterflies and report it at the end of each experimental session. The number of target stimuli was randomized between sessions.

2.4. ERP recording and averaging

EEG was continuously recorded on line from 62 scalp sites (Electrocap International montage, Eaton, OH, USA), with an additional row of low temporo-occipital electrodes TP9/10, P9/10, PO9/10 and O9/10 using a 64-channel system. The sampling rate was 500 Hz (bandpass 0.16–160 Hz). All electrodes were referenced against the nose. Eye movement and eye blink artifacts were monitored using vertical and horizontal electro-oculogram (EOG) recordings and corrected off-line by an automatic algorithm. EEG epochs extended from 200 ms before to 1200 ms after stimulus onset. Data were baseline corrected to the first 200 ms of the epoch. Epochs were carefully scanned, and the epochs presenting remaining artifacts were rejected before averaged to individual evoked potentials. Finally, a low-pass filter of 30 Hz was applied to the averaged data.

2.5. ERP analysis

Data were subjected to two independent analyses procedures consisting of (1) ERP waveform analysis and (2) analysis of ERP map topography combined with source localization techniques. For the former approach, we measured the face sensitive N170 component. In contrast, in the latter approach time periods of face processing were defined by applying spatio-temporal segmentation analysis. Moreover, in order to reveal race-specific brain activation, comparisons between Caucasian and Asian face data were performed on amplitudes of selected occipito-temporal electrodes and on three-dimensional (3D)-current density in occipital regions of interest. The target condition (butterflies) was analyzed for control purposes only.

2.5.1. ERP waveform analysis

Peak amplitudes and peak latencies were computed for each category over time between 140 and 190 ms post-stimulus for each selected occipito-temporal electrode ($n = 19$) and each condition at a single latency per component per subject. Repeated-measures analyses of variance (ANOVA) were conducted using Greenhouse-Geisser adjusted degrees of freedom. The electrodes of interest corresponded to electrodes Pz, P1/2, P5/6, P7/8, P9/P10, POz, PO3/4, PO7/8, PO9/10, Oz and O1/2. A first repeated-measures ANOVA was conducted with Condition (Caucasian Faces, Asian Faces, Cars, Furniture) and Electrode Site (Pz-O1/2) as within-subject factors in order to test face-specific activation within the N170 period. Scheffé tests were used for post-hoc comparisons between conditions. A second repeated-measures ANOVA restricted to the face conditions with Race (Caucasian vs. Asian) and Electrode (Pz-O1/2) as factors was performed in order to test for race-specific activation patterns.

2.5.2. Analysis of map topography: identifying time periods reflecting condition-specific information processing

2.5.2.1. Reducing real-time ERP map series to time segments of stable map topography (spatio-temporal ERP segmentation). For ERP topography analysis, a spatio-temporal segmentation procedure was applied (Lehmann, 1987; Michel et al., 1999b). The procedure aims to define those intervals where surface ERP map topographies remain stable for a certain time (segments of stable maps) and the time points where they change from one stable configuration into another (segment borders). Such stable segments are commonly observed in ERP data and presumably reflect different functional stages of the brain, also referred to as *microstates*, activated during information processing (Lehmann and Skrandeis, 1980; Brandeis and Lehmann, 1986; Michel et al., 1992). The segmentation procedure, driven by the evolution of the ERP map topographies over time, is applied to the grand-mean ERP data (across subjects averages of individual ERPs), rescaled against the average reference (Lehmann and Skrandeis, 1980). The map strength is represented by the global field power (GFP) which is the spatial standard deviation of the map's potential distribution. The segments and their borders are determined via calculation of the global map dissimilarity (GMD) between pairs of successive maps (see Fig. 3). This measure is inversely related to the spatial correlation coefficient between two maps (Brandeis et al., 1992). Over time, the GMD curve shows low values where maps remain stable and high values where maps rapidly change from one topography configuration into another. GMD minima thus indicate segment kernels and GMD peaks segment borders. Usually, low stability of map topography around GMD peaks coincides with low map strength. After defining segment borders, ERP maps are averaged within time segments, resulting in one unique representative map per segment (grand-mean segment maps). Again, grand-mean segment maps were fitted in the grand-mean ERP data and each time point was labeled with the segment map it was most highly correlated with. This fitting procedure was used to smooth and refine the borders of the segments. Finally, a unique grand-mean segment map was averaged in the newly defined time-borders (for additional methodological details see also Khateb et al., 1999).

2.5.2.2. Defining the functional significance of time segments and their maps. To define the time periods reflecting specific visual information processing, we searched for those time segments whose maps only appear in its own but are absent in the other condition, or vice versa. For this purpose, spatial ERP fitting procedures were applied to individual data (Pascual-Marqui et al., 1995). For each subject, we calculated the spatial correlation coefficients between a given segment map and the successive ERP maps of each condition in the corresponding time intervals. This procedure was conducted in order to assess how well a given segment map explains a given condition (goodness of fit = best explained variance, bev) (Pegna et al., 1997; Khateb et al., 1999, 2000; Thut et al., 1999, 2000; Morand et al., 2000; Lantz et al., 2001). Best explained variance was compared for each segment map between conditions using t tests. In a first step, comparisons were performed within the two face and two non-face conditions separately. We tested whether maps of a given segment differ within face and non-face object conditions respectively, by fitting to individual data a given segment map to the corresponding time segment of its own and the other condition. In a second step, face and non-face object maps of a given segment were averaged within their own category. Those maps of the face conditions significantly better explaining their own than the non-face object conditions are likely to reflect face-specific processing, and vice versa. The remaining maps with no differences between the 4 conditions can be interpreted to reflect visual information processing in general.

The ERP map-fitting procedure described above also provides information about when in time a given segment map is represented at best (time point of best explained variance, tpbev). This value was compared between conditions using *t* tests for all condition-specific segment maps in order to reveal differences in timing, i.e. latencies.

2.6. Source localization and analysis of regions of interest (ROIs)

To estimate the brain activity underlying segment map topography, two inverse solutions were calculated: LORETA (Pascual-Marqui et al., 1994) and BESA (Scherg and Van Crammon, 1985). LORETA is a modified weighted minimal norm solution that searches for the smoothest distribution by minimizing the norm of the Laplacian of the current vectors. A 3D spherical model was used. LORETA solutions were calculated within a regular grid of 1152 nodes, lying within the upper hemisphere of a sphere. Compared to dipole solutions, LORETA estimates the underlying generators without any a priori assumption on the number and locations of the sources. A critical review of this solution is provided elsewhere (Fuchs et al., 1999; Michel et al., 1999a). BESA allows the spatio-temporal modeling of multiple current dipoles over defined intervals. The orientation and the location of the dipoles were computed by an iterative least-square fit which minimizes the residual variance (% residual variance). This value indicates the percentage of data that cannot be explained by the model (for a detailed discussion of this method and its limitations see da Silva and Spekreijse, 1991; Scherg and Picton, 1991; Picton et al., 1999). Both inverse solutions were calculated using a spherical head model. These inverse solutions (LORETA

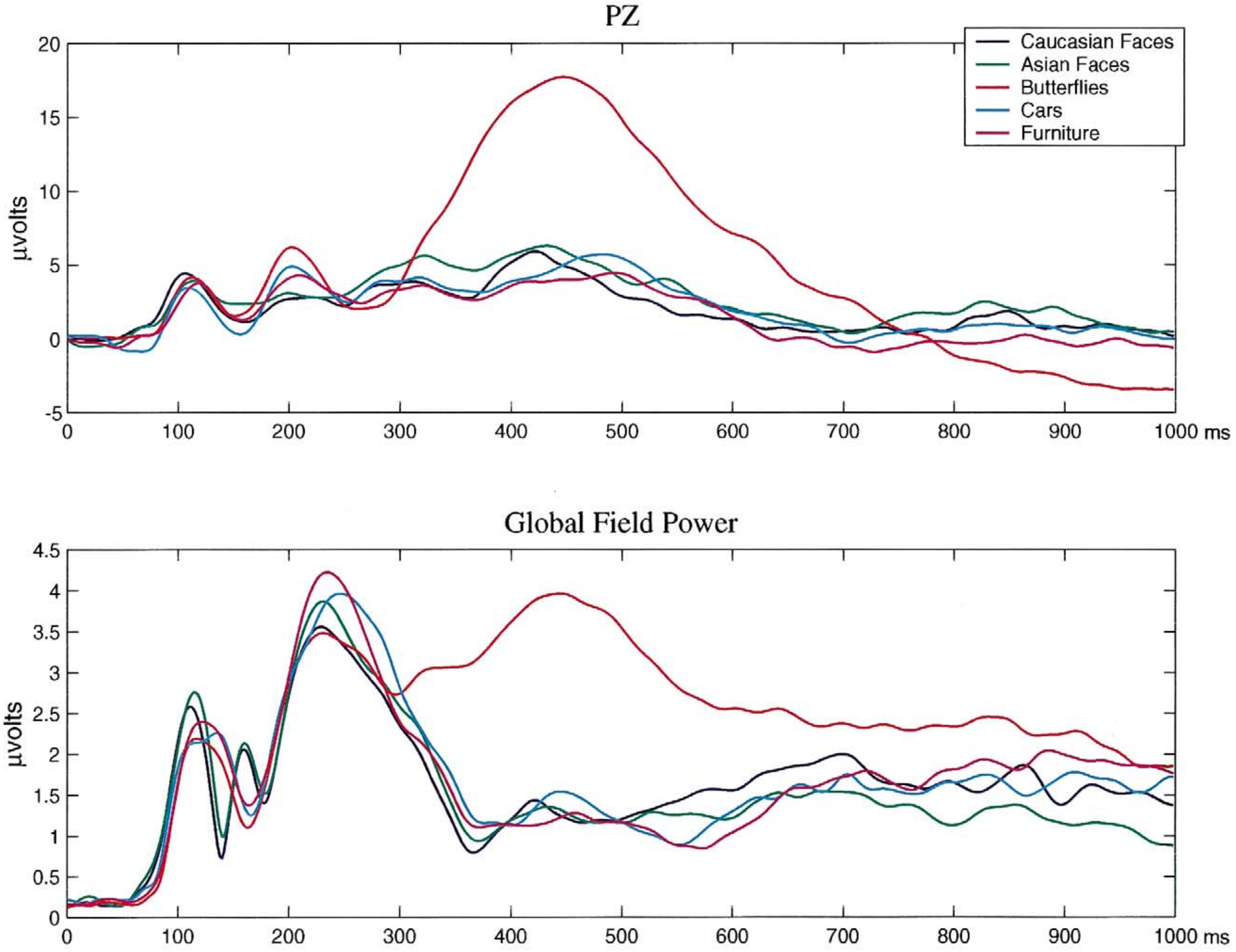

Fig. 1. ERP waveforms recorded over electrode Pz (upper part) and global field power (map strength) of successive ERP maps (lower part) represented for faces and non-face objects as well as the control stimuli (butterflies). Note the prominent P300 component observed in the control condition only and its correspondence with the GFP map strength. Positive values are up.

and BESA) were applied in the grand-mean average for segments that appeared to be specific for face or non-face object processing. The time window used was delimited by the segmentation analysis. An additional analysis based on individual segment maps was applied with LORETA only. Latter maps were calculated by averaging individual ERP maps within the face-specific time periods as determined by the grand-mean segmentation. LORETA results obtained from the Caucasian and Asian segment maps were used for ROI analysis in the occipito-temporal area in order to explore race effects regarding brain activation patterns.

3. Results

3.1. Behavioral results

This condition was analyzed for control purposes only. Both behavioral and ERP data revealed that subjects attended adequately to the delivered stimuli. The number of target stimuli was correctly reported in 98% of the trials and a prominent P300 component was observed for the butterflies, but not for any other stimulus type (Fig. 1).

3.2. ERP waveform analysis

A 4×19 repeated-measures ANOVA on peaks amplitudes, averaged within the time period of the N170 component, with Condition (Caucasian Faces, Asian Faces, Cars, Furniture) and Electrode Site as factors revealed a highly significant main effect for Condition ($F(3,33) = 19.76$, $P < 0.001$) as well as a significant interaction ($F(54,594) = 15.09$, $P < 0.001$). A partial repeated-measures ANOVA conducted to identify the origin of this interaction was computed for the electrodes P9/10 and P09/10 and revealed an effect of condition ($F(2.12, 23.34) = 53.78$, $P < 0.0000$). The ERP waveforms of these 4 electrodes are shown in Fig. 2. They revealed a prominent N170 component in the two face conditions. This was statistically confirmed by a post-hoc Scheffé test revealing that the face conditions were significantly different from the non-face object conditions with stronger negative amplitudes for faces than for non-face objects (see Table 1). Repeated-measures ANOVA of the N170 peak latencies show that the small differences between conditions (Caucasian faces = 160.5 ms; Asian faces = 161.1 ms; Cars = 164.6 ms; Furniture = 165.125 ms) were not significant ($F(2.18, 24) = 2.48$, $P = 0.1004$).

A 2×19 repeated-measures ANOVA performed on data of the face conditions only, showed a significant interaction between the factors Race and Electrode Site ($F(18,198) = 2.68$, $P = 0.042$). A partial repeated-measures ANOVA computed for O1/2, Oz electrodes revealed that Asian faces evoked stronger positive amplitudes than Caucasian ($F(1,11) = 6.10$, $P = 0.0312$). The waveforms on the Oz electrode are represented in Fig. 2. Peak latencies on these electrodes for OR faces (158.1 ms) and SR faces (155.6 ms) were not statistically different ($F(1,11) = 3.92$; $P = 0.0733$).

3.3. ERP analysis of map topography: identifying time periods reflecting condition-specific information processing

Fig. 3 depicts the global field power (GFP = map strength) as well as the global map dissimilarity (GMD) over time for the successive ERP maps of each of the 4 conditions (grand-mean ERPs). An ERP map represents the spatial potential configuration (map topography) of all 62 recorded electrodes at a given time point. Spatio-temporal segmentation of the grand-means using the GMD value as an indicator for map stability/instability reveals 6 time periods of stable map topography per condition (labeled with numbers). These time periods will be referred to as segments throughout the manuscript. The segment maps' topographies as well as their onset and offset times are shown in Fig. 4. Visual inspection reveals that map topography is very similar across conditions for maps occurring in similar time periods, except for maps 3. This map differs *between* but not *within* face and non-face object conditions. This was statistically confirmed by comparing map topography between conditions (segment-by-segment) using the results of ERP map fitting. Fitting each segment map of the Caucasian face condition in each subject to its own and the Asian face data showed that no segment map explained the Caucasian and the Asian face data significantly differently (see Table 2A, upper part). This suggests that the map topography of the two face conditions tends to be similar. Similarly, no significant differences were observed between the two non-face object conditions as revealed by fitting each 'Car' segment map to the corresponding time segments of the car and the furniture conditions (see Table 2A, lower part).

In a second step, face and non-face object maps of a given segment were averaged within their own category. These maps were then fitted to the individual data, also averaged within faces and non-face objects, in order to isolate those segment maps which are specific for face stimulation. Table 2B shows that segment maps 3 of the face conditions better explain their own conditions than the non-face object conditions. This map thus reflects face-specific activation patterns. Note that the map 3 occurs between 142 and 182 ms post-stimulus partially overlapping the N170 component in time. The ERP map fitting also provided information about when in time a given segment map was represented at best (time point of best explained variance, *tpbev*). This value was compared between face and non-face object segments 3 revealing that the face segment occurs significantly earlier (t = -3.625, $P = 0.003$; mean *tpbev*: 169.16 ms (faces) vs. 195.33 ms (non-face objects)).

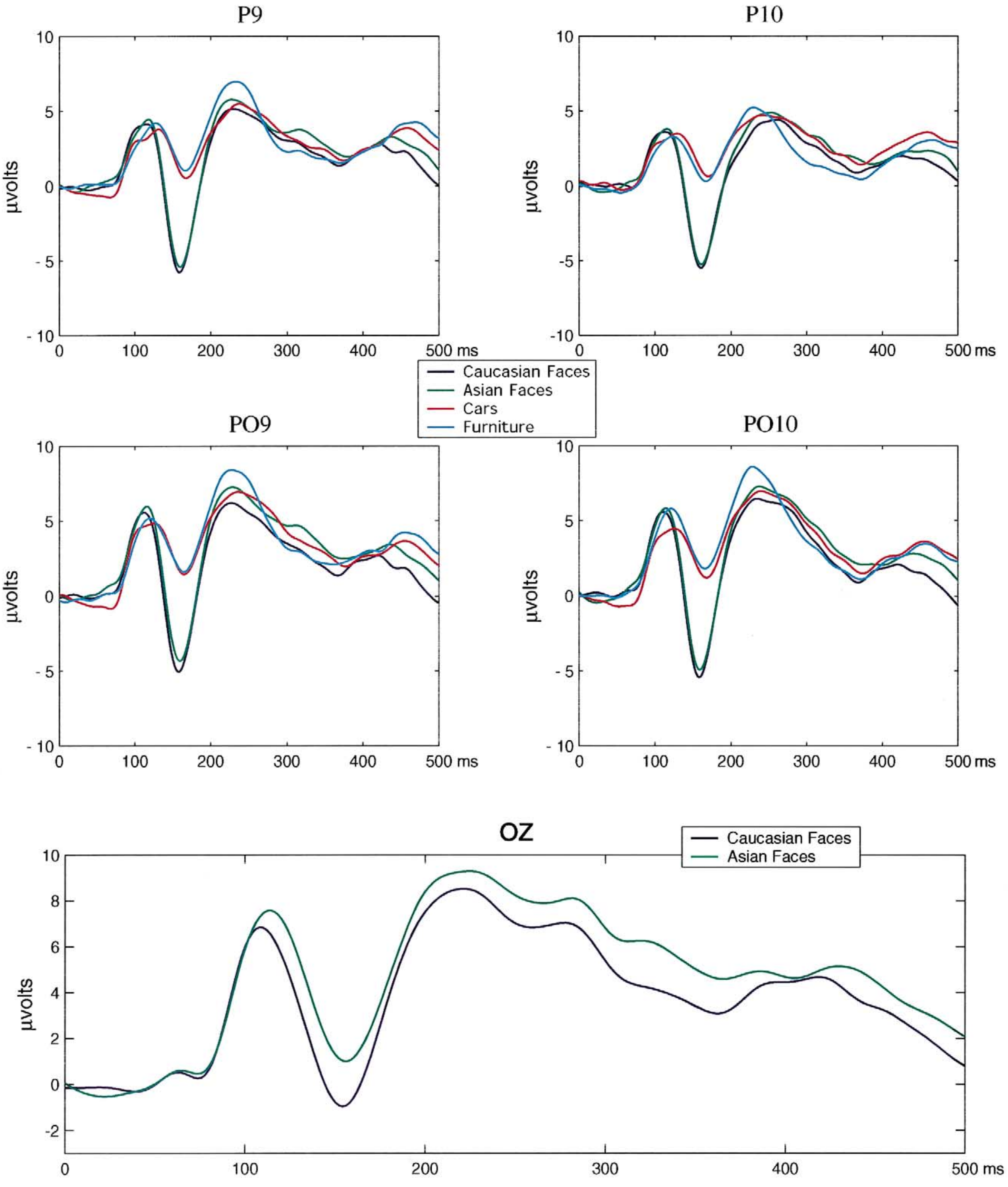

Fig. 2. (Top and middle) Grand-averaged ERP waveforms recorded at lateral temporo-occipital electrodes (P9/10 and PO9/10) in response to Caucasian and Asian faces as well as cars and furniture. (Bottom) Grand-averaged ERP waveforms recorded over central occipital electrode (Oz) in response to Caucasian and Asian faces. Positive values are up.

3.4. Source localization and ROI analysis

Within the time periods identified to reflect condition-specific activation patterns, two inverse solutions were applied: LORETA (Pascual-Marqui et al., 1994) and BESA (Scherg and Van Crammon, 1985). The source localization results are shown for the maps of segment 3 in Fig. 5. Visual inspection of the LORETA results

Table 1
P values of the Scheffé test for the factor Condition (Caucasian vs. Asian vs. Cars vs. Furniture) on peak amplitudes on the electrodes P9/PlO and P09/10 for the N170 component[a]

	Caucasian Faces (mean -5.78 μV)	Asian Faces (mean -5.34 μV)	Cars (mean 0.62 μV)	Furniture (mean 0.75 μV)
Caucasian faces	–	0.939	**<0.001**	**<0.001**
Asian faces	0.939	–	**<0.001**	**<0.001**
Cars	**<0.001**	**<0.001**		0.998
Furniture	**<0.001**	**<0.001**	0.998	–

[a] Significant effects are highlighted in bold type.

shows that the inverse solution of the face-specific segment map does qualitatively differ from the solution of the corresponding non-face object segment map. The solutions suggest that face-specific activity involves a larger bilateral occipito-temporal network than object-related activity. Moreover, Caucasian and Asian maps differ regarding their maxima with stronger medial occipital activity for Asian and stronger right occipito-temporal activity for Caucasian faces, although the activity distribution is similar between the two face stimulus types. To statistically test for Race effects regarding brain activity, the LORETA algorithm was applied to individual ERP maps (Caucasian and Asian data only) averaged over the face-specific time period as identified by the spatio-temporal segmentation procedure (segment 3). These results were subjected to ROI analyses. The ROIs were defined over medial occipital and bilateral occipito-temporal regions. Mean activity within the medial occipital ROI was significantly increased for Asian with respect to Caucasian faces as revealed by a *t* test (mean: 46.06 vs. 40.45) ($t = 2.68$, $P = 0.021$). No significant differences were observed for

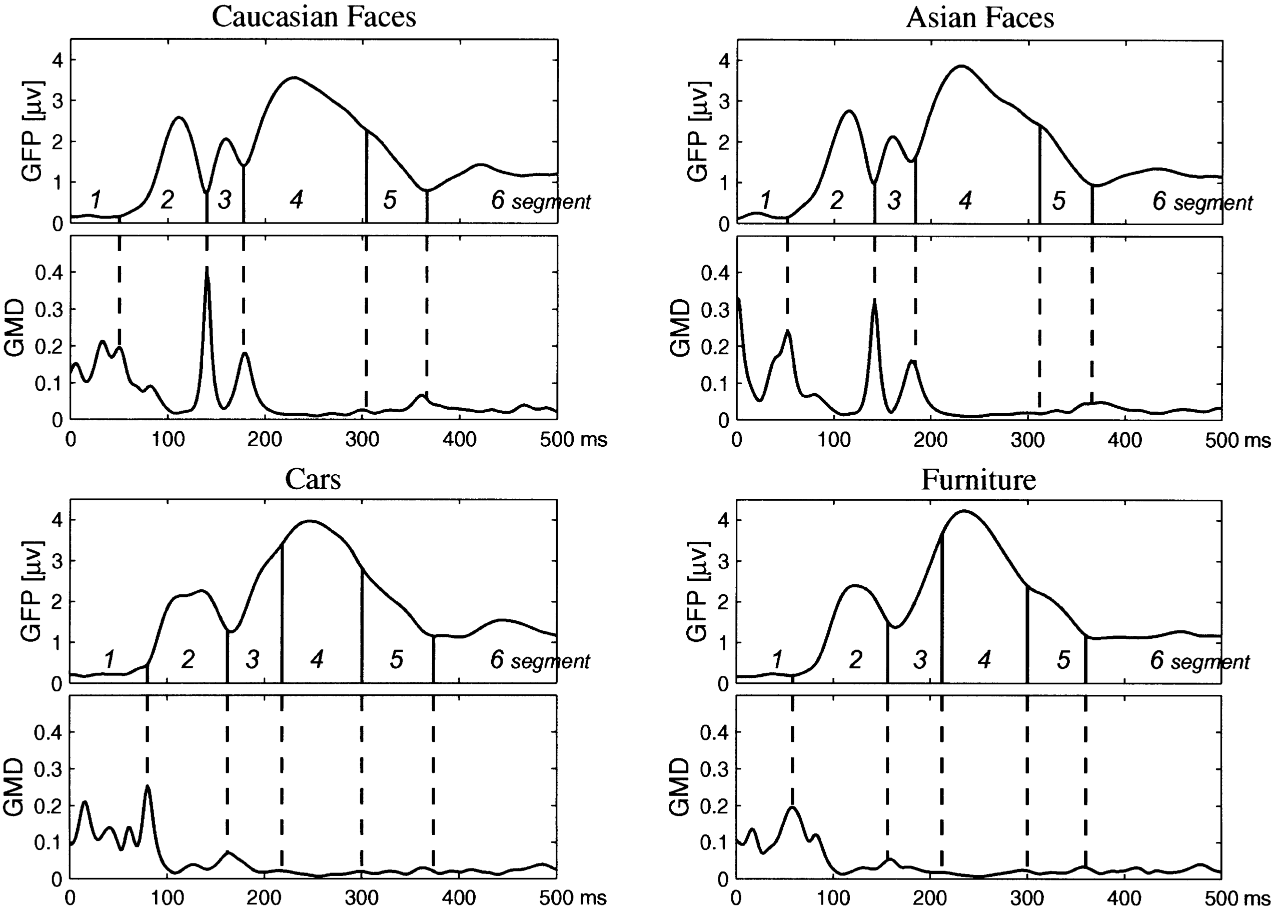

Fig. 3. Global field power indicating map strength (GFP, upper panels) as well as global map dissimilarity (GMD, lower panels) shown over time for the 4 grand mean ERPs. The time evolution of the GMD value was used for the spatio-temporal segmentation procedure to define time periods of stable map topography (low GMD values) and their borders (GMD peaks), the latter marked by vertical lines. Usually, low stability of map topography around GMD peaks coincides with low GFP values. Six periods of stable maps (segments) were identified per condition, labeled by numbers.

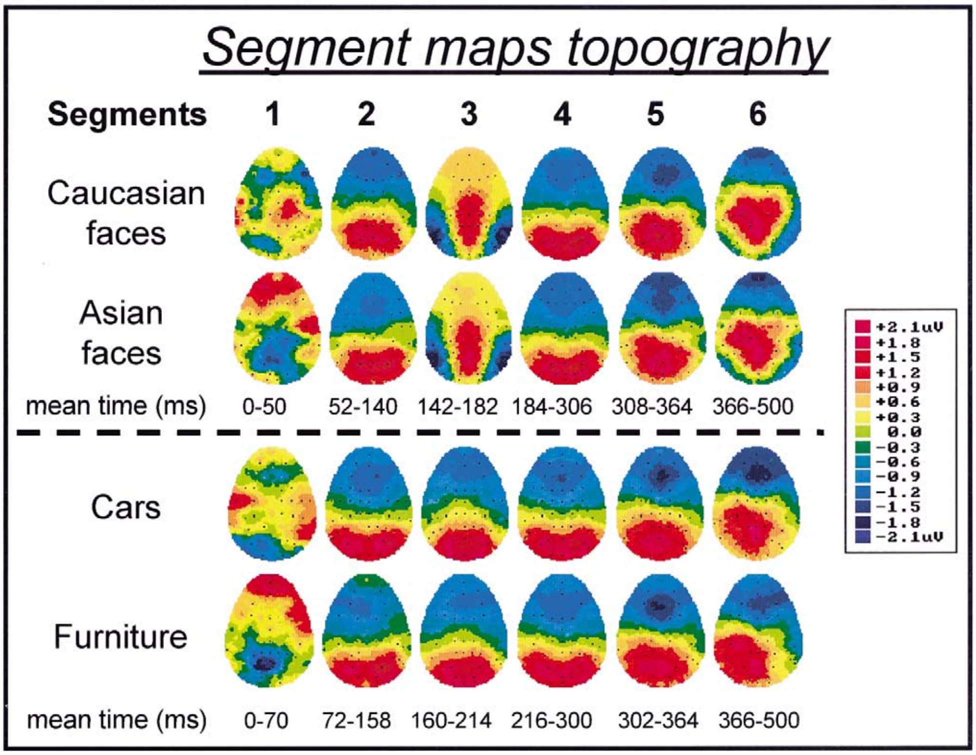

Fig. 4. Segment maps as defined by spatio-temporal segmentation of the grand-mean ERPs. Maps are represented in order of appearance (from left to right) for each condition separately (Caucasian faces, Asian faces, Cars and Furniture). All maps are rescaled against the average reference. The maps are viewed from the top, with the nose up and the left ear left. Their onsets and offsets are given below. Note that maps of overlapping time periods are usually very similar in topography between conditions, except map 3 which differs between face and non-face object conditions.

the lateral occipito-temporal ROI (mean: 34.3 vs. 32.8) ($t = 0.94$, $P = 0.355$).

Finally, BESA obtained a solution with 4 dipoles localized in the ventral occipito-temporal area for the face condition (% residual variance = 7.39), while two dipoles located in the medial part of the same area were sufficient to explain the non-face object data (% residual variance = 6.66). Thus, similar to LORETA, BESA retrieved qualitatively different solutions for faces than non-face objects.

4. Discussion

The present experimental design incorporated two com-

Table 2
t and *P* values for between-conditions comparisons on best explained variance (bev), performed segment by segment (1–6)[a]

		Segments					
		1	2	3	4	5	6
A							
Caucasian Maps in							
Caucasian faces vs.	*t*	−0.208	−0.701	1.203	−0.309	−1.506	0.089
Asian faces cond.	*P*	0.839	0.498	0.254	0.763	0.160	0.931
Car Maps in							
Cars vs.	*t*	−2.042	−1.382	−0.867	−1.337	1.634	1.172
Furniture cond.	*P*	0.066	0.194	0.405	0.208	0.131	0.266
B							
Face Maps in							
Faces vs.	*t*	−1.115	1.625	3.766	0.517	0.286	1.362
Non-face object cond.	*P*	0.289	0.133	**0.003**	0.615	0.781	0.201

[a] Significant effects are highlighted in bold type. A: Comparisons within face (Caucasian vs. Asian) and non-face object conditions (Cars vs. Furniture). B: Comparisons between face and non-face object conditions.

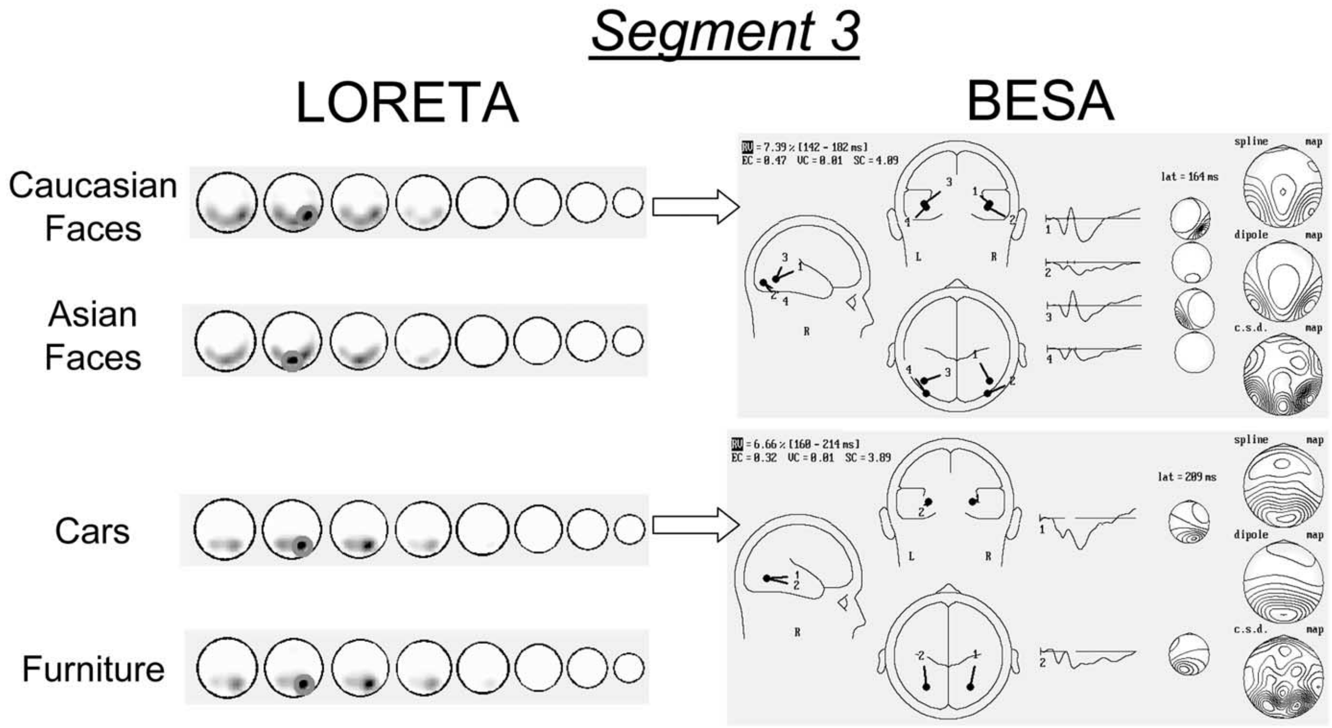

Fig. 5. 3D brain activity estimated for the surface maps n. 3 in face (Caucasian and Asian) and non-face object conditions (Cars and Furniture) using two inverse solutions (left: LORETA; right: BESA). LORETA: Solutions are represented in 8 transverse slices through the spherical head model with the lowest slices to the left (nose up, left ear left). BESA: The estimated 3D dipole locations within the head and the time varying activity of each dipole source are reported, along with their spline, dipole and scalp current density maps. For reasons of simplicity, the results of only 2 of the 4 conditions are shown. The remaining results are comparable to those illustrated here. Note that both LORETA and BESA solutions suggest activation of larger occipito-temporal regions in face as compared to non-face object conditions. Note also that despite similar source configurations for face conditions, LORETA solutions indicate that the location of maximum activity (blue circles) differs between Caucasian and Asian faces.

parisons: (1) perception of face and non-face object stimuli and (2) perception of same-race (SR) versus other-race (OR) faces. The results reported here are derived from an original combination of different surface ERP analyses and source localization procedures. Our data demonstrate for the first time a difference in electrical brain activity for the perception of SR versus OR faces. They also provide evidence for different and common stages in face and non-face object processing as information processing evolves (not only at the level of the N170), and allow us to describe these stages in terms of cerebral activation patterns across time. In Fig. 6, we propose a model that summarizes the time-course of these processing stages. These points are discussed below.

4.1. Face versus non-face object processing and the stages of information processing

Analysis of the evolution of ERP map topographies over time suggests that, as visual information processing unfolds, a face-specific stable map topography occurs between 140 and 210 ms. Several segments which are common to all types of stimuli are observed outside this time window. The first segment of all conditions is by default a noisy segment that follows the onset of the stimuli. Segment 2 peaks in strength at about 110 ms for all conditions. Undoubtedly, this segment map reflects the well-known P1 topography, which is associated with early visual cortical activation (primary visual cortex and extrastriate areas, e.g. Gomez Gonzalez et al., 1994). Both segments 1 and 2 are identical across face and non-face object conditions and are followed by the condition-specific segment 3. This segment overlaps in time the N170 component. It differs in map topography for face and non-face object conditions. In agreement with this result, the waveform analysis on the N170 component revealed a strong face-specificity for this component. Furthermore, both inverse solutions that we used, LORETA and BESA, returned in this time period different source localization results for the face and non-face object conditions. The inverse solutions indicate more distributed occipito-temporal sources for faces than non-face objects, both in terms of current density (LORETA) and numbers of dipoles (BESA). In addition, the inverse solutions indicated bilateral sources with more pronounced activity in the right hemisphere. In the case of face stimuli, this might reflect a bilateral activation of the face-sensitive areas, however, with a greater activation of the right than the left side (Dubois et al., 1999; Ishai et al., 1999; Rossion et al., 2000). As compared to the face conditions, the sources for non-face

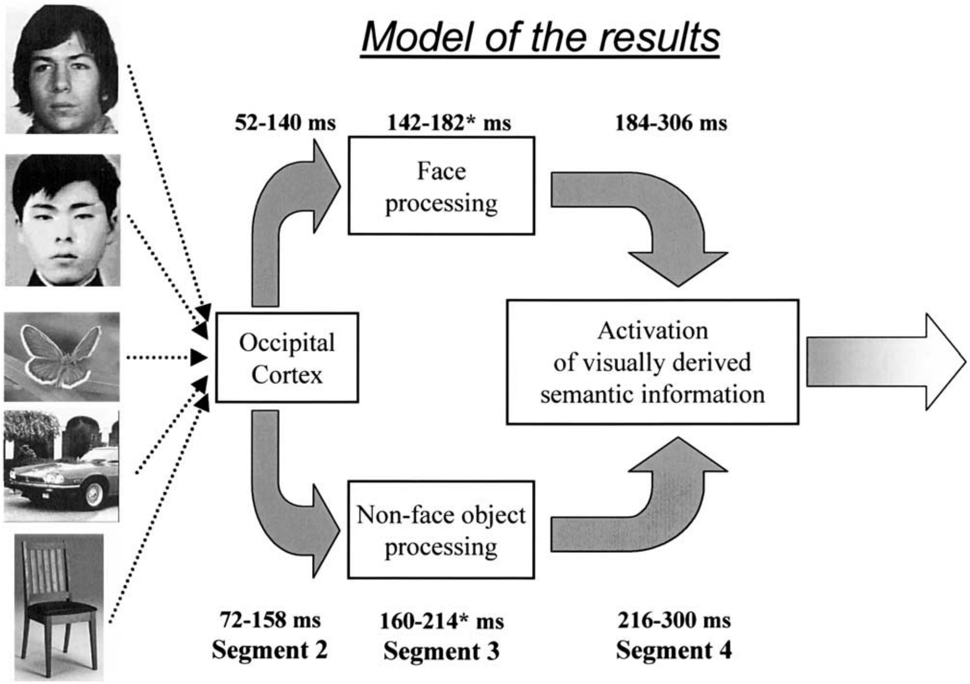

Fig. 6. Model of different stages of information processing over time associated with passive viewing of face (Caucasian and Asian faces) and non-face stimuli (cars and furniture) in Caucasian subjects. The 'butterfly' stimulus served as target (subjects had to silently count the occurrences of the target stimulus) and was not considered in the analysis. Note that the model representation is essentially inferred from the results of the ERP map segmentation analysis (providing clues on condition-specific stages of information processing). The star indicates the segment in which face processing appears significantly earlier than non-face object processing.

object stimuli were located more medially, consistently with recent neuroimaging studies (Epstein and Kanwisher, 1998; Chao et al., 1999; Ishai et al., 1999). In short, our results confirm that there are early face-sensitive processes taking place in occipito-temporal regions, at least using face passive viewing paradigms. Interestingly, segment 3 differed not only regarding electrical activation patterns between face and non-face object conditions but also regarding timing. As inferred from the analysis based on the time point of best explained variance of map topographies face processing was about 25 ms faster than non-face object processing, a result that is not found by peak analyses on the N170. This result may be interpreted as an evidence for a particular automated expertise for face perception in the temporal domain. Indeed, face perception may have a unique position in human visual perceptual skills, given its importance for social communication (see Kanwisher, 2000). Alternatively, an equally plausible explanation for this latency difference could be that the within-category visual similarity was likely to be substantially greater for faces than within the two other non-face object categories (cars, furniture). Future electrophysiological studies should also investigate whether visual expertise with non-face objects would lead to faster activation of the occipito-temporal cortex, as suggested by effects of expertise found at the level of the N170 (Tanaka and Curran, 2001; Rossion et al., 2002).

With respect to GFP strength, segment 4 is an important event that peaks at about 230 ms for all conditions. Its strength is similar to the strength of the P300 (Fig. 1) and, as previously demonstrated (Wackermann et al., 1993), it reflects a stable ERP topography, that is invariant across conditions in our experiment. Interestingly, the electrical brain response starts to differ between the target ('butterfly' detection) and non-target conditions immediately following segment 4 (see Fig. 1). At the end of segment 4, the GFP waveform splits for the butterfly condition. This indicates that a butterfly was perceived and correctly identified as a target immediately before the end of this segment, implying activation of the correctly derived semantic information in this segment's time period. This stage of processing is thus probably not face-specific but related to the dissociation between the target item ('Butterfly') and the other categories.

Regarding segments 5 and 6, the information provided by our study and available in the literature makes it difficult to provide any possible explanation of their functional significance.

4.2. Same-Race versus Other-Race face perception

Our data indicate that global correlates (ERP map topographies) of face processing occurring between 140 and 180 ms post-stimulus tend to be similar for SR and OR faces. In addition, no differences were observed between

OR and SR face conditions in the classical N170 face-sensitive component located at lateral occipito-temporal electrode sites (P9/P10 and PO9/PO10). This result would support the idea that the N170 component is not modulated by the level of expertise within the class of human faces. The fact that the FFA activation appears to be sensitive to the race of the face (Golby et al., 2001) but not the N170 is interesting. The precise relationship between the FFA activation and the N170 is unclear at the present state of knowledge. Previous ERP and neuroimaging studies reported similar functional modulations for the FFA and the N170, suggesting that the activation of the FFA contributes at least in part to the observation of the face-ERP component on the scalp (e.g. larger activation for faces than for objects, small but significant effects of inversion, etc., see Rossion and Gauthier, 2002). Our source localization data show that the activity reflected by the face sensitive N170 component is related to distributed occipito-temporal sources and not solely to the activation of a well-defined small fusiform regions such as the FFA. This assumption is based on the results of both LORETA and BESA (see also the discussion below concerning face versus non-face object processing). In addition, a more detailed analysis based on the LORETA solution that focused on the bilateral occipito-temporal ROI also failed to discriminate between SR and OR faces. This result suggests that the increase of activation for SR faces in the FFA observed in fMRI (Golby et al., 2001) may take place later than 200 ms.

However, amplitudes over medial occipital electrodes differed significantly between OR and SR faces. Likewise, an analysis of inverse solutions (LORETA) applied to this early stage of face processing confirmed that OR faces evoke more medial occipital activity than SR faces, although overall current density patterns were similar. This increase of early brain activity for OR faces can be highly surprising at first glance. However, some findings of previous studies help to interpret this observation. Two recent fMRI studies found only the amygdala to become more activated in response to OR as compared to SR faces (Hart et al., 2000; Phelps et al., 2000), suggesting a possible role of this structure in the encoding (Hart et al., 2000) and/or an unconscious evaluation about social groups (Phelps et al., 2000). Given its distribution on the scalp, the differential activity reported here for OR and SR is unlikely to arise and be recorded directly from the amygdala, but could be related to an amygdalar activation of early visual areas during face processing, as described by several studies (Amaral et al., 1992; Rolls, 1992). Moreover, both the amygdala and the posterior occipital lobe appear to present a higher level of activation to unfamiliar faces than familiar faces (Dubois et al., 1999), and it is conceivable that repeated presentations of SR faces makes them quickly familiar and leads to a decrease of activation in these regions, while this decrease is likely to be slower for OR faces.

An alternative explanation for the occipito-medial sources predominantly associated with OR face perception relates to behavioral findings in experiments using the pop-out effect. Using visual search tasks, Levin (1996, 2000) has shown that participants detect an OR face faster among SR faces than vice versa. Faster classification of OR faces has been interpreted as a pop-out effect for OR faces (Levin, 1996). According to Levin (1996), this performance may be due to the detection of a feature-positive present in OR but absent in SR faces (even if this face feature(s)-positive remains unknown). Thus, the greater activity in this area observed for OR faces may reflect a pre-attentive detection of a feature-positive. However, there is evidence that suggests rather a serial search than a pop-out effect for faces and facial expressions (Nothdurft, 1993). Moreover, the slopes of the reaction times (that increase with the number of targets) observed in the Levin (1996, 2000) studies also indicate a serial visual search mechanism, rather than a pop-out effect. For these reasons, we favor the interpretation that the stronger occipito-medial activation for OR faces reflects the detection of the relative unfamiliarity of OR faces rather than race detection through a face feature-positive.

Finally, although we carefully selected and controlled our stimuli it may still be that this differential activity between OR and SR is due to a difference in the stimuli per se (e.g. low-level visual properties) between Caucasian and Asian face stimuli. Future studies will be necessary to explore this early ‘face-race’ effect using, if possible, a fully cross-racial paradigm with two groups of subjects from different races. Moreover it will be interesting to use active tasks, that are possibly more sensitive to an effect of expertise for own race faces, such as face recognition and classification by race.

4.3. Methodological issues

In the present study, we combined different methods of ERP analysis involving classical waveform analysis, analysis based on ERP map topography (spatio-temporal segmentation) and inverse solutions. The first method takes only selected electrodes into account (that could be referred as a *local* approach), while the latter methods are based on multi-channel, whole-scalp recordings (as a *global* approach).

The results presented here turned out to be highly compatible but also complementary across these approaches. The remarkable correspondence between the POz electrode waveform and the GFP with respect to the P300 component (Fig. 1) is an example of such compatibility. Moreover, both local and global approaches, namely the inverse solutions, allowed us to identify differences in neuronal responses between OR versus SR faces and to describe some of the face- and non-face object specific components/segments. Note, however, that although inverse solutions were able to capture differences between OR and SR face conditions through ROI analysis procedures, an analysis of global map topography (spatio-temporal segmentation) failed to reveal any statistically significant effects. This demonstrates that a small and focal difference in activity may be masked, from a statistical point of view, when ERP analysis are based on global indices calculated over a multitude of recorded signals.

Thus, spatio-temporal segmentation analysis allowed us to obtain some results that would have been difficult to uncover using classical waveform analysis. Through segmentation analysis, we defined time-series of stable ERP map topographies and their evolution over time. The time windows defined by the spatio-temporal segmentation can represent an objective and useful criterion for determining the time windows used in the classical statistic waveform analysis. Moreover, identification of sub-stages of information processing and the assessment of their relative timing (showing for example that face processing is initiated faster than non-face object processing) have principally been made possible by this approach.

Finally, in order to strengthen possible interpretations regarding source localization, *two* inverse solution algorithms were applied (LORETA and BESA) and localized similar generators.

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