ACADEMIC PRESS

Available online at www.sciencedirect.com
SCIENCE DIRECT®

NeuroImage

NeuroImage 20 (2003) 1609–1624

www.elsevier.com/locate/ynimg

Early lateralization and orientation tuning for face, word, and object processing in the visual cortex

Bruno Rossion,[a,b,*] Carrie A. Joyce,[c] Garrison W. Cottrell,[c] and Michael J. Tarr[b]

[a] *Cognitive Neuroscience Unit, University of Louvain, Belgium*
[b] *Department of Cognitive and Linguistic Science, Brown University*
[c] *Computer Science and Engineering Department, University of California, San Diego, CA, USA*

Received 24 March 2003; revised 18 July 2003; accepted 18 July 2003

Abstract

Event-related potential (ERP) studies of the human brain have shown that object categories can be reliably distinguished as early as 130–170 ms on the surface of occipito-temporal cortex, peaking at the level of the N170 component. Consistent with this finding, neuropsychological and neuroimaging studies suggest major functional distinctions within the human object recognition system, particularly in hemispheric advantage, between the processing of words (left), faces (right), and objects (bilateral). Given these observations, our aim was to (1) characterize the differential response properties of the N170 to pictures of faces, objects, and words across hemispheres; and (2) test whether an effect of inversion for highly familiar and monooriented nonface stimuli such as printed words can be observed at the level of the N170. Scalp EEG (53 channels) was recorded in 15 subjects performing an orientation decision task with pictures of faces, words, and cars presented upright or inverted. All three categories elicited at the same latency a robust N170 component associated with a positive counterpart at centro-frontal sites (vertex-positive potential, VPP). While there were minor amplitude differences at the level of the occipital medial P1 between linguistic and nonlinguistic categories, scalp topographies and source analyses indicated strong hemispheric and orientation effects starting at the level of the N170, which was right lateralized for faces, smaller and bilateral for cars, and as large for printed words in the left hemisphere as for faces. The entire N170/VPP complex was accounted for by two dipolar sources located in the lateral inferior occipital cortex/posterior fusiform gyrus. These two locations were roughly equivalent across conditions but differed in strength and lateralization. Inversion delayed the N170 (and VPP) response for all categories, with an increasing delay for cars, words, and faces, respectively, as suggested by source modeling analysis. Such results show that early processes in object recognition respond to category-specific visual information, and are associated with strong lateralization and orientation bias.

Introduction

A critical task of human vision is to classify incoming signals into perceptual categories. Event-related potential (ERP) studies of the human brain have shown that object categories can be distinguished by their electrophysiological activity recorded on the surface of the occipito-temporal cortex. Early face-sensitive responses have been reported in a few EEG and MEG (magnetoencephalography) studies before 60 ms (Braeutigam et al., 2001), or around 100 ms at the level of the P1 (EEG; Halit et al., 2000; Itier and Taylor, 2002; Linkenkaer-Hansen et al., 1998) or the M1 (MEG; Halgren et al., 2000; see Taylor, 2002), but the differences between faces and other object categories at these latencies are likely to be related to low-level visual differences (Halgren et al., 2000). By contrast, the largest and most consistent ERP/MEG difference has been observed as early as 130–170 ms, between pictures of faces and other objects at occipito-temporal (Bentin et al., 1996; Botzel et al., 1995; Eimer, 2000a, 2000b; Halgren et al., 2000; Liu et al., 2000; Rossion et al., 2000; Schendan et al., 1998) or centro-frontal sites (Jeffreys, 1989, 1996; VanRullen and Thorpe, 2001). More precisely, the N1, or the first negative occipito-temporal component evoked by any complex visual stimulus presented foveally, is greatly enhanced when elicited by

* Corresponding author. Unite de Neurosciences Cognitive, Universite Catholique de Louvain, 10 Place du Cardinal Mercier, 1348 Louvain-la-Neuve, Belgium. Fax: +32-10-47-37-74.
E-mail address: bruno.rossion@psp.ucl.ac.be (B. Rossion).

1053-8119/$ – see front matter © 2003 Elsevier Inc. All rights reserved.
doi:10.1016/j.neuroimage.2003.07.010

pictures of faces, and is usually referred to as the N170 "face potential" (e.g., Bentin et al., 1996; Eimer, 2000a; Rossion et al., 2000). This component follows the occipital P1 (which peaks at around 100 ms following stimulus onset) and is temporally coincident with a large positive potential at centro-frontal sites, the P2 vertex or vertex-positive potential (VPP; following Botzel et al., 1995; Jeffreys, 1989, 1996; Schendan et al., 1998).[1] The temporal coincidence of the N170 and VPP, their opposite polarity, and surface localization, as well as their remarkable functional similarity (e.g., Itier and Taylor, 2002; Rossion et al., 1999a, 1999b; see Jeffreys, 1996) strongly suggest that these two peaks form part of the same dipolar complex. In particular, both the temporally coincident N170 and VPP are the earliest markers of a reliable processing difference between faces and objects (Bentin et al., 1996; Jeffreys, 1996; Rossion et al., 2000).

Complementary evidence from behavioral, neuroimaging, and patient studies supports this distinction between faces and objects at the functional and neural level in humans. Neuropsychological studies have reported a number of brain-damaged patients who exhibit disproportionate impairment for recognizing faces as compared to other objects, a deficit referred to as prosopagnosia (Bodamer, 1947/1990). Prosopagnosia is usually associated with bilateral or right unilateral occipito-temporal lesions (e.g., Damasio et al., 1982; Farah, 1991; Landis et al., 1988). The opposite deficit—object agnosia without prosopagnosia—has been also described in rare cases (e.g., Moscovitch et al., 1997).

In addition to the clear differences observed between faces and nonface objects, a distinction within the object recognition system can be made between the recognition of printed words/characters and common objects. A number of neuropsychological patients have been described with an inability to read printed words in the absence of object (and face) recognition deficits, and whose other forms of language-related processing (including spoken language comprehension and written language production) are preserved (Farah, 1994). As noted by Farah (1991), these cases of "pure alexia" or "agnosic alexia" appear to result from damage to some aspect of visual processing, and not to language processes per se. Interestingly, the localization of the lesions responsible for pure alexia is also at the level of the occipito-temporal cortex, and is either bilateral or restricted to the left hemisphere (Farah, 1991).

Such dissociations between the processing of words, faces, and objects suggest major functional distinctions within the human object recognition system, associated with different left (words) and right (faces) hemispheric advantages.

As noted earlier, several scalp ERP studies have compared the processing of faces to objects and have found substantially larger N170 for pictures of faces than other object categories at bilateral occipito-temporal sites, with some studies describing a larger difference at right hemisphere electrode locations (e.g., Bentin et al., 1996). However, few scalp ERP studies that have used printed words as stimuli have investigated the *visual* ERP components, instead concentrating on the high-level analysis of words as linguistic entities (e.g., for a review, see Kutas and Van Petten, 1990). Nevertheless, a large scalp occipito-temporal N170 component in response to visually presented words has been reported (e.g., Bentin et al., 1999; Nobre and McCarthy, 1994; see also Nobre et al., 1994, for intracranial evidence). This component is bilateral and appears to be identical for words and nonwords, but is larger in amplitude to orthographic than nonorthographic stimuli (e.g., forms, symbols) only in the left hemisphere (Bentin et al., 1999).

To our knowledge, only one previous scalp ERP study has directly compared the processing of words, faces, and objects in the same experiment, in order to characterize the nature and onset of the first perceptual processing differences between linguistic and nonlinguistic stimuli (Schendan et al., 1998). The main finding of this study was that the VPP was as large for faces and words, and larger for these two categories than for pictures of common objects, an observation that led the authors to conclude that the VPP amplitude varies with the cumulative experience people have discriminating among individual instances within visual categories (e.g., words, faces; Schendan et al., 1998). No significant VPP scalp distribution differences among words, faces, and objects were reported. With regard to the Schendan et al. study, one caveat is in order regarding the location of the reference electrode at the mastoids. This prevented an unbiased comparison of the N170/VPP complex to faces, objects, and words, since the mastoid electrode sites are located where the N170 to faces is particularly large. In the present study, we compared the early visual processing of faces, objects, and words with a large number of electrodes and a common average reference (Bertrand et al., 1985), in order to describe the differential pattern of response (amplitude, latency, and topographical distribution) of both the N170 and the VPP complex to these stimuli.

We also investigated the ERP responses to picture-plane inversion of these three object categories. Previous studies have shown that inversion significantly delays the N170 to faces (Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000a; Goffaux et al., 2003a; Itier and Taylor, 2002; Linkenkaer-Hansen et al., 1998; Liu et al., 2000; Rebai et al., 2001; Rossion et al., 1999b, 2000, 2002; Sagiv and Bentin, 2001; Taylor et al., 2001; Watanabe et al., 2003) but not to pictures of other objects (e.g., houses, chairs, cars, or shoes, Eimer, 2000a; Rebai et al., 2001, Rossion et al., 2000). Some of these studies have also found an increase in amplitude of the N170 to inverted faces (de Haan et al.,

[1] The VPP or P2 vertex, like the N170, presents a large variability in peak latency (between 140 and 200 ms; see Jeffreys, 1996) and has been also referred to in the literature as the P150 (e.g., Schendan et al., 1998) or the P190 (Bentin et al., 1996). We will use the most common terminology, the VPP (following Jeffreys, 1989).

2002; Itier and Taylor, 2002; Linkenkaer-Hansen et al., 1998; Rebai et al., 2001; Rossion et al., 1999b, 2000, 2002; Sagiv and Bentin, 2001; Taylor et al., 2001) but not to other objects (Rebai et al., 2001; Rossion et al., 2000). However, there is some evidence that expertise training with nonface objects may also lead to a delay of the N170 to inverted stimuli (Rossion et al., 2002). This suggests that the effect of stimulus inversion on the N170 is not restricted to faces and can at least be observed for highly familiar visual stimuli with a strong canonical orientation. Here we tested whether pictures of words, which are perfectly consistent with this definition, also produce a delay of the occipito-temporal N170 when presented upside down. Behaviorally, robust effects of orientation have been obtained for letters in both mental rotation (Cooper and Shepard, 1973) and identification (Jolicoeur, 1990) tasks, suggesting that, similar to faces (Yin, 1969), there may be early visual mechanisms tuned to the orientation of familiar letterstring stimuli. Finally, we compared faces and words to a nonface object category that is also familiar and monooriented, namely pictures of cars.

To summarize, we presented our subjects with upright and picture-plane inverted pictures of words, cars, and faces while recording ERPs with a large number of scalp electrodes. Specific questions using these methods focus on the N170 occipito-temporal response, thought to reflect differential high-level visual processing of face and nonface object categories. Our hypotheses were twofold: (1) that the pattern of N170 responses will be different between faces, objects, and words, possibly reflecting a left(words)/right-(faces) bias, as suggested indirectly by previous studies and neuropsychological reports; (2) that the N170 will be delayed in latency not only to inverted pictures of faces, but also to inverted words, which are highly familiar monooriented stimuli. These hypotheses were tested by means of peak analyses as well as topographical and dipole localization procedures.

Methods

Subjects

Subjects were 16 students (10 males, 6 females, all right handed) from the University of California, San Diego, between the ages of 21–39 (mean = 27.5) who were paid for participating in a single, 2 h experimental session. One subject's data were excluded because of poor signal-to-noise ratio.

Stimuli

Stimuli were 16 grayscale images of cars, 16 grayscale images of faces, and 16 words, each presented on a gray background (see Fig. 1). All cars were presented in a 3/4 right-facing view while face images were full-front views of Caucasian females (8) and males (8) with neutral expressions and with clothing, backgrounds, and hair removed (see Fig. 1). The word stimuli were 16 nouns, 4–7 letters in length, presented in black, Helvetica font.[2] At a 100-cm distance from the monitor, face images (7.32 × 8.87 cm) subtended ~4.19 × 5.08° of visual angle; cars and words (12.17 × 5.26 cm) subtended ~6.96 × 3.01° of visual angle Inverted versions of the 48 stimuli were created by rotating the images 180° for words and faces. Upside-down pictures of cars were obtained by flipping the stimuli horizontally instead of rotating them, thus keeping constant the side (right) to which the car was pointing between inverted and upright conditions. This resulted in the 96 different stimulus items used in this experiment.

Procedure

Following electrode application, subjects were seated in a sound-attenuating, electrically shielded chamber facing a computer monitor (~100 cm). They were told to fixate the center of the screen during the presentation of four consecutive blocks (with about a 1-min pause between blocks) of 96 trials each. On each trial, subjects were presented with an image of a car, a face, or a word for 250 ms in either its upright or inverted orientation. The interstimulus interval between trials varied randomly from 1250 to 1750 ms. Subjects pressed a button with the index finger of their dominant hand if the image was in the upright orientation, and a button with the middle finger of their dominant hand if the image was in the inverted orientation. Each stimulus was presented to each subject 8 times, 4 times in the upright orientation, and 4 times in the inverted orientation. All stimuli were centered in the computer monitor and the stimulus order was random in all blocks.

EEG recording

Subjects were instructed to refrain from blinking and moving their eyes and bodies, as the corresponding artifacts interfere with the recording of the electroencephalogram (EEG). Scalp recordings were made via 53 tin electrodes (10–20 system + additional sites) embedded in an elastic cap. Four additional electrodes were used to monitor eye movement and blinks: one placed under each eye and one placed on the outer canthus of each eye. The online reference was an electrode placed on the left mastoid. Electrical activity was amplified with a bandpass filter of 0.01–100 Hz and digitized at a rate of 500 Hz.

EEG/ERP analyses

EEG data were analyzed using EEprobe 2.0 (ANT, Inc.) running on Red Hat Linux 7.0. The EEG was filtered with

[2] The 16 words were dog, hat, job, baby, farm, game, idea, king, mine, note, rock, chair, labor, plant, table, and voice.

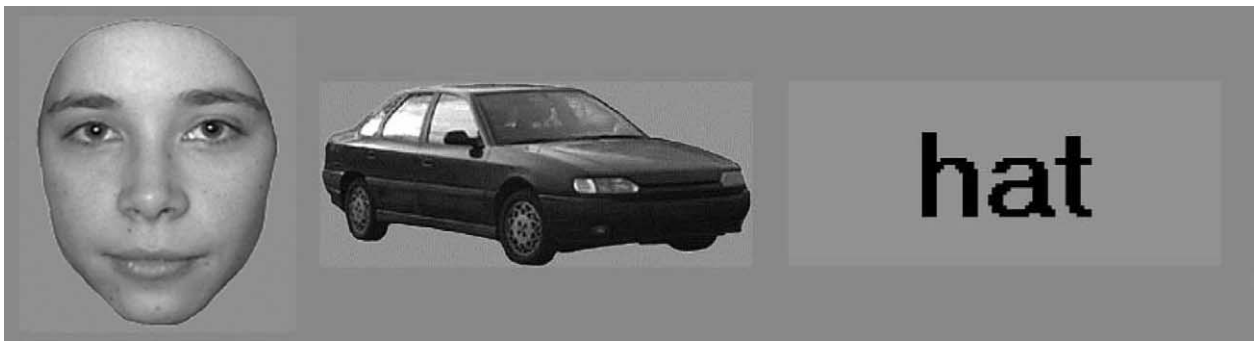

Fig. 1. Examples of the face, car, and word stimuli.

a 201-point digital 30 Hz low-pass filter, with cutoff frequencies of 29 (−3 dB point), and a stop-band attenuation of −63.3 dB (50 Hz and above). Then EEG and EOG artifacts were removed using a [−40; +40 μV] deviation over 200-ms intervals on frontal electrodes and using a [−35; +35 μV] deviation over 200-ms intervals on all other electrodes. In case of too many blink artifacts (in 7 subjects), they were corrected by a subtraction of VEOG prop-

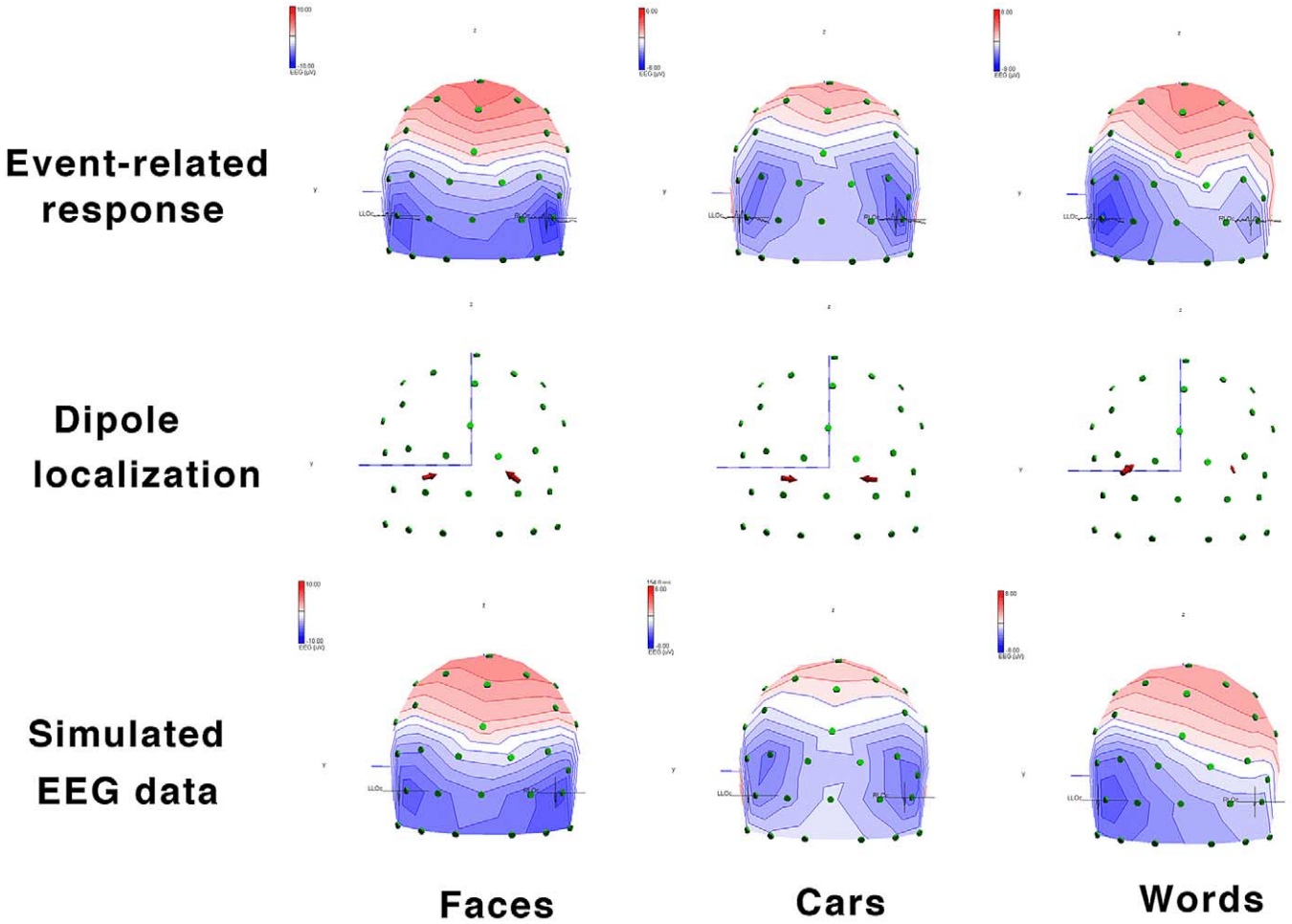

Fig. 2. Top row. Topographical maps (back of the head) of the N170 (154 ms) for the three categories of stimuli presented in this study (upright stimuli). The scale has been adapted for each category for a better display of all topographical similarities and differences (−8/8 μV for faces; −6/6 μV for words; −4/4 μV for cars). Middle row. Localization of the two dipoles accounting for more than 95% of the variance of the whole signal for each condition. Strength is reflected by the size of the dipole. Note the larger dipole in the right hemisphere for faces and the particularly large dipole in the left hemisphere for words. Lower row. The simulated EEG from the dipoles during the time interval. Each dipole configuration accounts for both the N170 and the VPP. Note that the simulated and real EEGs look almost identical for every condition.

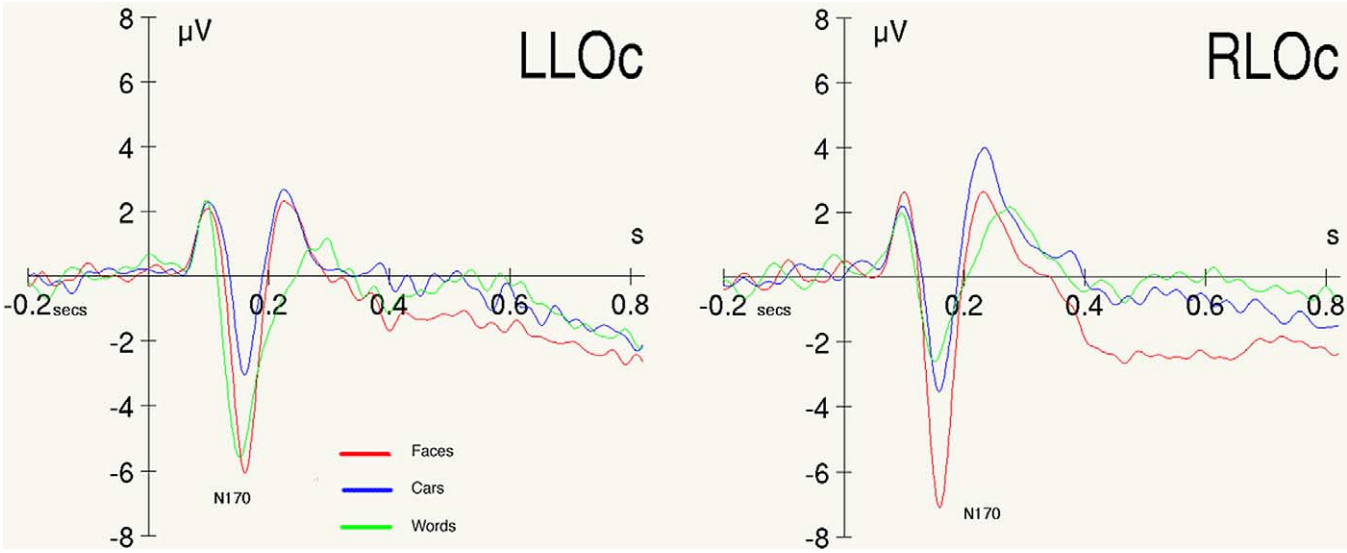

Fig. 3. The N170 obtained in response to all three categories (upright stimuli) at left and right (low) occipito-temporal sites. Note the larger difference between faces and other categories in the right hemisphere, and the large N170 to words in the left hemisphere.

agation factors, based on PCA-transformed EOG components (Nowagk and Pfeifer, 1996). Averaged ERPs were rereferenced using a common average reference.

Statistical analysis

After examination of the grand average topographies in all conditions (see Fig. 2), peak latency values of the N170 were extracted automatically at the maximum (negative) amplitude value between 130 and 210 ms at the occipito-temporal electrode site in the left and right hemisphere where the component peaked maximally in all conditions (LLOC/RLOC; i.e., left and right lateral occipital channels; see Fig. 2). These sites correspond to locations roughly 2 cm below T5 and T6, respectively. At these sites as well at occipital medial sites, the peak latency value of the preceding positivity (P1) was also extracted (70–140 ms). The VPP (and preceding negativity) measurements were made on a centro-frontal electrode (MIFR = FCZ, maximum positivity) using the same time window. The amplitude values were measured for both the P1 and N170 on five pairs of posterior channels where both of these peaks were prominent (occipital lateral, occipital medial, occipital inferior, temporal inferior, temporo-occipito-parietal). They were measured over 20-ms windows centered around the peak latency of the maximum amplitude on grand-averaged data, separately for each hemisphere and condition.

Repeated-measures ANOVAs were computed on behavioral measures, as well as on peak latencies and amplitudes of the N170, the VPP, and the P1. Post hoc *t* tests were performed when necessary and considered significant at $P < 0.05$, corrected for multiple comparisons (Bonferroni). Topographical displays and dipole analyses based on the whole scalp regions provided complementary information to the electrode peak analyses.

Dipole modeling

Dipole source models of the N170/VPP complex for each condition were determined on the grand averages by using a constrained multiple dipole fit procedure in Advanced Source Analysis (ASA 2.2, ANT, Inc.), with a realistic 3D head-shaped model based on the Montreal Neurological Institute MRI Atlas, AC/PC coordinates (Evans et al., 1993). The *X* axis of the coordinate system is a line joining electrodes T3 and T4 (left/right axis), the *Y* axis passes through FPZ and OZ (anterior/posterior axis), and the vertical *Z* axis passes through the center of the head and electrode CZ. Practically, a source model is derived by fitting the source model iteratively to the data until a minimum in residual variance (RV) is reached; i.e., the percentage of variance in the recorded potential distribution not accounted for by the source model is minimized. Similar to previous studies of N170 dipole modeling (Botzel et al., 1995; Itier and Taylor, 2002; Rossion et al., 1999a; Schweinberger et al., 2002), the dipoles of a pair were symmetrically constrained along the sagittal plane, assuming bilateral sources, in order to limit the number of parameters estimated. No other constraints with respect to localization or orientation of the dipoles were used. The independent variables were thus (for each condition): the *localization* of the dipoles, their *orientation* relative to the scalp, and their *strength* or dipole moment (in nA m). One pair of stationary dipoles was fitted in the time window around the peak latency of the N170 component (140–180 ms) for all conditions. We also modeled the subtraction waveforms of upright stimuli (*Faces–cars; words–cars; Faces–words*) for a better comparison with neuroimaging studies, where face-sensitive activations are always found *relative* to objects in inferior occipital and fusiform gyry.

Table 1
Mean (±SD) latency and amplitude values of the N170 (and preceding P1) at peak maximum (lateral occipito-temporal electrode site)

		Faces		Cars		Words	
		Up	Inverted	Up	Inverted	Up	Inverted
N170	L	162 ± 12	168 ± 13	164 ± 14	169 ± 14	156 ± 20	159 ± 18
Latency (ms)							
	R	162 ± 12	169 ± 12	163 ± 14	170 ± 13	158 ± 22	162 ± 22
Amplitude (μV)	L	−5.7 ± 3.3	−5.8 ± 3.5	−2.8 ± 3.1	−2.8 ± 3.7	−5.4 ± 5.4	−5.5 ± 4.5
	R	−6.7 ± 5.1	−6.5 ± 4.8	−3.3 ± 4.1	−3.0 ± 4.1	−2.5 ± 4.1	−3.8 ± 3.8
P1							
Latency (ms)	L	100 ± 17	105 ± 17	107 ± 19	108 ± 17	102 ± 12	94 ± 16
	R	106 ± 13	107 ± 15	105 ± 18	107 ± 19	104 ± 18	98 ± 17
Amplitude (μV)	L	2.0 ± 2.2	1.7 ± 2.4	2.2 ± 2.6	2.8 ± 2.2	2.1 ± 2.3	1.2 ± 2.2
	R	2.5 ± 2.2	2.5 ± 2.2	2.1 ± 2.0	2.1 ± 1.6	1.8 ± 1.6	1.8 ± 2.1
VPP							
Latency (ms)		160 ± 12	171 ± 17	165 ± 18	169 ± 19	152 ± 17	155 ± 19
Amplitude (μV)		4.2 ± 3.4	3.8 ± 3.1	1.5 ± 2.8	1.3 ± 3.2	2.4 ± 3.6	2.8 ± 3.3

Note. VPP values are measured at peak maximum, on a fronto-central site (between Cz and Fz). The amplitude values are computed over 20-ms windows centered on the peak latency (see Methods).

The initial localization of dipoles in the head model was identical for all conditions (0, 0, and 60 mm). Depending on the quality of the solution found, one additional dipole pair or a single dipole was added sequentially.

Results

Behavioral data

For both accuracy ($F(1, 14) = 3.82$, $P = 0.054$) and RTs ($F(1, 14) = 3.11$, $P = 0.09$), there were marginal effects of orientation, with the decision being slightly easier (97.3% vs 95.4%) and faster (548 ms vs 576 ms) for upright than inverted stimuli, with no interaction with object category.

ERP data

P1 and N170 latencies

At the level of the P1, there was a significant effect of *Category* on peak latency ($F(2, 28) = 4.21$, $P < 0.05$), the P1 peaking earlier for words compared to cars ($P < 0.01$) but not to faces ($P = 0.12$); cars and faces did not differ ($P = 0.36$). The interaction between *Category* and *Orientation* showed that these differences were due to a faster P1 for words compared to other categories when presented inverted ($P < 0.01$) but not upright ($P = 0.6$).

There was a main effect of *Category* on the N170 latency ($F(2, 28) = 4.98$, $P < 0.05$), mainly due to a faster response to pictures of words vs cars: $P = 0.023$ and a nonsignificant trend compared to faces ($P = 0.068$). The N170 latency did not differ between faces and cars ($P = 0.29$). There was also a main effect of *Orientation* ($F(2, 28) = 64.29$, $P < 0.001$), reflected by a longer N170 latency for upside-down presentations for all categories, marginally significant for words (see Fig. 4; Faces: $P < 0.001$; Cars: $P < 0.001$; Words: $P = 0.054$). Measuring peak latency differences using peak-to-peak latency analyses (a subtraction between N170 and P1 latency values) revealed a single significant main effect of *Orientation* ($F(2, 28) = 21.12$, $P < 0.001$) reflecting the delayed response to inverted pictures, with no differences between *Categories* (all other effects: $P > 0.2$). Thus, the latency difference between cars vs words emerged significantly at the level of the N170, but resulted from an additive effect (as indicated on Table 1) starting before the P1 peak, whereas the effects of *Orientation* for all categories were absent at the level of the P1 and highly significant at the level of the N170.

P1 and N170 amplitudes

At the level of the P1, there was a main effect of *Category* ($F(2, 28) = 5.6$, $P < 0.01$), due to a larger P1 for faces and cars compared to words ($P < 0.05$ and $P < 0.01$, respectively). There was no significant difference between faces and cars ($P = 0.98$). Because there was a significant interaction between the 4 factors (*Category*, *Orientation*, *Hemisphere*, and *Electrode*), post hoc *t* tests were run at each site. These tests revealed only significant differences (after Bonferroni correction for multiple tests) between faces and words at one electrode site (occipital medial) for inverted stimuli in the two hemispheres (all *P*s < 0.05), and in the right hemisphere only for upright stimuli. Differences were also observed at these sites between cars and words but were not significant after a Bonferroni correction. Faces and cars did not differ at these sites, but for inverted stimuli only, in the left hemisphere, there was a larger P1 amplitude for faces at lateral occipital sites ($P < 0.01$), and for cars vs faces at occipito-parietal sites ($P < 0.01$). In sum, there were local amplitude differences here and there at the level of the P1, but no differential lateralization pattern for categories, nor any effect of orientation. At occipital medial

sites, words appeared to elicit smaller responses, as observed previously (Schendan et al., 1998).

For the N170, there was a main effect of *Category* ($F(2, 28) = 34.26$, $P < 0.0001$), reflected by a larger component for faces compared to words ($P < 0.001$) and cars ($P < 0.0001$). These two latter categories were also different (words > cars, $P < 0.01$). However, these effects were qualified by a highly significant interaction between *Category* and *Hemisphere* ($F(2, 28) = 11.75$, $P < 0.001$), reflecting a larger N170 for faces compared to words in the right hemisphere only ($P < 0.0001$; left: $P > 0.2$), and compared to cars in both hemispheres (P's < 0.0001). Words elicited a large N170 than cars in the left hemisphere ($P < 0.001$) but not in the right hemisphere ($P = 0.65$). These effects are illustrated on Figs. 2 and 3. They were qualified by an interaction of these two factors with *Electrode* site, because the face-N170 was not significantly larger than cars on an occipito-parietal site of the left hemisphere ($P = 0.8$) and in addition to being significantly larger in the right hemisphere, it differed compared to words on an inferior occipital site of the left hemisphere ($P < 0.05$). There was also a triple interaction among *Category*, *Orientation*, and *Hemisphere* ($F(2, 28) = 4.47$, $P < 0.05$) due to the N170 to words, which was lower when presented inverted than upright, in the RH only ($P < 0.01$).

Accounting for P1 amplitude differences using peak-to-peak differences confirmed these effects. The main effect of *Category* ($F(2, 28) = 22.67$, $P < 0.0001$) was significant, reflecting the larger component for faces compared to words ($P < 0.001$) and cars ($P < 0.0001$). These two latter categories did not differ ($P = 0.25$). These effects were also qualified by a highly significant interaction between *Category* and *Hemisphere* ($F(2, 28) = 11.63$, $P < 0.001$), reflecting a larger N170 for faces compared to words in the right hemisphere only ($P < 0.0001$; left: $P > 0.15$), and compared to cars in both hemispheres (P's < 0.0001). Words elicited a larger N170 than cars in the left hemisphere ($P < 0.05$) but not in the right hemisphere ($P = 0.28$). The triple interaction among *Category*, *Hemisphere*, and *Electrode* was also significant ($F(8, 112) = 5.63$, $P < 0.0001$), because a difference between faces and words could also be observed at two sites on the left hemisphere, but it did not reach significance.

VPP latency

VPP latency effects were identical to those observed at the N170 (see Fig. 5). There were main effects of *Category* ($F(2, 28) = 9.22$, $P < 0.001$) due to earlier peak latency for words, and of *Orientation* ($F(2, 28) = 22.62$, $P < 0.001$) due to the delay resulting from inversion. These effects were qualified by a significant interaction between the two factors ($F(2, 28) = 4.89$, $P < 0.05$). The delay with inversion was significant for faces ($P < 0.001$) and cars ($P < 0.01$), but not for words ($P = 0.31$).

At the level of the preceding peak (central N100), there was a main effect of *Category* ($F(2, 28) = 11.96$, $P < 0.001$), again due to an earlier peak in response to words compared to cars ($P < 0.01$) and faces ($P < 0.01$), which did not differ from each other ($P = 0.2$).

As with the N170, taking into account these variations at the level of the central N100 in a peak-to-peak analysis did not change the pattern of VPP results, except that there was only a main effect of *Orientation* (delayed for upside-down presentations, ($F(2, 28) = 11.47$, $P < 0.01$), but no effect of *Category* ($F(2, 28) = 0.95$, $P = 0.4$). The two factors did not interact ($F < 1$).

VPP amplitude

For VPP amplitude, there was a main effect of *Category* ($F(2, 28) = 44.13$, $P < 0.0001$), with the peak elicited by faces being larger than for cars ($P < 0.001$) and words ($P < 0.001$), and the VPP to words being larger than to cars ($P < 0.05$; see Fig. 5). At the level of the preceding positivity, there was also a main effect of *Category* $F(2, 28) = 4.25$, $P < 0.005$, due to a smaller response to words compared to faces ($P < 0.05$) and cars (marginally significant: $P = 0.06$), with no difference between these two categories ($P = 0.27$). VPP-corrected amplitude was significantly affected by *Category* ($F(2, 28) = 13.14$, $P < 0.001$), but not by *Orientation* or an interaction of *Category* with *Orientation* (F's < 1). The main effect of category was related to a larger VPP for faces than words ($P < 0.05$) and cars ($P < 0.001$), but was not significant between words and cars ($P = 0.6$).

Summary of the results

As illustrated on Figs. 2 and 3 and Table 1, the N170 was significantly larger for faces than other categories, with a right hemisphere advantage. The N170 in response to cars was smaller and bilateral, whereas words elicited a component that was strongly lateralized, being as large as for faces in the left hemisphere. All these amplitude differences appeared at the level of the N170, as they were observed for both the measures compared to the prestimulus baseline, and to the preceding peak. At this earlier level, there was only a medial occipital P1 (and centro-frontal N1) reduction of amplitude for words, but no differences between faces and cars. Words elicited also a slightly faster P1/frontal N1 than other stimuli, but the processing taking place between this component and the N170 was as fast for all categories. As for orientation effects, they clearly emerged at the level of the N170 (Table 1, Fig. 3) with a delay to inverted stimuli significant for all categories at this level.

Dipole localization

The dipole localization was performed on grand-average data. Table 2 presents the summary results of the dipole localization obtained on grand averages for each condition, in the time window of 140–180 ms. For the three categories of stimuli, the localization of the reconstructed intracranial sources was highly similar: equivalent dipoles were located

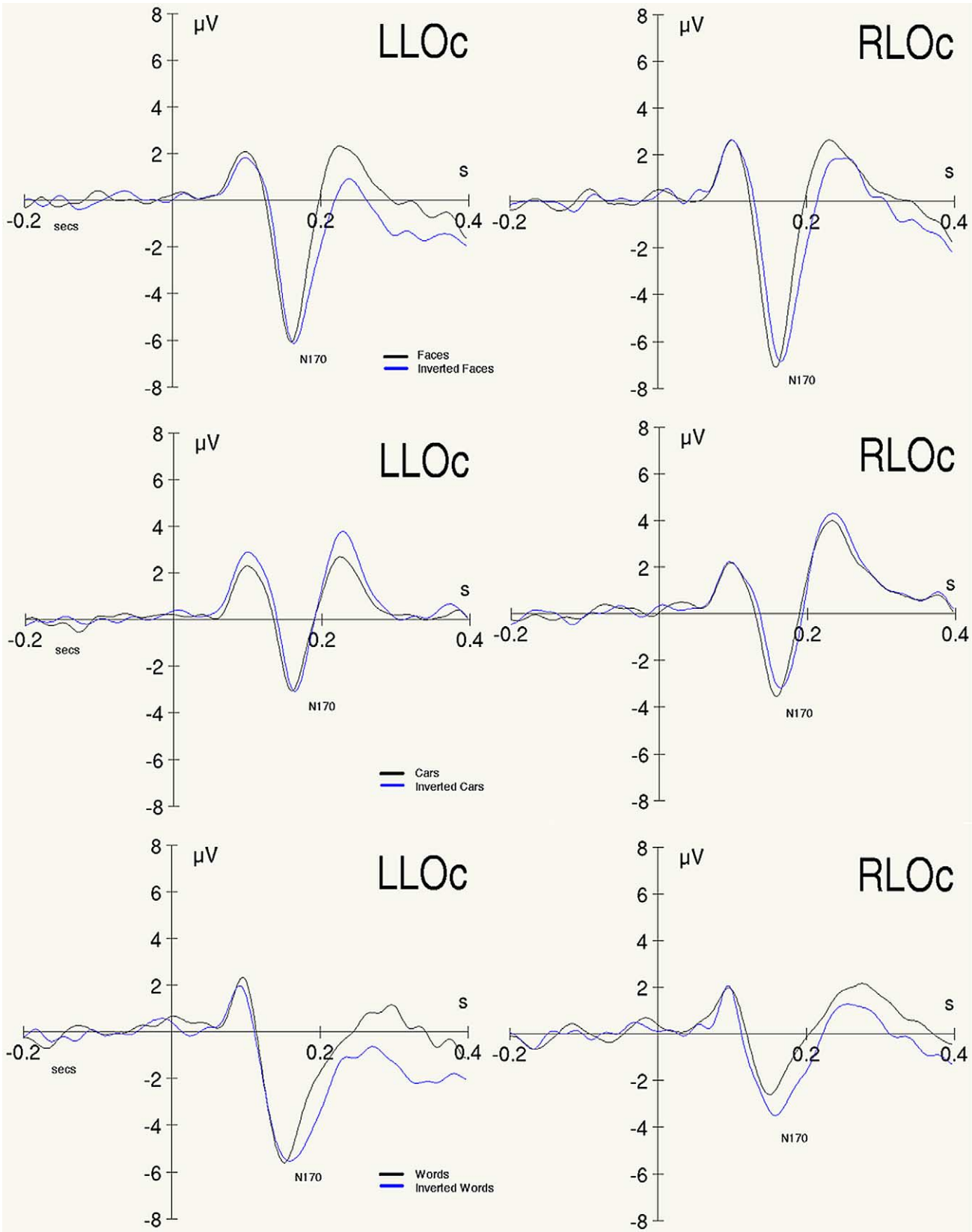

Fig. 4. The delay observed at the level of the N170 on left and right lateral occipito-temporal sites (LLOC/RLOC) for upside-down pictures of faces, cars, and words. Note that the delay starts at the level of the N170 and is absent at the level of the previous P1 component.

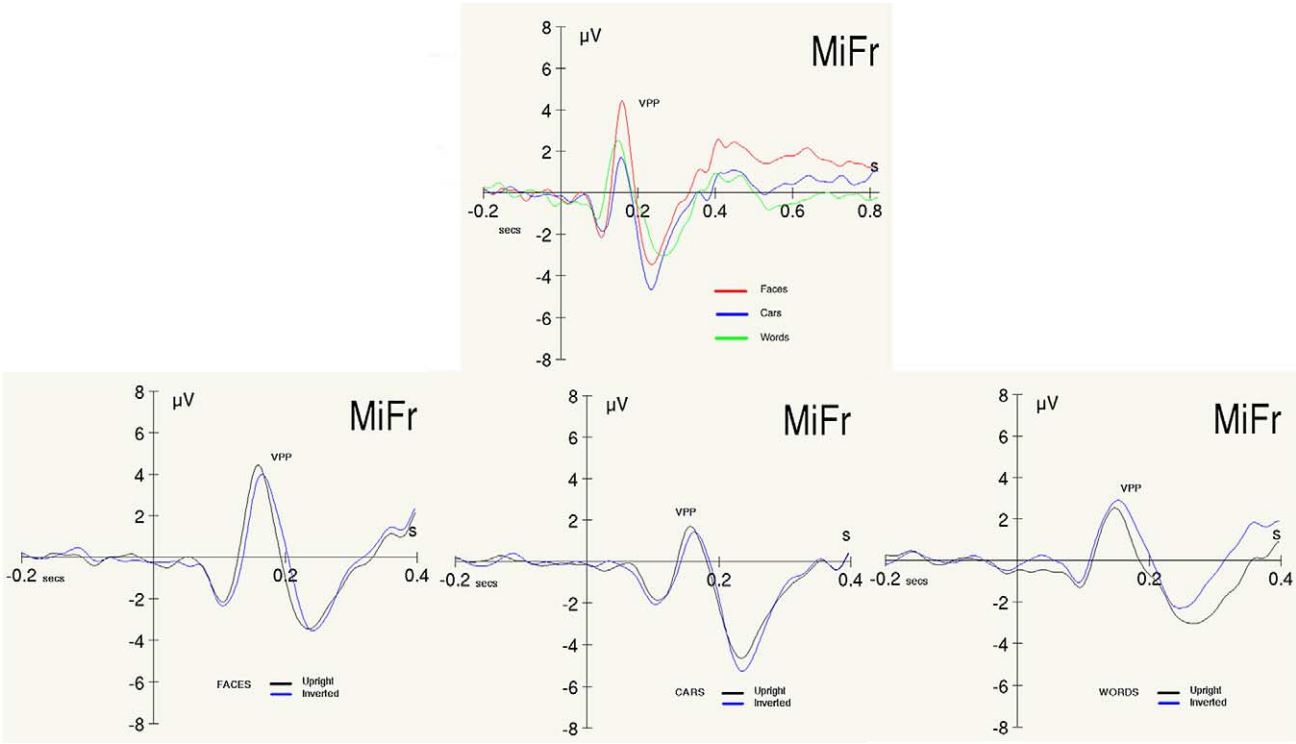

Fig. 5. The response properties of the vertex-positive potential (.VPP) at a middle centro-frontal site (MIFR, corresponding to FCZ). The above, left panel shows the difference between the three categories of objects used as stimuli: a large VPP for faces as compared to for words or cars. The other three panels show the delay observed with inversion at the level of the VPP for each object category.

in the infero-posterior part the visual cortex, at the level of the posterior fusiform gyrus (Figs. 2 and 6, Table 2). The orientation of the dipoles was such that a single dipole pair could explain almost all of the variance in the signal over the scalp, for all conditions (Table 2; Fig. 2). The EEG recomputed from these dipole pairs was almost indistinguishable from the original EEG data (see Fig. 2), thus accounting for both the negative N170 and the positivity at the vertex. When another single dipole or a pair of dipoles was added, the system failed to find a reliable solution and stopped after a few iterations. The localization of dipoles was highly similar between conditions, although the sources were oriented more tangentially for cars (Table 2; Fig. 2). The strength of the dipoles and the latency of the minimum residual variance during the sample (140–180 ms) differed across conditions and hemispheres. For faces, there was greater strength for the right hemisphere dipole, which peaked much earlier for upright faces than for inverted faces (in both hemispheres). For cars, the strength of the dipoles was much smaller, but fairly equal between hemispheres, peaking slightly later for inverted pictures in both hemispheres. For words, there was a large difference between hemispheres, the strength of the left hemisphere dipole being more than two times larger than the strength of the right hemisphere dipole. The delay observed with inversion appeared larger for face stimuli than for words and for cars, respectively (Table 2). Finally, the dipole localization on the *Faces–cars* subtracted grand-averaged waveforms (Fig. 7) gave an almost identical localization compared to the dipoles accounting for the face pictures alone, and also exhibited a right hemisphere advantage. The RH advantage was even larger for faces minus words, whereas the LH advantage was large when subtracting cars from words (Fig. 7). For these two latter subtractions, a single dipole solution accounted for as much of the variance as the symmetrical dipole pair, with no difference in localization for the dominant dipole. The single dipole solution was located in the left hemisphere for *words–cars* and in the right hemisphere for *faces–words* (Table 3).

Discussion

The N170 response pattern to objects, faces, and words

As early as 130–160 ms (peak of the N170/VPP), clear spatio-temporal response patterns emerge for pictures of faces, objects, and words, most likely originating from occipito-temporal cortex, as indicated by topographical displays and source reconstruction analyses. At these sites, there is no evidence of earlier differences between the three categories (Fig. 3), but as in a previous ERP study comparing linguistic and nonlinguistic visual images (Schendan et al., 1998), differences between printed words and other categories could be observed focally at medial occipital sites on the P1. As noted previously (Schendan et al., 1998),

Table 2
Summary of dipole modeling parameters

Condition	Hemisphere	Localization (mm) and orientation (head model:*x*, *y*, *z*)	Max Strength (nA m)	Minimum of residual variance (RV)	Latency of min. RV (ms)
Faces—upright	Right	−64, −36, −9.7 0.31, 0.75, 0.58	100	1.32	158
	Left	−64, 36, −9.7 0.37, −0.9, 0.24	89		
Faces—inverted	Right	−65, −38, −8.9 0.35, 0.8, 0.49	97	0.885	174
	Left	−65, 38, −8.9 −0.37, 0.89, −0.27	90		
Cars—upright	Right	−65, −35, −10 0.26, 0.93, 0.11	67	1.73	162
	Left	−65, 35, −10 −0.46, 0.88, 0.12	66		
Cars—inverted	Right	−71, −39, −2.8 0.31, 0.94, 0.12	54	3.35	166
	Left	−71, 39, −2.8 0.48, −0.87, −0.12	55	3.35	166
Words—upright	Right	−61, −47, 1.6 0.14, 0.42, 0.9	26	5.3	150
	Left	−61, 47, 1.6 0.61, −0.64, 0.46	55		
Words—inverted	Right	−74, −38, −3.1 0.45, 0.84, 0.3	59	1.67	160
	Left	−74, 38, −3.1 0.43, −0.89, 0.17	75		

Note. For all the conditions, the dipoles were located in the inferior occipital gyrus (BA19).

these occipital differences probably do not reflect neural operations that have become specialized for aspects of linguistic vs nonlinguistic patterns, but rather differences related to low-level visual properties and impossible to control completely, such as spatial frequency spectra (De Valois and De Valois, 1990) or perhaps spatial dimensions (length of words vs objects and faces). As a matter of fact, there was no such early difference between pictures of cars and faces, which were more comparable for low-level visual features, in the present study. In any case, hemispheric differences and orientation effects arose later than this P1 component, at the level of the N170.

How similar are the N170/VPP responses to the three stimulus categories used here? First, insofar as upright pre-

Table 3
Summary of dipole modeling parameters on subtraction waves

Condition	Hemisphere	Localization (mm) and orientation (head model:*x*, *y*, *z*)	Max Strength (nA m)	Minimum of residual variance (RV)	Latency of min. RV (ms)
Faces–cars	Right	−65, −35, −8.3 0.23, 0.51, 0.88	56	1.37	156
	Left	−65, 35, −8.3 0.053, −0.73, 0.69	37		
Faces–words	Right	−33, −41, −4.4 0.43, 0.34, 0.83	67	3.99	162
Words–cars	Left	−74, 23, 10 0.36, −0.45, 0.82	61	4.46	138

Note. The difference between faces and cars was bilateral and was best modeled with a pair of dipoles, which were located close to the location of the sources for faces alone (Table 2). A model with a single source gave a dipole component at a much more anterior and medial location compared to any of the two source solutions. However, the difference between words and cars could be modeled with a single dipole source located in the left hemisphere in an almost identical location (−21 −75 9.3; 4.25 of residual variance at 130 ms) compared to the left hemispheric dipole found in the two dipole solutions. Similarly, the difference between faces and words could be accounted for by a single right hemispheric dipole (36 −34 1; 3.91 of RV at 164 ms) which was located more anteriorly than in the other solutions. The subtraction wave was maximal early on for words compared to cars due to the earlier deflection observed for words. The dipoles located in the inferior occipital gyrus (BA19) for faces–cars, in the inferior temporal gyrus (BA20) for faces–words, and in the middle occipital gyrus (BA18) for words–cars.

sentations are compared and earlier differences accounted for, we found no significant peak latency difference between the three categories at the level of the N170/VPP. In short, there is no evidence that particular object categories are processed faster than others in the time interval spanning the preceding low-level visual processes and this early object categorization stage (see Rossion et al., 2002). A second striking similarity between the N170 evoked by these three categories of stimuli is its highly similar scalp distribution (peaking at the same electrode site, Fig. 2), albeit ignoring lateralization effects and quantitative local increases of activation that are addressed next.

Indeed, the three categories of objects used in the present study also produce significant electrophysiological differences at this early object categorization stage. Whereas the N170 in response to faces is bilateral with a small right hemisphere advantage, the same component is strongly left lateralized for printed words (Figs. 2 and 3). For pictures of cars, it is bilateral and much smaller relative to the response to faces in both hemispheres, as well as relative to the left-lateralized N170 response to words (Fig. 3). To our knowledge, the present study is the first to characterize these spatio-temporal differences between faces, objects, and words at a global level. Nevertheless, these results are consistent with evidence from previous scalp and intracranial ERP studies, as well as neuroimaging and neuropsychological reports.

As noted in the Introduction, earlier ERP studies have described a larger right than left hemisphere N170 amplitude response to faces as compared to other objects (e.g., Bentin et al., 1996). Compared to previous observations (e.g., Bentin et al., 1999; Schendan et al, 1998; Vogel and Luck, 2000), the left lateralization of the N170 in response to printed words in our study is striking. Bentin et al. (1999) observed an equally large response in left and right hemisphere to linguistic stimuli, but a significant N170 difference between linguistic and nonlinguistic (forms, symbols) patterns restricted to the left hemisphere. However, a left lateralization of the N170 to printed words has also been noted previously (Nobre and McCarthy, 1994). Recording field potentials directly at the surface of the brains of patients being evaluated for seizure disorders, Allison and colleagues (1999) described N200 potentials in response to faces, which were recorded from regions of the (right and left) fusiform gyrus and the inferior temporal gyri. These intracranial components were spatially distinct from N200s recorded to letterstring stimuli and nonface objects in other studies (see Allison et al., 1994, 1999). The timing[3] and location of the N200s suggest that these local field potentials contribute directly to the equivalent dipole generators responsible for the N170/VPP complex, as proposed by others (Bentin et al., 1996; Jeffreys, 1989; Schendan et al., 1998).

A large number of imaging studies have shown that compared to other objects, pictures of faces activate the occipito-temporal cortex (posterior and middle fusiform gyrus) bilaterally, with a right hemisphere advantage (e.g., Hasson et al., 2002; Puce et al., 1996; Sergent et al., 1992). In contrast, letterstrings evoke activation that is primarily restricted to the left lateral fusiform gyrus and occipitotemporal sulcus (Hasson et al., 2002; Polk et al., 2002; Puce et al., 1996; Sergent et al., 1994). Other PET and fMRI studies have also described a left lateralization pattern for pictures of common objects (e.g., Sergent et al., 1992), but this pattern of lateralization is not consistently found (e.g., Hasson et al., 2002) and may well be related to the use of semantic categorization tasks (e.g., Sergent et al., 1992) rather than to an early processing bias toward the left hemisphere for nonface object categorization. Such semantic factors are unlikely to play a role in the left lateralization bias found for words in the present ERP response patterns, because the task used here was a simple orientation decision and the onset time of these lateralization effects occurs well before the time at which electrophysiological effects of semantic processing on words, faces, and objects are usually reported (i.e., at the level of the N400; see, e.g., Bentin et al., 1999; Kiefer, 2001; Nobre and McCarthy, 1994). In short, the strong left lateralization for printed words as compared to objects and faces found in the present study can be related to aspects of visual pattern recognition (i.e., letters) and not to language (i.e., lexical, semantic, syntactic) processes per se. Accordingly, they should also be observed with pseudowords or even string of consonants, since there is no amplitude difference between words and nonwords at the level of the N170 (e.g., Bentin et al., 1999; Schendan et al., 1998), such differences usually being found later, around 250 ms (Bentin et al., 1999; Dehaene, 1995).

The differential patterns of early lateralization for faces, words, and objects reported here are also consistent with the neuropsychological literature on object recognition deficits. Impairments in face perception usually follow bilateral lesions of the occipito-temporal cortex (e.g., Damasio et al., 1982; Farah, 1991), although a right unilateral lesion may be sufficient to produce prosopagnosia (e.g., Landis, 1988). By contrast, pure alexia is found with either bilateral or left unilateral ventral lesions (Farah, 1991). Interestingly, a review of 99 cases of object agnosia published over the last century (Farah, 1991) indicates that it is systematically associated with either pure alexia or prosopagnosia (or both), and can thus be observed following unilateral left or right hemispheric, or bilateral lesions.

Our scalp ERP findings are thus consistent with findings collected with a wide variety of methods. At the same time, our results clarify the spatio-temporal brain response at

[3] As noted previously by several authors (Bentin et al., 1996; Jeffreys, 1996; Schendan et al., 1998), the apparent discrepancies between the peak latencies of the scalp N170/VPP and the intracranial N200s may be accounted for by several factors. First, both the N170/VPP and the N200s actually range between 140 and 200 ms. Second, the responses of normal brains are compared with those of patients under medication and this may also account for some differences in onset and peak latency of these cortical components.

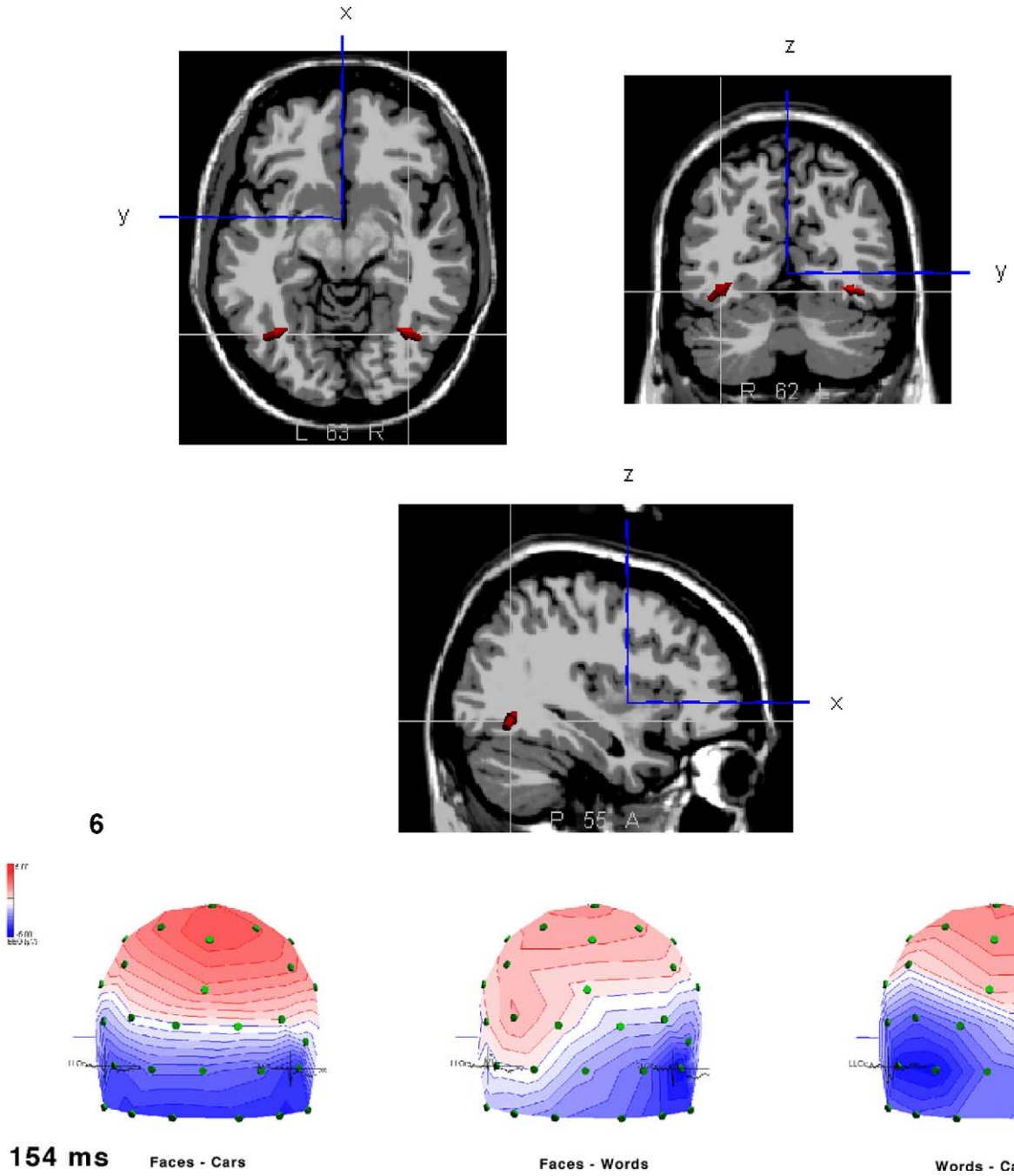

Fig. 6. Localization of the equivalent dipolar sources for faces superimposed on a standard structural MRI model, average of 50 subjects (Evans et al., 1993).

Fig. 7. Topographical maps of the subtractions maps between faces and cars, faces and words, words and cars, at the N170/VPP complex peak latency for all conditions (154 ms).

which these three object categories are differentiated. That is, recording ERPs at the scalp allows one to capture neural activity at a global level, and, in particular, to characterize temporal patterns of lateralization that may be missed using other techniques (Regan, 1989).

Although, as we have already noted, our results are consistent with those of many other studies, the differences between faces and words obtained here stand in contrast to the absence of topographical differences for faces and words found by Schendan and colleagues (1998). These discrepancies may be related to methodological differences, as well as to different objectives of the two studies. First, Schendan and colleagues chose to concentrate on the VPP response using a mastoid reference that almost eliminated the N170 component in their study. However, they do note (Schendan et al., 1998, p. 246, Fig. 3) a small left lateral-

ization of the N170 response to words, and a right hemisphere advantage for faces and objects, which they did not describe as reliable. Second, they used far fewer electrode sites (half) as compared to the present study, in particular, at posterior sites. In any case, our observation of a larger N170 and VPP response to faces compared to words does not contradict their conclusion that the amplitude of the VPP response is related to the cumulative experience people have with a particular category, a view that other studies on the N170 have corroborated (Gauthier et al., 2003; Rossion et al., 2003; Tanaka and Curran, 2001). However, our findings suggest that such experience is probably just one of the multiple factors contributing to the differential amplitude of the N170/VPP complex. We turn to this question next.

What drives the different N170 response patterns to faces, objects, and words?

The spatio-temporal differences among faces, words, and objects might be interpreted as evidence that the processing of information in the human object recognition system is divided early into three functionally independent subsystems, or modules, each specialized to process one type of visual form information. Such an interpretation has been offered by Bentin and colleagues (1996) to account for the N170 amplitude difference found between faces and other objects, that is, as the manifestation of an early face categorization ("detection") stage. Similarly, these authors described a difference between orthographic and nonorthographic stimuli at the level of the N170 (Bentin et al., 1999) that was interpreted as the manifestation of an early system tuned to process linguistic information. This modularist view has also been adopted by a number of authors interpreting activation differences between faces and objects in the regions of the inferior occipital gyrus and middle fusiform gyrus (e.g., Kanwisher et al., 1997; Sergent et al., 1992; Puce et al., 1996; see Haxby et al., 2000), and in the left fusiform gyrus for letterstrings compared to numbers and shapes (the "letter area," Polk et al., 2002). There are, however, a number of general problems with the modular interpretation of these findings (see Tarr and Gauthier, 2000).

As we are primarily concerned with electrophysiological findings, a number of empirical ERP studies have shown that the N170 amplitude response not only differentiates between nonface object categories (Rossion et al., 2000), but is also sensitive to attention (Eimer, 2000b; Holmes et al., 2003; but see Severac-Cauquil et al., 2000), task factors (Tanaka et al., 1999; Vogel and Luck, 2000), and diagnosticity of the facial information for the task at hand (Goffaux et al., 2003b) and is related to visual experience one has accumulated with the object category (Gauthier et al., 2003; Rossion et al., 2003; Tanaka and Curran, 2001). Recent evidence also suggests that this component may be sensitive to face familiarity (Caharel et al., 2003; Jemel et al., 2003). These findings suggest that the N170 reflects the activation of many different subprocesses (and areas) in the occipito-temporal pathway, and can be used as a tool to study the parameters affecting object recognition, including the recognition of faces (see Rossion et al., 2002).

The effect of inversion

A major finding of the present study was that all object categories led to a significant delay of the N170 (and VPP) when inverted. Several previous studies have described such a latency delay for inverted face presentations at the level of the N170/M170 (e.g., Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000a; Goffaux et al., 2003a; Itier and Taylor, 2002; Linkenkaer-Hansen et al., 1998; Liu et al., 2000; Rebai et al., 2001; Rossion et al., 1999b, 2000, 2002; Sagiv and Bentin, 2001; Taylor et al., 2001; Watanabe et al., 2003) or the VPP when measured (Jeffreys, 1993; Rossion et al., 1999b). Although an amplitude increase to inverted faces has also been reported (de Haan et al., 2002; Itier and Taylor, 2002; Linkenkaer-Hansen et al., 1998; Rebai et al., 2001; Rossion et al., 1999b, 2000; 2002; Sagiv and Bentin, 2001; Taylor et al., 2001), this effect is less consistent (see Rossion and Gauthier, 2002). In the present study, we did not find such an amplitude increase, the N170 being as large for upright and inverted presentations for all categories of stimuli. Interestingly, the delay of the N170/VPP complex with inversion was not only characterized by a local peak latency delay, but by the dipole analysis showing that the best fit for this dipolar component was systematically delayed for inverted stimuli (Table 2). This finding illustrates another way of quantifying the delay of N170-related processes when faces are presented in an unusual orientation, taking into account the entire signal during a specific time window (see also Halgren et al., 2000; Michel et al., 2001).

Since the N170 latency delay has been reported previously only for faces or a nonface category (Greebles) to which subjects had been familiarized (Rossion et al., 2002), we predicted that the N170 to inverted presentations of highly monooriented stimuli such as printed words would also be delayed, and this indeed is what we found. However, presenting pictures of cars upside down also significantly delayed the N170, a finding inconsistent with our previous results (Rossion et al., 2000). This was somewhat surprising in that we used similar stimuli (pictures of cars) and the same task (an orientation judgment). However, several factors may account for this empirical discrepancy. First, we observed the maximum peak latency of the N170 at lower occipito-temporal sites than in our previous study. Second, compared to our previous study, pictures of cars were no longer presented in a full-front view (see Rossion et al., 2000, Fig. 1), but in a 3/4 view. Preliminary data recorded comparing full-front and 3/4 views suggests that the N170 response is significantly shorter in latency for 3/4 views of cars than full-front views, and is closer to full-front presentation of faces, suggesting that the optimal view for presenting pictures of cars may be a 3/4 profile view. Thus, view

canonicality in depth (Blanz et al., 1999; Palmer et al., 1981) may also affect the N170 response.

Although when pictures of cars are presented in their (depth) canonical view, the N170 can be delayed to inverted images, the dipole analysis suggests that the delay of the N170/VPP complex related to inversion increases gradually for cars, words, and faces, respectively (Table 2). The necessary and sufficient factors to trigger this effect and modulate its magnitude should be investigated more precisely in future ERP studies. As for printed words, our prediction would be that, similarly to the left hemisphere advantage, this inversion effect should be found for nonwords as well, in our view, being more related to the perception of inverted individual letters than of the combinations of these letters forming words.

The N170 and the VPP: Two faces of the same dipolar activity?

Lastly, besides its interest for the spatio-temporal processing aspects of object categories, our study provides a number of arguments supporting the view that the VPP and N170 should be viewed as two sides of the same dipolar configuration: First, the two components are temporally coincident, generally occurring between 140 and 200 ms, and at almost identical latencies in the same study. Second, they present identical functional responses. In particular, a larger response to faces than objects is found on both components (Bentin et al., 1996; Botzel et al., 1995), leading them both to be defined as electrophysiological correlates of the "structural encoding stage" within Bruce and Young's (1986) functional face processing model (Bentin, 1996; Eimer, 1998; Jeffreys, 1989). Identical effects of face (and object) inversion are also found on the N170 and VPP during inversion (Rossion et al., 1999b; the present study; Itier and Taylor, 2002), switching face components (George et al., 1996), contrast inversion (Itier and Taylor, 2002), and spatial frequency filtering (Goffaux et al., 2003a). Finally, they can be both accounted for by the same dipole configuration rooted in the inferior occipital cortex/posterior fusiform gyrus and pointing toward the vertex, as in previous ERP (Botzel et al., 1995; Itier and Taylor; 2002; Rossion et al., 1999b; Schweinberger et al., 2002) and MEG studies (Halgren et al., 2000; Watanabe et al., 2003). This is consistent with the outcome of spatial principal component analysis (PCA) during the time window of the N170/VPP component, which also points to a single component accounting for most of the variance in the scalp EEG data (Schweinberger et al., 2002).[4] Taken together, these observations strongly suggest that the VPP peak recorded at centro-frontal sites reflects volume-conducted activity originally generated in occipito-temporal cortex.

[4] Only Botzel et al. (1995) found a reliable solution with two different pairs of dipoles for the N170 (peak C in their study) and the VPP (peak D), but the decrease of residual variance was small and this additional solution could be found only when they fitted the two pairs at different time windows.

Conclusion

The human visual object recognition system distinguishes between faces, objects, and words as early as 130 to 170 ms. This effect is reflected by variations of the amplitude and lateralization pattern at the level of the N170/VPP complex, originating from single equivalent dipolar sources located bilaterally in the occipito-temporal cortex. Whereas the right hemisphere has an advantage in the early categorization of faces, objects are processed bilaterally, and there is a strong left hemisphere bias for word-like stimuli that does not seem to be related to language (i.e., semantic, syntactic, or lexical) processes per se. Further studies will have to clarify the respective role of the structural differences between these categories and of the differential visual experience of human subjects with them in shaping these early differences. Moreover, these early stages of visual processing can also be tuned to specific views of objects, such that the presentation of a familiar object category in a noncanonical view delays the associated ERP components.

Acknowledgments

Bruno Rossion is supported by the Belgian National Fund for Scientific Research (FNRS). This work was supported by awards from the James S. McDonnell Foundation (Perceptual Expertise Network, 15573-S6 (supporting C.A.J.) and the National Science Foundation (BCS-0094491) to M.J.T., and an award from the NIMH (MH57075) to G.W.C. The authors thank Marta Kutas for use of her facilities, David L. Molfese for assistance during data collection, Maarten van de Velde and Michiel van Burik for help with data conversion and source localization, Christine Schiltz and two anonymous reviewers for their helpful comments on a previous version of this manuscript.

References

Allison, T., Ginter, H., McCarthy, G., Nobre, A.C., Puce, A., Luby, M., Spencer, D.D., 1994. Face recognition in human extrastriate cortex. J. Neurophysiol. 71, 821–825.

Allison, T., Puce, A., Spencer, D.D., McCarthy, G., 1999. Electrophysiological studies of human face perception: potentials generated in occipitotemporal cortex by face and nonface stimuli. Cereb. Cortex 9, 415–430.

Bentin, S., Allison, T., Puce, A., Perez, A., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. J. Cogn. Neurosci. 8, 551–565.

Bentin, S., Mouchetant-Rostaing, Y., Giard, M.H., Echallier, J.F., Pernier, J., 1999. ERP manifestations of processing printed words at different psycholinguistic levels: time course and scalp distribution. J. Cogn. Neurosci. 11, 235–260.

Bertrand, O., Perrin, F., Pernier, J., 1985. A theoretical justification of the average reference in topographic evoked potential studies. Electroenceph. Clin. Neurophysiol. 62, 462–464.

Blanz, V., Tarr, M.J., Bülthoff, H.H., 1999. What object attributes determine canonical views? Perception 28, 575–600.

Bodamer, J., 1947. Die-Prosop-agnosie. Arch. Psychiatr. Nervenkrankh, 179, 6–54. English translation by Ellis, H.D., Florence, M., 1990. Cogn. Neuropsychol. 7, 81–105.

Bötzel, K., Schulze, S., Stodieck, R.G., 1995. Scalp topography and analysis of intracranial sources of face-evoked potentials. Exp. Brain Res. 104, 135–143.

Braeutigam, S., Bailey, A.J., Swithenby, S.J., 2001. Task-dependent early latency (30–60 ms) visual processing of human faces and other objects. NeuroReport 12, 1531–1536.

Bruce, V., Young, A.W., 1986. Understanding face recognition. Br. J. Psychol. 77, 305–327.

Caharel, S., Poiroux, S., Bernard, C., Thibaut, F., Lalonde, R., Rebai, M., 2002. ERPs associated with familiarity and degree of familiarity during face recognition. Int. J. Neurosci. 112, 1499–1512.

Cooper, L. A., Shepard, R. N., 1973. Chronometric studies of the rotation of mental images, in: Chase, W.G., (Ed.), Visual Information Processing, New York, Academic Press.

Curran, T., Tanaka, J. W., Weiskopf, D. M., 2002. An electrophysiological comparison of visual categorization and recognition memory. Cogn. Affect. Behav. Neurosci. 2, 1–18.

Damasio, A.R., Damasio, H., Van Hoesen, G.W., 1982. Prosopagnosia: anatomic basis and behavioral mechanisms. Neurology 32, 331–341.

De Valois, R. L., De Valois, K. K., 1990. Spatial Vision. Oxford Univ. Press, New York.

De Haan, M., Pascalis, O., Johnson, M.J., 2002. Specialization of neural mechanisms underlying face recognition in human infants. J. Cogn. Neurosci. 14, 199–209.

Dehaene, S., 1995. Electrophysiological evidence for category-specific word processing in the normal human brain. NeuroReport 6, 2153–7.

Eimer, M., 1998. Does the face-specific N170 component reflect the activity of a specialized eye processor? Neuroreport 9, 2945–2948.

Eimer, M., 2000a. Effects of face inversion on the structural encoding and recognition of faces—evidence from event-related brain potentials. Cogn. Brain Res. 10, 145–158.

Eimer, M., 2000b. Attentional modulations of event-related brain potentials sensitive to faces. Cogn. Neuropsychol. 17, 103–116.

Evans, A.C., Collins, D.L., Mills, S.R., Brown, E.D., Kelly, R.L., Peters, T.M., 1993. 3D statistical neuroanatomical models from 305 MRI. volumes. Proc. IEEE-Nuclear Science Symposium and Medical Imaging Conference, pp. 1813–1817.

Farah, M.J., 1991. Patterns of co-occurrence among the associative agnosias: implications for visual object representation. Cogn. Neuropsychol. 8, 1–19.

Farah, M.J., 1994. Specialization within visual object recognition: clues from prosopagnosia and alexia. in: Farah, M.J., Ratcliff, G. (Eds.), The Neuropsychology of High-Level Vision. Erlbaum, Hillsdale, NJ, pp. 133–146.

Gauthier, I., Curran, T., Curby, K.M., Collins, D., 2003. Perceptual interference supports a non-modular account of face processing. Nature Neurosci. 6, 428–432.

George, N., Evans, J., Fiori, N., Davidoff, J., Renault, B., 1996. Brain events related to normal and moderately scrambled faces. Cogn. Brain Res. 4, 65–76.

Goffaux, V., Gauthier, I., Rossion, B., 2003a. Spatial scale contribution to early visual differences between face and object processing. Cogn. Brain Res. 16, 416–424.

Goffaux, V., Jemel, B., Jacques, C., Rossion, B., Schyns, P., 2003b. ERP evidence for task modulations on face perceptual processing at different spatial scales. Cogn. Sci. 27, 313–325.

Halgren, E., Raij, T., Marinkovic, K., Jousmaki, V., Hari, R., 2000. Cognitive response profile of the human fusiform face area as determined by MEG. Cereb. Cortex 10, 69–81.

Hasson, U., Levy, I., Behrmann, M., Hendler, T., Malach, R., 2002. Eccentricity bias as an organizing principle for human high-order object areas. Neuron 34, 479–490.

Halit, H., de Haan, M., Johnson, M.H., 2000. Modulation of event-related potentials by prototypical and atypical faces. NeuroReport 11, 1871–1875.

Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. Trends Cogn. Sci. 4, 223–233.

Holmes, A., Vuilleumier, P., Eimer, M., 2003. The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials. Cogn. Brain Res. 16, 174–184.

Itier, R.J., Taylor, M.J., 2002. Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. NeuroImage 15, 353–72.

Jeffreys, D.A., 1989. A face-responsive potential recorded from the human scalp. Exp. Brain Res. 78, 193–202.

Jeffreys, D.A., 1993. The influence of stimulus orientation on the vertex positive scalp potential evoked by faces. Exp. Brain Res. 96, 163–172.

Jeffreys, D.A., 1996. Evoked studies of face and object processing. Visual Cogn. 3, 1–38.

Jemel, B., Pisani, M., Calabria, M., Crommelinck, M., Bruyer, R., 2003. Is the early face-sensitive component cognitively penetrable? Evidence from repetition priming of Mooney faces of familiar and unfamiliar persons. Cogn. Brain Res. in press.

Jolicoeur, P., 1990. Orientation congruency effects on the identification of disoriented shapes. J. Exp. Psychol. Hum. Percep. Perform. 16, 351–64.

Kanwisher, N., McDermott, J., Chun, M-M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. 17, 4302–4311.

Kiefer, M., 2001. Perceptual and semantic sources of category-specific effects: event-related potentials during picture and word categorization. Memory Cogn. 29, 100–16.

Kutas, M., Van Petten, C., 1990. Electrophysiological perspectives on comprehending written language. Electroenceph. Clin. Neurophysiol. 41, 155–67.

Landis, T., Regard, M., Bliestle, A., Kleihues, P., 1988. Prosopagnosia and agnosia from noncanonical views. An autopsied case. Brain. 11, 1287–1297.

Linkenkaer-Hansen, K., Palva, J.M., Sams, M., Hietanen, J.K., Aronen, H.J., Ilmoniemi, R.J., 1998. Face-selective processing in human extrastriate cortex around 120 ms after stimulus onset revealed by magneto- and electroencephalography. Neurosci. Lett. 253, 147–150.

Liu, J., Higuchi, M., Marantz, A., Kanwisher, N., 2000. The selectivity of the occipitotemporal M170 for faces. Neuroreport 11, 337–341.

Michel, C.M., Thut, G., Morand, S., Khateb, A., Pegna, A.J., Grave de Peralta, R., Gonzales, S., Seeck, M., Landis, T., 2001. Electric source imaging of human brain functions. Brain Res. Rev. 36, 108–118.

Moscovitch, M., Behrmann, M., Winocur, G., 1997. What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. J. Cogn. Neurosci. 9, 555–604.

Nobre, A.C., Allison, T., McCarthy, G., 1994. Word recognition in the human inferior temporal lobe. Nature 372, 260–263.

Nobre, A.C., McCarthy, G., 1994. Language-related ERPs-Scalp distribution and modulation by word type and semantic priming. J. Cogn. Neurosci. 6, 233–255.

Nowagk, R., Pfeifer, E., 1996. Unix implementation of the ERP evaluation package (EEP 3.0). In Annual Report of Max-Planck-Institute of Cognitive Neuroscience (Eds. Friederici, A. D., & Von cramon, D. Y).

Palmer, S., Rosch, E., Chase, P., 1981. Canonical perspectives and the perception of objects, in: Long, J., Baddeley, A. (Eds.), Attention and Performance, IX. Erlbaum, Hillsdale, NJ, pp. 135–151.

Polk, T.A., Stallcup, M., Aguirre, G.K., Alsop, D.C., D'Esposito, M., Detre, J.A., Farah, M.J., 2002. Neural specialization for letter recognition. J. Cogn. Neurosci. 14, 145–159.

Puce, A., Allison, T., Asgari, M., Gore, J.C., McCarthy, G., 1996. Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. J. Neurosci. 16, 5205–5215.

Rebai, M., Poiroux, S., Bernard, C., Lalonde, R., 2001. Event-related potentials for category-specific information during passive viewing of faces and objects. Int. J. Neurosci. 106, 209–226.

Regan, D., 1989. Human Brain Electrophysiology: Evoked Potentials and Evoked Magnetic Fields in Science and Medicine. Elsevier, New York.

Rossion, B., Campanella, S., Gomez, C., Delinte, A., Debatisse, D., Liard, L., Dubois, S., Bruyer, R., Crommelinck, M., Guerit, J.-M., 1999a. Task modulation of brain activity related to familiar and unfamiliar face processing: an ERP Study. Clin. Neurophysiol. 110, 449–462.

Rossion, B., Curran, T., Gauthier, I., 2002. A defense of the subordinate-expertise account for the N170 component. Cognition 85, 189–96.

Rossion, B., Delvenne, J.F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., Guérit, J.-M., 1999b. Spatio-temporal localization of the face inversion effect: an event-related potentials study. Biol. Psychol. 50, 173–189.

Rossion, B., Gauthier, I., 2002. How does the brain process upright and inverted faces? Behav. Cogn. Neurosci. Rev. 1, 63–75.

Rossion, B., Gauthier, I., Goffaux, V., Tarr, M.J., Crommelinck, M., 2002. Expertise training with novel objects leads to left lateralized face-like electrophysiological responses. Psychol. Sci. 13, 250–257.

Rossion, B., Gauthier, I., Tarr, M.J., Despland, P.A., Bruyer, R., Linotte, S., Crommelinck, M., 2000. The N170 occipito-temporal component is enhanced and delayed to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. NeuroReport 11, 69–74.

Rossion, B., Kung, C.-C., Tarr, M.J., 2003. Greeble expertise reduces the N170 response to faces: electrophysiological evidence for visual competition between faces and non-face objects of expertise. J. Cogn. Neurosci. C301 Suppl. S 2003.

Rumiati, R.I., Humphreys, G.W., 1997. Visual object agnosia without alexia or prosopagnosia: arguments for separate knowledge stores. Visual Cogn. 4, 207–217.

Sagiv, N., Bentin, S., 2001. Structural encoding of human and schematic faces: holistic and part-based processes. J. Cogn. Neurosci. 13, 937–951.

Schendan, H.E., Ganis, G., Kutas, M., 1998. Neurophysiological evidence for visual perceptual categorization of words and faces within 150 ms. Psychophysiology 35, 240–51.

Scherg, M., 1990. Fundamentals of dipole source potential analysis, in: Grandori, F., Hoke, M., Romani, GL (Eds.), Auditory Evoked Magnetic and Magnetic and Electric Potentials. Karger, Basel, pp. 40–69.

Schweinberger, S.R., Pickering, E.C., Jentzsch, I., Burton, A.M., Kaufmann, J.M., 2002. Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. Cogn. Brain Res., in press.

Sergent, J., MacDonald, B., Zuck, E., 1994. Structural and functional organisation of knowledge about faces and proper names: a positron emission tomography study. in: Umiltà, C., Moscovitch, M. (Eds.), Attention and Performance, Vol. 15. M.I.T. Press, Cambridge, pp. 203–208.

Sergent, J., Otha, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing. A positron emission tomography study. Brain 115, 15–36.

Severac-Cauquil, A.S., Edmonds, G. E., Taylor, M.J., 2000. Is the face sensitive N170 the only ERP not affected by selective attention? NeuroReport 11, 2167–2171.

Tanaka, J.W., Curran, T., 2001. A neural basis for expert object recognition. Psychol. Sci. 12, 43–47.

Tanaka, J.W., Luu, P., Weisbrod, M., Kiefer, M., 1999. Tracking the time course of object categorization using event-related potentials. NeuroReport 10, 829–835.

Tarr, M.J., Gauthier, I., 2000. FFA: a flexible fusiform area for subordinate-level visual processing automatized by expertise. Nature Neurosci. 3, 764–769.

Taylor, M.J., 2002. Non-spatial attentional effects on P1. Clin. Neurophysiol. 113, 1903–1908.

Taylor, M.J., McCarthy, G., Saliba, E., Degiovanni, E., 1999. ERP evidence of developmental changes in processing of faces. Clin. Neurophysiol. 110, 910–915.

Taylor, M.J., Edmonds, G.E., McCarthy, G., Allison, T., 2001. Eyes first! Eye processing develops before face processing in children. NeuroReport 12, 1671–1676.

VanRullen, R., Thorpe, S.J., 2001. The time course of visual processing: from early perception to decision-making. J. Cogn. Neurosci. 13, 454–61.

Tovée, M.J., 1998. Face processing: getting by with a little help from its friends. Curr. Biol. 8, R17–R320.

Vogel, E.K., Luck, S.J., 2000. The visual N1 component as an index of a discrimination process. Psychophysiology 37, 190–203.

Watanabe, S., Kakigi, R., Puce, A., 2003. The spatiotemporal dynamics of the face inversion effect: a magneto- and electro-encephalographic study. Neuroscience 116, 879–895.

Yin, R.K., 1969. Looking at upside-down faces. J. Exp. Psychol. 81, 41–145.