Spatio-temporal localization of the face inversion effect: an event-related potentials study

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Abstract

Event-related potentials (ERPs) from 58 electrodes at standard EEG sites were recorded while 14 subjects performed a delayed-matching task on normal and inverted faces. A large and single difference between normal and inverted face processing was observed at occipito-temporal sites about 160 ms following stimulus onset, mainly in the right hemisphere (RH). Although the topographies indicate that similar areas are involved at this latency in processing the two types of stimuli, the electrophysiological activity, which corresponds to the previously described N170, was larger and delayed for inverted as compared to normal face processing. These results complement and specify, at a neural level, previous behavioral and divided visual field studies which have suggested that the loss of configural face information by inversion may slow down and increase the difficulty of face processing, particularly in the RH. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

The question as to whether face and object recognition involve different processes underlined by different neural structures, is a central concern of visual cognitive neuroscience. Several lines of evidence from cognitive psychology (Yin, 1969; Bruce, 1988; Tanaka and Farah, 1993), neuropsychology (Farah, 1991; Moscovitch et al., 1997), neurophysiology (Desimone, 1991; Perrett et al., 1992) and more recently neuroimaging studies (Sergent et al., 1992; Kanwisher et al., 1997; McCarthy et al., 1997) support the thesis of an autonomous processing system specifically dedicated to faces. An alternative view challenges the notion of a specialized face system and argues that general recognition mechanisms are sufficiently complex and plastic to account for apparently face-specific effects obtained with normal and brain-injured subjects (Damasio et al., 1982; Gauthier and Tarr, 1997; Gauthier et al., 1999).

According to the dominant modular view, faces are special because their recognition relies more on configural[1] information than recognition of other visual objects (Tanaka and Farah, 1993; Rhodes, 1993; Moscovitch et al., 1997). This configural information, such as the spatial relations between different parts of the face, plays a more important role in face processing than isolated features. Strong support for this view comes from studies showing that vertical inversion, which disrupts the coding of configural cues (Rhodes et al., 1993; Rhodes, 1993; Young et al., 1987), impairs recognition of faces more than recognition of other classes of mono-oriented objects. This disproportionate inversion effect has been regarded as the first evidence for specialized face recognition mechanisms (Yin, 1969, 1970; Diamond and Carey, 1986; Tanaka and Farah, 1993). To summarize, inversion of a face preserves the low-level visual features but would not involve specific face configural mechanisms (Moscovitch et al., 1997).

Studying how the human brain processes normal as compared to inverted faces may thus be a first critical stage to the understanding of the spatio-temporal neural networks involved in configural face processing.

Few studies have addressed directly the question of face inversion processing with respect to its neural basis and characteristics. A recent fMRI study (Kanwisher et al., 1998) showed a reduced activation of the 'face fusiform area', a right-hemisphere region previously described as being face specific (Kanwisher et al., 1997), for inverted faces but the difference between normal and inverted faces was small and inconsistent across subjects. Moreover, subjects were scanned in two conditions: a passive stimulation of both kinds of stimuli, and an active 1-back matching

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[1] The terms configural or holistic information are often used interchangeably in the face recognition litterature (Tanaka and Farah, 1993; Kanwisher et al., 1997). Here, we will avoid the term holistic as it is not clear whether the holistic information conveyed by faces refers to the canonical configuration shared by all faces (the first order configuration, according to Diamond and Carey, 1986) or the individual variations within the fixed configuration, termed the second order relational features (Diamond and Carey, 1986). Following Rhodes (1993), the simpler term configural information will be used throughout the paper to refer to the latter, which is the only kind of configural information that varies between faces and used with expertise.

task in which subjects had to press a button whenever they saw two identical pictures in a row. The difference between normal and inverted faces was seen in all subjects for the passive-viewing condition but was small and observed in only six out of ten subjects for the active discrimination task. Differences in activation in the fusiform face area and other occipito-temporal regions between upright and inverted faces were also observed in another recent study (Gauthier et al., 1999). This last study also demonstrated that expertise with non-face objects leads to a comparable difference between normal and inverted stimuli in the face area for these objects. Also recently, Haxby et al. (1999) observed an increase of activity in regions involved in object recognition when faces were inverted. Again, face inversion had minimal effects on the activity in face-selective regions. The conclusion of the authors was consistent with previous behavioral and neuropsychological studies which have suggested that inverted faces leads to the recruitment of processing ressources in the object perception systems (Moscovitch et al., 1997)

However, the low temporal resolution of the technique, especially in blocked fMRI designs (Kanwisher et al., 1997; Gauthier et al., 1999), does not allow to specify whether normal and inverted faces are processed differently at early stages of visual categorization. Even at later stages of face processing, latency differences between onset of activity for the two kinds of stimuli would not be detectable by hemodynamic techniques such as PET or fMRI. To detect such temporal differences, one has to turn to neurophysiological studies in animals and humans. Studies in macaque have failed to find differential response amplitudes of face-selective cells in the infero-temporal cortex to normal and inverted faces (Perrett et al., 1988). The same authors also first described greater response latencies to inverted faces (Perrett et al., 1988) but they recently acknowledged this last effect may reflect an artifact of measurement as following studies failed to replicate the latency difference (Perrett et al., 1998). In any case, such response latency effects cannot be detected by fMRI.

Previous event-related potentials (ERPs) studies have compared the presentation of normal and inverted faces. Allison et al. (1994) recorded intracranial potentials to normal and inverted faces in an epileptic patient and observed a reduced and delayed face-specific N200 to inverted faces in the right hemisphere (RH) only. To our knowledge, these investigations have not been extended to a sample of normal subjects. Jeffreys (1993, 1996) observed a latency delay of the so-called VPP ('vertex positive potential') defined as a face-specific potential occuring between 140 and 180 ms, when horizontal and inverted faces were presented, as compared to normal faces. No amplitude modification with rotation of faces was observed. Only a few subjects were recorded and no quantitative measurements or statistical analysis were made. In one of their experiments, Bentin et al. (1996) also described a significant latency delay of the occipito-temporal N170 for inverted faces. This effect was not discussed in their paper. Moreover, these last studies used passive stimulation paradigms, in which the subjects did not have to make any discrimination on the normal and inverted faces. Accordingly, these studies did not record the electrophysiological correlate of the behavioral difference observed when processing normal and inverted faces. The present study aims at clarifying this question by

means of ERPs recorded on a high number of electrodes when subjects are involved in a discrimination task on normal and inverted faces.

2. Methods

Fourteen young normal subjects (mean age: 25 years; five females; three left-handed) took part in the experiment.

Twenty-eight different faces sharing the same face outline (chin, head, ears) but with all different internal features (eyes, nose, mouth; see Fig. 1) were made (Mac-a-Mug®). Every stimulus was black on a white background. Inverted versions of the 28 faces were also prepared for the experiment. These 56 faces and 20 faces used for the training before the experiment were displayed on a monitor using a commercial visual stimulator (STIM, Neuroscan SCAN®). All stimuli had a size of approximately 6×8 cm, and thus sustained a visual angle of 2.28¡ (viewing distance = 150 cm).

During the experiment, subjects sat on a comfortable chair in a dark room with the head restrained by a chin rest and were instructed to fixate a point on the center of the screen. Following two training blocks, subjects were presented with 28 blocks (14 of each condition) of 28 pairs of stimuli each. The block order was the same for all subjects. For half of them, the first block was made of normal faces while the other half received the inverted faces first. Blocks of normal and inverted faces were alternated.

Each trial consisted of a prime face and a target face. Each of the 28 faces appeared once as a prime and once as a target in a given block. In total, all faces were seen as many times, and as many times in same and different pairs. The order

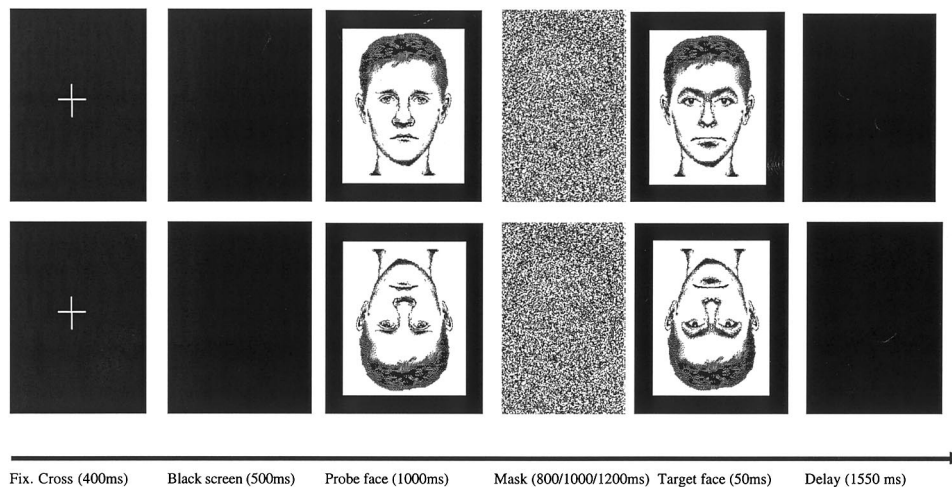| Fix. Cross (400ms) | Black screen (500ms) | Probe face (1000ms) | Mask (800/1000/1200ms) | Target face (50ms) | Delay (1550 ms) |

Fig. 1. Stimuli and timing used in the experiment. Above: condition 1, delayed matching of normal faces. Below: condition 2, delayed matching of inverted faces.

of pairs for the first block of normal faces was the same as the order of pairs for the last block of inverted faces and vice versa. Half of them were followed in the pair by the same face while the other half were followed by a different face. Each different pair was presented only once. Trials were presented in a random order in each block but all subjects saw the same series of stimuli. The beginning of each trial was signaled by a small white cross that remained on the center of the black screen for 400 ms (see Fig. 1). Then, a black screen was displayed for 500 ms, followed by a prime face presented in the center of the screen for 1000 ms. Following the prime face, a perceptual mask was presented for 800, 1000, or 1200 ms, randomly. After the mask had disappeared, the target face was shown for 50 ms. The intertrial interval was set at 1550 ms (black screen). Each trial lasted thus 4500 ms on average. The very short presentation time of the target was used in order to reinforce a high level of attention during the whole experiment and to prevent subjects from using feature-scanning strategies and ocular saccades. Moreover, pre-testing had shown that even with such a short presentation time, subjects can achieve a very high level of performance. The task was to decide as quickly and as accurately as possible whether the target and prime faces were the same or not. Subjects had to press the left (different) or right (same) key on a computer mouse (right hand for all subjects) to indicate their choice. The whole experiment lasted about 2.5 h, including setup of the electrode cap.

Correct response times (RTs) and percentage of errors were computed and analyzed with Systat 5.1®. Correct responses below 200 ms and above 1200 ms were considered as errors.

EOG was recorded bipolarly from electrodes placed on the outer canthi of the eyes, and in the inferior and superior areas of the orbit. Scalp EEG was recorded from 58 electrodes mounted in an electrode cap (Fig. 2). Electrode positions included the standard 10–20 system locations and additional intermediate positions. Recordings were performed with a left ear reference. EEG was amplified with a gain of 30K and bandpass filtered at 0.01–100 Hz. Electrode impedance was kept below 5 kΩ. EEG was continuously acquired at a rate of 500 Hz and stored on disk for off-line analyses. After removal of EEG and EOG artifacts, epochs beginning 100 ms prior to stimulus onset and continuing for 924 ms were made. They were rereferenced off-line to a common average reference. Codes synchronized to stimulus delivery were used to selectively average epochs associated with upright and inverted target faces. This coding allowed to compute different ERP averages, which were made for each subject. The main analyses were made on averages for matching ('same' decision) trials. Only correct trials were included in averages. The data were low pass filtered at 45 Hz and displayed off-line in the forms of waveforms and topographical maps (Fig. 3).

Peak amplitude (mean over a 20 ms time-window around the peak with respect to a 100 ms pre-stimulus baseline) and latencies of different components at selected electrodes were obtained for the different conditions for each subject individually, and were tested using paired t-tests and repeated-measures analyses of variance (ANOVAs) with the stimulus orientation and lateralization as factors. Subtraction maps (between grand averages and also for each subject) on each time-point of the waveforms were also computed automatically by the Neuroscan software.
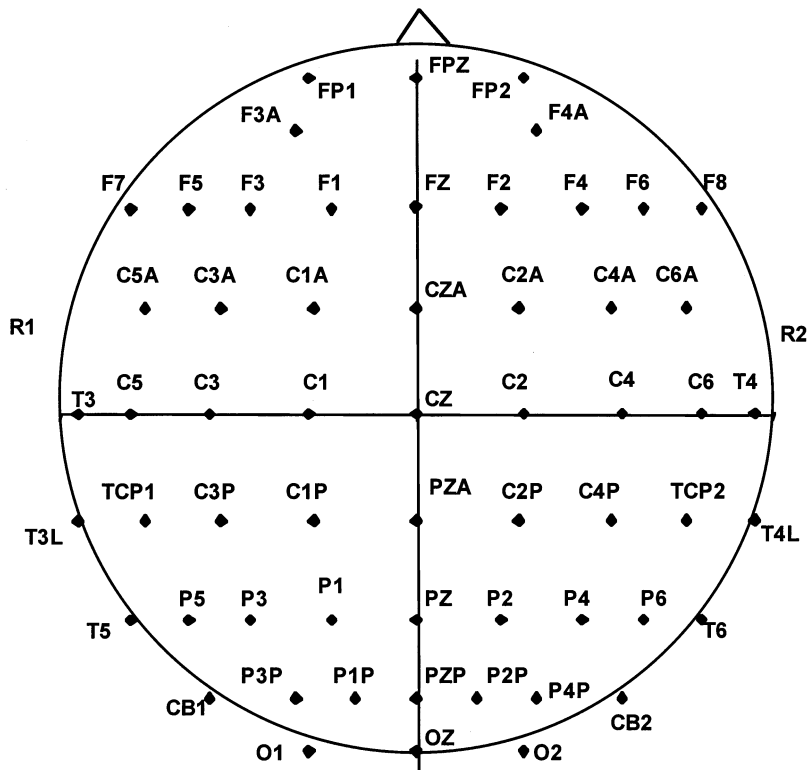
Fig. 2. Electrode locations on the scalp.

3. Results

An advantage of normal over inverted faces was observed both in percentage of correct responses ($90.2 \pm 7.9\%$ vs $82.7 \pm 7.7\%$; paired t-test: $t_{13} = 11.5$, $P < 0.001$) and correct RTs (685 ± 88 ms vs 726 ± 79: $t_{13} = 5.3$ $P < 0.001$) thus confirming the face inversion effect with a delayed-matching paradigm. Similar effects were found for matching trials only ($88.5 \pm 9.3\%$ vs $79.7 \pm 10.8\%$; $t_{13} = 7.3$, $P < 0.001$; RTs: 700 ± 106 ms vs 726 ± 94; $t_{13} = 2.12$; $P = 0.05$).

Grand average ERP waveforms elicited by normal and inverted target faces are illustrated in Fig. 3. Following stimulus onset, three clear electrophysiological components, best described as dipolar complexes (see Fig. 3; Table 1), were observed. The first component was the P1 (all subjects) which culminated (Oz) at 114 ms for normal faces and 117 ms for inverted faces (mean latencies) and was characterized by a large positivity over all posterior electrodes with polarity reversal at central and frontal sites. There was no significant difference in peak (Oz) latency ($t_{13} = 1.54$ $P = 0.147$) or voltage amplitude ($t_{13} = 0.405$, $P = 0.692$) of P1 in normal and inverted face conditions. An ANOVA with face orientation and lateralization (O1 and O2) did not show any effect on latencies (lateralization: $F_{1,13} = 2.1$,
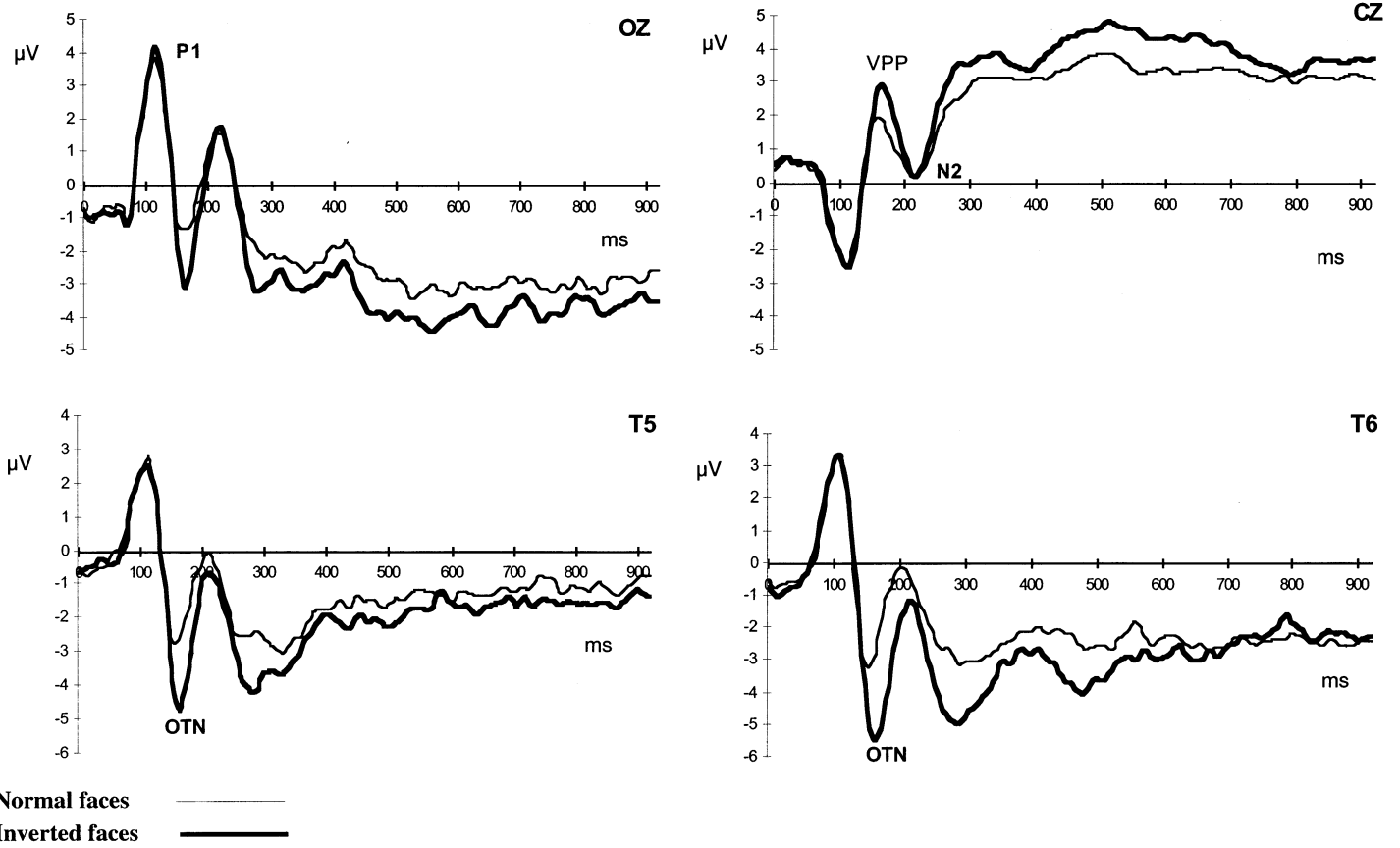
Fig. 3. Event-related potentials recorded at central (Cz), occipital (Oz), right (T6) and left (T5) occipito-temporal sites for matching trials.

Table 1
Latencies following stimulus onset and amplitudes of the event-related potentials components observed during normal and inverted face processing

	Latencies (ms)		Amplitudes (µV)	
	Normal faces	Inverted faces	Normal faces	Inverted faces
P1 (Oz) ($N = 14$)	114 ± 11	117 ± 13	4.57 ± 3.4	4.46 ± 3.5
OTN[a] (T6) ($N = 13$)	156 ± 8	167 ± 9	-3.53 ± 2.4	-6.03 ± 2.83
OTN[a] (T5) ($N = 13$)	157 ± 10	167 ± 8	-2.93 ± 3.5	-5.08 ± 4.51
VPP (Cz) ($N = 13$)	157 ± 8	170 ± 9	2.28 ± 1.56	3.28 ± 2.36
N2 (Cz) ($N = 11$)	219 ± 20.5	224 ± 9	-0.77 ± 1.45	-0.74 ± 1.95

[a] OTN, occipito-temporal negativity.

$P = 0.171$; orientation: $F_{1,13} = 1.364$, $P = 0.264$; interaction: $F_{1,13} = 0.445$; $P = 0.516$) and peak amplitudes (all Fs < 1).

Secondly, large occipito-temporal negativities (OTNs; 13 subjects) reversing polarity at central sites (Fig. 3, vertex positivity) were observed. In two subjects, they peaked at CB1/CB2 (Fig. 2) for both normal and inverted faces but were also large at T5/T6 while the largest amplitudes were observed at these latter sites for the other 11 subjects. They were measured at T5/T6 for all subjects. Inter-subject variability in terms of peak latencies (Table 1) and scalp distribution was low. The OTNs peaked at 156 and 157 ms for normal faces (T6 and T5, respectively) and at 167 and 167.5 ms for inverted faces. The ANOVA confirmed large effects of orientation for both latencies ($F_{1,12} = 30$, $P < 0.001$) and voltage amplitudes ($F_{1,12} = 22.09$, $P = 0.001$): the latency of OTNs was longer and their amplitude larger for inverted faces than normal faces. All other effects failed to reach a statistically significant level ($P > 0.25$). The OTNs peaked slightly later at Oz for inverted faces (163 and 170 ms, respectively (see Fig. 3). The VPP peaked at Cz (Fig. 3) at 157 and 170 ms for normal and inverted faces, respectively, and was observed for the same subjects as the OTNs. There was also a significantly larger amplitude for the VPP observed on inverted faces than on normal faces ($t_{12} = 3.147$, $P = 0.008$). As for the OTNs, the latency delay for inverted faces was also significant ($t_{13} = 5.456$, $P < 0.001$).

A third-negative-centro-frontal component, (N2; 11 subjects; normal faces 219 ms; inverted faces: 224 ms at Cz), best observed at central sites and also reversing polarity at posterior locations (Fig. 3) followed these laterally located potentials. Paired *t*-test failed to show any significant difference between normal and inverted faces neither in latencies ($t_{1,10} = 0.77$, $P = 0.459$) nor in peak amplitude ($t_{1,10} = 0.088$, $P = 0.932$).

Fig. 4. Scalp topographies of brain activity (grand average over 14 subjects) related to normal and inverted face processing during the time course of the occipito-temporal negativities (OTNs). Top: for both conditions, the critical activity starts in the right hemisphere. Note the longer duration and the larger amplitude of activity for inverted faces at the level of occipito-temporal sites, particularly in the right hemisphere. Below: substraction maps (inverted-normal) displayed on the same time epoch as the raw activity (top views and right hemisphere views).

Normal Faces

Inverted Faces

132/140 ms   142/150   152/160   162/170   172/180   182/190   192/200   202/210 ms

Subtraction Maps, Top View

Subtraction Maps, Right View

132/140 ms   142/150   152/160   162/170   172/180   182/190   192/200   202/210 ms
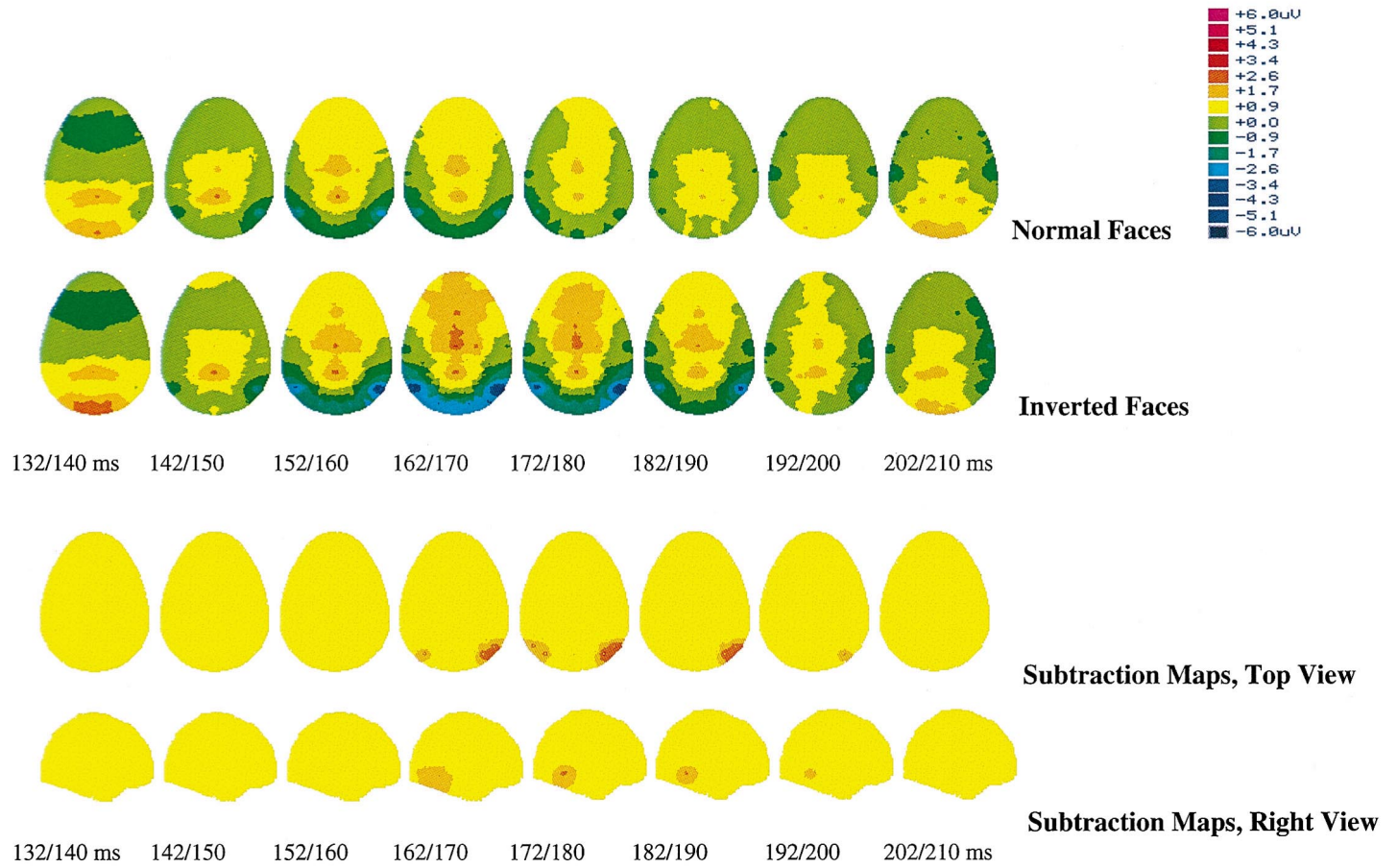
Fig. 4.

The only significant difference between ERPs recorded during normal and inverted face processing concerned the occipito-temporal activities occurring about 160 ms after stimulus presentation. Although the topographies of OTNs were similar for both conditions (Fig. 4), the activity was clearly delayed and larger for inverted faces. Additional analyses were thus performed on these occipito-temporal activities for target stimuli[2].

Subtraction maps computed on grand averages on each time point showed a large amplitude difference between normal and inverted faces which was slightly delayed with regard to the raw activity (OTNs; Fig. 4)[3]. This effect was observed in 11 subjects out of the 13. The voltage amplitude difference reached -2.67 μV on the left side and -3.79 μV on the right side (Fig. 3). Differential amplitude values (20 ms around the peak with a latency determined on grand average subtraction maps) were computed for each subject to perform statistical tests. The difference was statistically significant at both sides (right (T6): $t_{12} = 5.29$; $P < 0.001$; left (T5): $t_{12} = 5.29$; $P < 0.001$) and there was a statistically significant difference between the differential amplitudes on the two sides ($t_{12} = 2.187$; $P < 0.05$), reflecting a larger difference between normal and inverted faces on the right occipito-temporal sites (Fig. 3). This interaction between lateralization and orientation was larger when only right-handed subjects (10) were included in the analyses. The ANOVA conducted on these subjects still evidenced large effects of orientation for both latencies ($F_{1,12} = 30$, $P < 0.001$) and voltage amplitudes ($F_{1,9} = 12.26$, $P = 0.007$) and also a significant interaction between lateralization and orientation for amplitudes ($F_{1,9} = 8.75$, $P = 0.016$) as the difference between normal and inverted faces was significantly larger in the right than in left hemisphere. Other effects failed to reach a statistically significant level ($P_s > 0.31$).

We also performed a correlation analysis between the difference in RTs (normal-inverted faces) and both the differences in peak latencies and amplitudes. This analysis failed to find any significant correlation (latencies: T6, $r = 0.224$, $P = 0.948$; T5, $r = 0.222$, $P = 0.466$; amplitudes: T6, $r = 0.324$, $P = 0.281$; T5, $r = 0.318$, $P = 0.291$). An identical analysis was made on accuracy rates and revealed interesting non-significant trends for the correlation with: T6, $r = 0.469$, $P = 0.106$; T5, $r = 0.519$, $P = 0.069$. Behavioral effects of inversion were thus slightly associated with differences in voltage amplitude between normal and inverted faces. The correlation between latencies and accuracy rates was not significant (T6: $r = 0.314$, $P = 0.297$; T5: $r = 0.213$, $P = 0.484$).

Finally, we computed the correlation between the two electrophysiological effects observed on occipito-temporal negativities and observed a significant correlation

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[2] Peak latencies and amplitudes were also computed for all ('same' and 'different' decisions) target stimuli, as well as for mismatch trials only and identical effects were obtained.

[3] This delay was simply a result of the delay of about 10 ms observed between normal and inverted faces: when the OTNs for inverted faces reach their maximum amplitude, the corresponding activity for normal faces already decreases. Although such a latency difference between conditions might cause an apparent voltage amplitude difference in some cases, in the present study, the raw waveforms (Fig. 3) as well as the topographies (Fig. 4) illustrate the large amplitude difference occurring in OTNs for normal and inverted faces.

between the amplitude difference and the latency difference at T6 ($r = 0.607$, $P = 0.028$) but not at T5 ($r = 0.284$, $P = 0.347$).

4. Discussion

An early and single difference between normal and inverted faces was found at occipito-temporal sites about 160 ms following stimulus onset. This observation strongly suggests that visual processing taking place before 160 ms are common to normal and inverted face processing. This result could be expected as inversion does not modify the low-level visual features of faces (Kanwisher et al., 1998).

Bilateral occipito-temporal regions activated by normal faces at around 160 ms are also engaged during processing of inverted faces with a significant delay (around 10 ms) and the scalp distribution of ERPs suggests that similar brain regions are involved in processing the two types of stimuli (Fig. 4) at this latency. However, inverted faces evoked larger activity at this latency as observed both on occipito-temporal and central sites (Fig. 3 and Fig. 4).

The two concurrent potentials observed at central and occipito-temporal electrodes in the present study have been previously observed at similar latencies (Jeffreys, 1996; Bentin et al., 1996) and identified as the VPP and the N170, respectively. In these studies, the amplitude of these components was larger for faces than objects (Bötzel et al., 1995; Bentin et al., 1996; Jeffreys, 1996; Eimer, 1998) and accordingly, these activities have been described as 'face-specific potentials' (Bentin et al., 1996; Jeffreys, 1996). Whether the VPP is the positive counterpart of the N170 is still a matter of debate (Bötzel et al., 1995; George et al., 1996). The present data argue for common generators of both potentials, probably located in occipito-temporal regions where the potentials are larger with a neutral common average reference and where face-specific activity has been observed in neuroimaging studies (e.g. Kanwisher et al., 1997). To support this statement, we refer to the high temporal synchrony between the two peaks, the absence of VPP when the N170 cannot be detected (1 subject in the present study), and the electrophysiological differences between normal and inverted faces that may be observed on both potentials but not on preceding and following components (P1 and N2). However, the VPP has usually been characterized as a 'face structural encoding stage' (Jeffreys, 1996) while Bentin et al. (1996) argued that the N170 should reflect the activation of a cortical region involved in human eyes detection, as the amplitude of the N170 was particularly large for eyes presented in isolation in this latter study. The amplitude of the N170 was also found to be as large for distorted faces as for isolated eyes but significantly lower for whole faces (Bentin et al., 1996). This interpretation of a human-eye-sensitive detector has, however, been ruled out by a recent study (Eimer, 1998) as the N170 amplitude was not affected by the presence or absence of eyes. Rather, it was also suggested that the N170 was caused by the structural encoding of different face components (Eimer, 1998).

In the present study, a latency delay for the N170 and its positive counterpart has been observed when processing inverted faces as compared with normal faces. This

result is entirely compatible with Jeffreys (1993, 1996) and Bentin et al. (1996) observations in passive stimulations though it was not systematically analyzed and discussed in these studies. Bentin et al. (1996) also observed a latency delay for isolated eyes. More recently, a N170 latency delay was observed when faces without eyes were presented (Eimer, 1998) or when subjects had to focus on the eyes of the face to perform a task (Jemel et al., 1999). A slight scrambling of the face also delays the occipito-temporal negativities and the VPP, though not significantly for this latter component (George et al., 1996). Taken together, these observations suggest that disrupting the face configuration either by modifying relationships between features (George et al., 1996), removing one (Eimer, 1998; Jemel et al., 1999) or many features (Bentin et al., 1996), or inverting the face (Bentin et al., 1996; Jeffreys, 1993; the present study) delays the face-specific activity observed at 170 ms following stimulus onset in occipito-temporal regions.

This latency delay observed on face components when facial configuration information is lacking is compatible with both functional and neurophysiological studies.

Functionally, faces are regarded as containing two kinds of information: facial features themselves and configuration or spatial relationships between these different features (Sergent, 1984; Tanaka and Farah, 1993). According to the functional model of face processing (Bruce and Young, 1986), this information is processed first in an initial structural encoding stage, aimed at providing an invariant face representation to higher processes devoted to face recognition or visual categorization (such as gender decision or expression analysis). When available, configural information is particularly important to face encoding (Young et al., 1987) and it has been shown that a description of the overall face configuration can be quickly obtained and be used to guide the elaboration of fine-scaled details of the various face parts (Mermelstein et al., 1979; Bruce, 1988; Suzuki and Cavanagh, 1995). Accordingly, recognition of the whole face or of face parts is more accurate and quicker than recognition of an isolated feature or an inverted face (Tanaka and Farah, 1993). In other words, the loss of configural information by inversion slows down and increase the difficulty of facial encoding. These behavioral observations are compatible with the quicker face-specific activity observed in occipito-temporal regions for normal faces as compared with faces whose configuration has been disrupted by various transformations. Additional evidence supporting this explanation comes from recent ERP studies (Han et al., 1997; Proverbio et al., 1998) that have demonstrated temporal precedence of different parieto- and fronto-central ERP components to global processing than to local processing of non-face stimuli.

Many neurophysiological studies recorded cells in monkey infero-temporal cortex and superior temporal sulcus that respond selectively to faces (e.g. Gross et al., 1972; Desimone, 1991; Perrett et al., 1987). Most of these cells selectively responsive to faces are view- and orientation-sensitive (Wachsmuth and Perrett, 1997). As most experience of faces occurs in the upright orientation, it is suggested that more cells in the temporal cortex become selectively tuned for the upright orientation of the faces (Perrett et al., 1998). Moreover, there appear to be some cells responding only to one facial region (e.g. the eyes), other cells which exhibit independent tuning

to several facial parts (e.g. eyes or mouth) and some cells that respond only when multiple features are presented simultaneously (Perrett et al., 1982). Normal faces presented in a familiar orientation are thus likely to recruit a larger amount of cells than any of the faces whose configuration has been modified. Previous studies by Perrett et al. (1988) had revealed comparable response amplitudes to upright and inverted faces but different onset latencies. However, these authors acknowledged recently that there is no systematic variation in onset latency of responses and viewing conditions of these cells (Perrett et al., 1998) and that previous reports of increased response latencies to rotated images of faces may reflect an artifact measurement. If we consider the scalp potentials to reflect the neural activity of face cells populations in occipito-temporal cortex, how can we account then for the quicker response activity observed in the present study when the face configuration is normal as compared to inverted and transformed faces? Perrett et al. (1998) hypothesize that differential timing of activity in cell populations can arise as a result of the differential number of cells coding for various face views of face parts. As normal faces recruit a larger amount of cells than any of the faces whose configuration has been modified, the cumulative reponse curve (number of spikes) to these first stimuli in a population will exceed a certain level above background activity (a threshold) sooner than for the transformed images.

If true, this — still speculative — model does not exclude functional interpretations of the latency difference between normal and inverted faces as observed in scalp potentials in the present study. Rather, it encompasses them in a single neurophysiological framework. In such a model, the difference in N170 peak latency between normal and inverted faces should have been correlated with the difference for RTs. However, several hundreds of milliseconds and several processes separate the occurrence of the potentials and the effective response of the subject. This may have added variance to the data and thus 'blurred' any correlation effect. Nevertheless, the origin of the differential performance for upright and inverted faces is proposed to come from this face encoding stage reflected by the N170. The delayed-matching task used in the present study necessitates not only encoding the target face but also comparing it with a representation of the prime face held in visual short-term memory. A decision is then based on this comparison and a motor response is programmed and performed. As the difference between normal and inverted faces is identical for matching and mismatch trials (see note iv), this reinforces the proposition that this difference takes place at the encoding stage.

In the present study, we also observed a larger amplitude of the N170 and VPP for inverted faces. This effect was larger for the RH, especially when only right-handed subjects were considered. Can this effect be also accounted by the loss of configuration when inverting faces? One could argue that the additional processing of configuration occurs only for normal faces and consequently that a larger activity, if any, should be observed for processing of normal faces. However, as discussed above, configural information facilitates face processing, and it is also revealed in the behavioral measures recorded in the present study. The loss of configuration with inversion could have resulted in a selective amplification of neural activity devoted to faces because of an increase of difficulty. In favor of the

hypothesis that the loss of configuration by inversion causes not only a peak delay latency, but also a larger activity, is the significant correlation between the difference in peak latencies and the same difference for the amplitudes in the RH. Bentin et al. (1996) also observed a non-significant trend for a larger N170 amplitude for inverted faces as compared to normal faces. A significant larger amplitude was observed for isolated eyes in the same study and George et al. (1996) also observed larger occipito-temporal negativities for processing scrambled faces as compared with normal faces. In this latter study, which also used an active discrimination paradigm, the data suggest that the occipito-temporal negativities to scrambled faces are enhanced by the presence of an additional long lasting temporal negativity associated with the difficulty of the stimulus processing. This explanation is compatible with the observations of the present study, and in particular with the observation that large behavioral effects of inversion were correlated with large differences in voltage amplitude between normal and inverted faces, although the correlation failed to reach statistical significance. Note also that the temporal processing negativity described by George et al. (1996) lasts from 150 ms until at least 350 ms whereas in our study, the larger activity for inverted faces is observed mainly at around 160 ms and is small or non-existent at the level of the following potential (N2, 220 ms). Thus, the temporally localized difference between normal and inverted faces in the present study may be a result of a selective amplification of face-specific activity because of attentional processes related to difficulty rather than to the superimposition of a general processing negativity in temporal regions. An alternative explanation of this larger amplitude for inverted faces may be proposed with regard to recent fMRI evidence from Haxby et al. (1999). These authors show that face inversion does not significantly decrease the neural activity within face-selective regions but increases the response in ventral extrastriate regions that respond to another visual category (houses). Thus, the larger amplitude observed for inverted faces might be a result of the recruitment of additional processing resources in object perception systems. Such interpretations of our results based on fMRI studies must, however, be taken with caution as no indication of the precise temporal course of activity in visual regions is available from these studies.

To summarize, the present study suggests that identical functional components and cortical regions are involved in the initial processing of normal and inverted faces, albeit with a different timing and amplitude of activity: inverted faces are processed slowly and require more neural activity than normal faces, at least in an active discrimination task in which inverted faces are more difficult to process than normal faces. This latter effect is particularly observed in right occipito-temporal hemisphere structures. Consistent with the lateralization effects found in this study, it has been proposed that the RH superiority for face processing may be related to a specific or even a more general superiority for configural/holistic processing (Hillger and Koenig, 1991). Accordingly, the RH superiority disappears when faces are inverted, as has been demonstrated by divided visual field experiments (Hillger and Koenig, 1991). Moreover, right brain injured patients do not demonstrate the classical face inversion effects (Yin, 1970) and prosopagnosics, who are thought to

have lost specific processes dedicated to face recognition, may even show better performance for processing inverted than normal faces (Farah et al., 1995). This last effect has been recently extended to visual objects (de Gelder et al., 1998) and animal faces (de Gelder and Rouw, 1999). Given that the use of configural information in face processing is a consequence of a visual expertise[4] that may apply to other categories of objects (Diamond and Carey, 1986; Bruyer and Crispeels, 1992; Gauthier and Tarr, 1997), it would also be interesting to test whether the neurophysiological correlate of the inversion effect observed in the present study is specific to faces, or can be observed for other kinds of objects with and without visual expertise. Such studies are currently in progress in our laboratory.

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References

Allison, T., Ginter, H., McCarty, G., Nobie, A.C., Puce, A., Luby, N., Spencer, D.D., 1994. Face recognition in human extrastriate cortex. Journal of Neurophysiology 2, 821–823.

Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. Journal of Cognitive Neuroscience 8, 551–565.

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

Bruce, V., 1988. Recognising faces. Lawrence Erlbaum, London.

Bruce, V., Young, A.W., 1986. Understanding face recognition. British Journal of Psychology 77, 305–327.

Bruyer, R., Crispeels, G., 1992. Experise in person recognition. Bulletin of the Psychonomic Society 30, 501–504.

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

de Gelder, B., Bachoud-Lévi, A.-C., Degos, J.-D., 1998. Inversion superiority in visual agnosia may be common to a variety of orientation polarised objects besides faces. Vision Research. 38, 2855–2861.

de Gelder, B., Rouw, R. Spared configural processing of faces in prosopagnosia. Cognitive Neuropsychology (in press).

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[4] Visual experts can be defined as people who are trained to perform subordinate recognition of exemplars of a large class of objects on a repeated basis and thus improve dramatically to the point of performing such subordinate recognition using different perceptual mechanisms as most people. A typical example is bird watchers, who can easily discriminate between species of birds (see Tanaka and Gauthier, 1997, pp. 87–88).

Desimone, R., 1991. Face-selective cells in the temporal cortex of monkeys. Journal of Cognitive Neuroscience 3, 1–8.

Diamond, R., Carey, S., 1986. Why faces are and are not special: an effect of expertise. Journal of Experimental Psychology: General 115, 107–117.

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

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

Farah, M.J, Wilson, K., Drain, H., Tanaka, J.R., 1995. The inverted face inversion effect in prosopagnosia: evidence for mandatory, face-specific perceptual mechanisms. Vision Research 35, 2089–2093.

Haxby, J.V., Ungerleider, L.G., Clarck, V.P., Scouten, J.L., Hoffman, E.A., Martin, A., 1999. The effect of face inversion on activity in human neural systems for face and object perception. Neuron 22, 189–199.

Gauthier, I., Tarr, M.J., 1997. Becoming a 'greeble' expert: exploring the face recognition mechanism. Vision Research 37, 1673–1682.

Gauthier, I, Tarr, M.J., Anderson, A.W., Skudlarski, P., Gore, J.C.. Expertise with novel objects can recruit the face area. Nature Neuroscience (in press).

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

Gross, C.G., Rocha-Miranda, C.E., Bender, D.B., 1972. Visual properties of neurons in infertemporal cortex of the macaque. Journal of Neurophysiology 35, 96–111.

Han, S., Fan, S., Chen, L., Zhuo, Y., 1997. On the different processing of wholes and parts: a psychophysiological analysis. Journal of Cognitive Neuroscience 9, 687–698.

Hillger, L.A., Koenig, O., 1991. Separable mechanisms in face processing: evidence from hemispheric specialization. Journal of Cognitive Neuroscience 3, 42–58.

Jeffreys, D.A., 1993. The influence of stimulus orientation on the vertex positive scalp potential evoked by faces. Experimental Brain Research 96, 340–350.

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

Jemel, B., George, N., Olivares, E., Fiori, N., Renault, B. (1999). Event-related potentials to structural familiar face incongruity processing. Psychophysiology (in press).

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

Kanwisher, N, Tong, F., Nakayama, K., 1998. The effect of face inversion on the human fusiform face area. Cognition 68, B1–B11.

McCarthy, G., Puce, A., Gore, J.C., Allison, T., 1997. Face-specific processing in the human fusiform gyrus. Journal of Cognitive Neuroscience 9, 605–610.

Mermelstein, R., Banks, W., Prinzmetal, W., 1979. Figural goodness effects in perception and memory. Perception and Psychophysics 26, 472–480.

Moscovitch, M, Winocur, G., Behrmann, M., 1997. What is special about face recognition? nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. Journal of Cognitive Neuroscience 9, 555–604.

Perrett, D.I., Rolls, E.T., Caan, W., 1982. Visual neurons responsive to faces in the monkey temporal cortex. Experimental Brain Research 47, 329–342.

Perrett, D.I., Mistlin, A.J., Chitty, A.J., 1987. Visual neurons responsive to faces. Trends in Neurosciences 10, 358–364.

Perrett, D.I., Mistlin, A.J., Chitty, A.J., Smith, P.A.J., Potter, D.D., Brönnimann, R., Harries, M.H., 1988. Specialised face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction times studies. Behavioral Brain Research 29, 245–258.

Perrett, D.I., Heitanen, J.K., Oram, M.W., Benson, P.J., 1992. Organization and functions of cells responsive to faces in the temporal cortex. Philosophical Transactions of the Royal Society of London 335, 23–30.

Perrett, D.I., Oram, M.W., Ashbridge, E., 1998. Evidence accumulation in cell populations responsive to faces: an account of generalisation of recognition without mental transformations. Cognition 67, 111–145.

Proverbio, A.M., Mimritic, A., Zani, A., 1998. Electrophysiological evidence of a perceptual precedence of global vs. local visual information. Cognitive Brain Research 6, 321–334.

Rhodes, G., 1993. Configural coding, expertise, and the right hemisphere advantage for face recognition. Brain and Cognition 22, 19–41.

Rhodes, G., Brake, S., Atkinson, A.P., 1993. What's lost in inverted faces? Cognition 47, 25–57.

Sergent, J., 1984. An investigation into component and configural processes underlying face recognition. British Journal of Psychology 75, 221–242.

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

Suzuki, S., Cavanagh, P., 1995. Facial organization blocks access to lower-level feastures: an object inferiority effect. Journal of Experimental Psychology 21, 901–913.

Tanaka, J., Farah, M.J., 1993. Parts and wholes in face recognition. The Quarterly Journal of Experimental Psychology 46A, 225–245.

Tanaka, J., Gauthier, I., 1997. Expertise in object and face recognition. In: Goldstone, R.L., Schyns, P.G., et Medin, D.L. (Eds.), The Psychology of Learning and Motivation, vol. 36. Academic Press, San Diego, CA, pp. 83–125.

Wachsmuth, E., Perrett, D.I., 1997. Generalising accross object orientation and size. In: Walsh, V., Butler, S. (Eds.), Perceptual Constancies. Oxford University Press, Oxford.

Yin, R.K., 1969. Looking at upside-down faces. Journal of Experimental Psychology 81, 141–145.

Yin, R.K., 1970. Face recognition by brain-injured patients: a dissociable ability? Neuropsychologia 8, 395–402.

Young, A.W., Hellawell, D., Hay, D.C., 1987. Configural information in face perception. Perception 16, 747–775.