Available online at www.sciencedirect.com
SCIENCE DIRECT®

Cognitive Brain Research 16 (2003) 416–424

COGNITIVE BRAIN RESEARCH

www.elsevier.com/locate/cogbrainres

Research report

Spatial scale contribution to early visual differences between face and object processing

Valérie Goffaux[a,b,*], Isabel Gauthier[c], Bruno Rossion[a,d]

[a] *Unité de Neurosciences Cognitives (NESC), UCL, Place Cardinal Mercier 10, 1348 Louvain La Neuve, Belgium*
[b] *Laboratoire de Neurophysiologie (NEFY), UCL, Avenue Hippocrate 54, 1200 Bruxelles, Belgium*
[c] *Department of Psychology, Vanderbilt University, Nashville, TN 37240, USA*
[d] *Department of Cognitive and Linguistic Sciences, Brown University, Providence, RI 02912, USA*

Accepted 18 December 2002

Abstract

Event-related potential (ERP) studies have highlighted an occipito-temporal potential, the N170, which is larger for faces than for other categories and delayed by stimulus inversion of faces, but not of other objects. We examined how high-pass and low-pass filtering modulate such early differences between the processing of faces and objects. Sixteen grey-scale pictures of faces and cars were filtered to preserve only relatively low (LSF) or high (HSF) spatial frequencies and were presented upright or upside-down. Subjects reported the orientation of the faces and cars in broad-pass and filtered conditions. In the broad-pass condition, we replicated typical N170 face-specific effects of amplitude and delay with inversion. These effects were also present in the LSF condition. However, a completely different pattern was revealed by the HSF condition: (1) a similar N170 amplitude for cars as compared to faces and (2) an absence of N170 latency delay with face inversion. These results show that the source of early processing differences between faces and objects is related to the extraction of information contained mostly in the LSF, which conveys coarse configuration cues particularly salient for face processing.

Theme: Neural basis of behaviour

Topic: Cognition

Keywords: Face processing; Specificity; N170; Configuration; Spatial scales

1. Introduction

The question of whether face recognition depends on a domain-specific module has motivated numerous studies using behavioral, neuropsychological, ERP, single-unit recordings in animals and humans, and neuroimaging methodologies [16,34]. In the last few years, a relatively early ERP component differentiating between faces and other objects has been described in the normal human brain [2,5,27]. This brain signature consists of a large bilateral negative occipito-temporal potential, peaking around 170 ms following the onset of the stimulus, called the N170. The N170 appears to be a crucial step in face perceptual processing since its amplitude is larger for faces than for other object categories [2,5,27] and a consistent latency delay is observed on the N170 with upside-down inversion of faces[1] only [2,10,27,28]. These findings corroborate the view that the presentation of a face to the visual system automatically activates early category-specific mechanisms. However, modulations of the N170 have also been observed in response to non-face stimuli when subjects were extensively trained to discriminate between individual objects: the N170 amplitude increases (in

*Corresponding author. Unité de Neurosciences Cognitives (NESC), UCL, Place Cardinal Mercier 10, 1348 Louvain La Neuve, Belgium. Tel.: +32-10-478-767; fax: +32-10-473-774.
E-mail address: valerie.goffaux@psp.ucl.ac.be (V. Goffaux).

[1] Behavioral studies have consistently demonstrated that inversion of a face disrupts its configuration, i.e. spatial relationships between features [11,19,24]. The fact that it is almost exclusively observed at the level of the N170 in ERP studies thus provides a link between the processing of configural cues and the N170. This argument has been developed in detail in a recent review on the face inversion effect [26].

0926-6410/03/$ – see front matter
doi:10.1016/S0926-6410(03)00056-9

natural dogs and bird experts [33]) and its latency is delayed with upside-down inversion (in Greebles experts [29]). These results favor the view that faces per se are not handled by an early special processor. Instead, extensive expertise and the resulting perceptual tuning toward configural cues [9,12] are likely candidates contributing to the emergence of so-called face-specific effects on the N170.

The coarse and fine scales (or LSF and HSF, respectively) supply the visual system with different visual cues about a face. LSF only preserve configuration, particularly important in face processing, whereas HSF provide the visual system with discrete facial features and other fine details such as wrinkles [7,8,21,31,32]. We therefore examined how SF filtering modulates the face-specific effects typically observed on the N170. Given the prevalence of LSF in face configural processing, we hypothesized that the early differences described for broad-pass faces and objects would be mainly supported by LSF. In this case, the differences between faces and objects at the level of the N170 should be viewed as reflecting the different perceptual processing at stake in the two categories rather than the activation of a module exclusively dedicated to detection of a face per se, operating independently of visual information available to the system [2,30].

To test this hypothesis, we compared N170 evoked by faces and cars presented upright and upside-down when the stimuli were presented in broad-pass, in LSF and in HSF.

2. Materials and methods

2.1. Subjects

Thirteen naive paid subjects took part in the experiment (five female; mean age 25; 11 right-handed).

2.2. Stimuli

Sixteen pictures of faces (half male, half female) and 16 pictures of cars were used in the experiment (Fig. 1). All stimuli were presented in 3/4 views. Viewed at a distance of 70 cm, they subtended 5.3/4.8° of visual angle. Each stimulus set was filtered, preserving either the HSF (above 32 cycles per image, or 6.5 cycles per degree) or the LSF

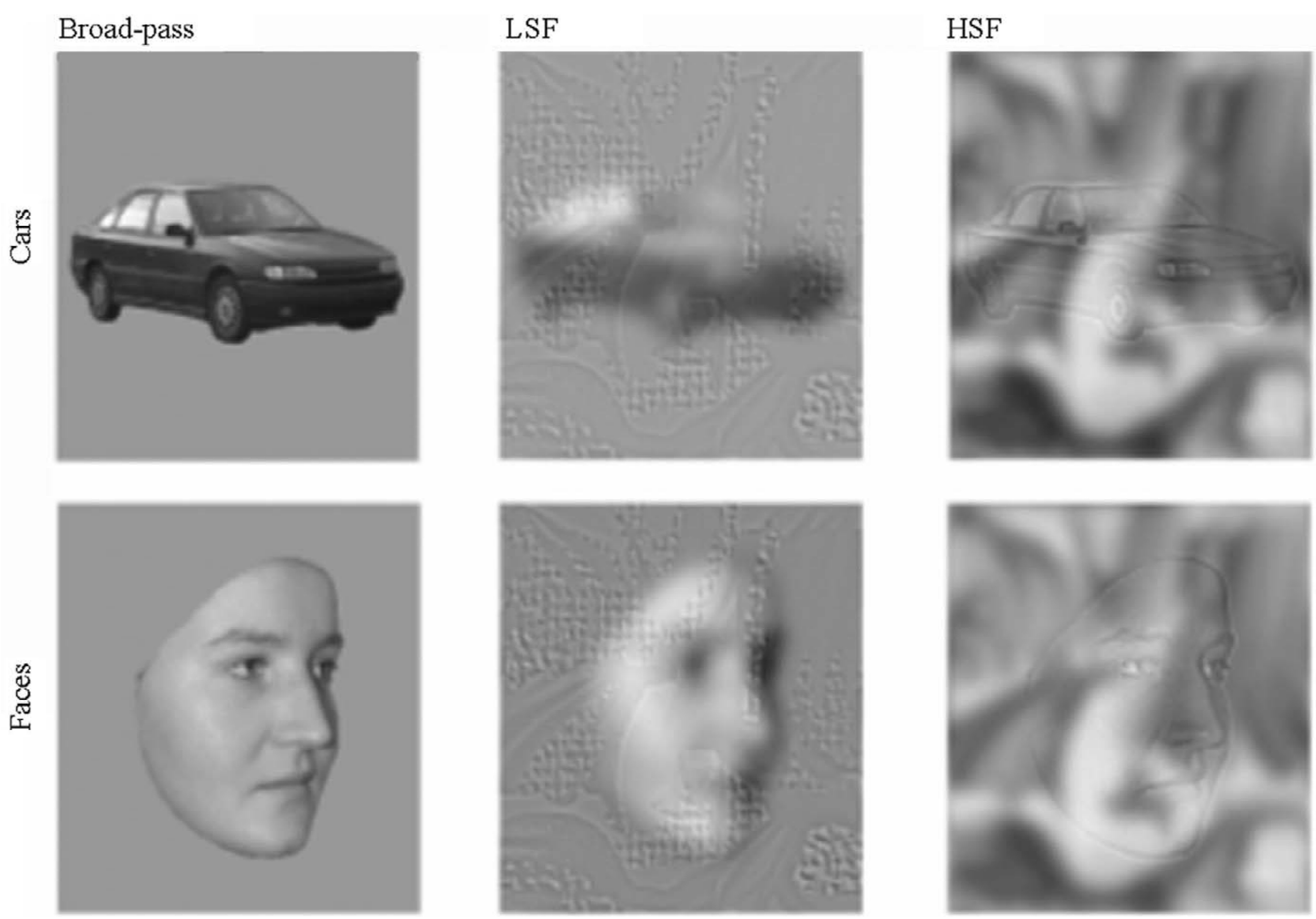

Fig. 1. Illustration of the stimuli used in the experiment. For cars (top row) and faces (bottom row), broad-pass, LSF and HSF versions are displayed.

(below 8 cycles per image, or 1.6 cycles per degree) (Fig. 1). In HSF cars and faces, a LSF texture background was added; in LSF stimuli, the same background was displayed in its HSF version. Hence, LSF and HSF stimuli were identical with respect to their SF content and controlled for spectral energy. The face and car images were also rotated in the picture plane by 180°, resulting in 12 stimulus conditions: Category (faces–cars)×Spatial frequency (broad-pass-LSF-HSF)×Orientation (upright–inverted). The 'broad-pass' condition refers to the unfiltered stimuli.

2.3. Design and procedure

Subjects were seated in a comfortable chair in a dimly lit and electrically shielded room. They received 64 randomized trials of each stimulus condition (each stimulus repeated four times, 768 trials in total). The stimuli appeared one by one at the centre of the screen, on a black background, for 400 ms. The mean inter-trial interval was 1500 ms (randomized between 1400 and 1600 ms). Subjects reported as quickly and accurately as possible the orientation of each stimulus by pressing the right (inverted) or left (upright) key on a response pad. The orientation decision was not aimed at precisely tapping the face inversion effect. It was used, as in previous studies [27,28], to maintain the subject's attention constant throughout the experiment. Response times and accuracy were recorded. Every 50 trials, subjects marked a pause. The experiment lasted for about 40 min.

2.4. EEG recordings

EEG was recorded by 64 electrodes mounted in an electrode cap (Quickcap, Neuromedical Supplies). Electrode positions included the standard 10–20 system locations and additional intermediate positions (see Fig. 2). Horizontal and vertical EOG were monitored using four facial bipolar electrodes placed on the outer canthi of the eyes and in the inferior and superior areas of the orbit. EEG was continuously recorded, digitized at a rate of 500 Hz with a linked mastoids reference. The signal was amplified by SYNAMPS (Neuroscan) amplifiers with a gain of 30 K and band-pass filtered at 0.01–40 Hz, and stored on a disk for off-line analysis. We performed epoching 200 ms prior to and 800 ms after stimulus onset. After VEOG correction and rejection of artifacts (−50/50 μV threshold), a common average reference was recomputed for all electrodes. Finally, the averages were band-pass filtered between 1 and 30 Hz.

2.5. Data analysis

N170 latency and amplitude values (with regard to a −200 ms baseline) for the different conditions were automatically extracted at the peak maximum electrodes located in occipito-temporal areas over the right and left hemispheres (PO8 and PO7, see Fig. 2). We computed repeated-measures ANOVA on the behavioral and electrophysiological data with factors of Category (cars–faces), Spatial frequency (broad-pass-LSF-HSF), Orientation (upright–inverted) and electrode Laterality (left–right). Polynomial contrasts were used for post-hoc comparisons. All effects with two or more degrees of freedom in the numerator were adjusted for violations of sphericity according to the GreenHouse–Geisser correction [35]. To ascertain that effects on N170 amplitude and latency did not stem from earlier effects, i.e. P100 modulations, we performed analyses on P100 values as well on relative N170 values, which were corrected using P100 as baseline. P100 amplitude and latency were automatically extracted at the peak maximum (with regard to a −200 ms baseline) on PO8 and PO7 electrodes. Relative N170 amplitude and latency were corrected by subtracting the P100 amplitude and latency from initial N170 values. For sake of clarity, and since our main focus was on N170 modulations, results of these analyses are reported in Appendix A.

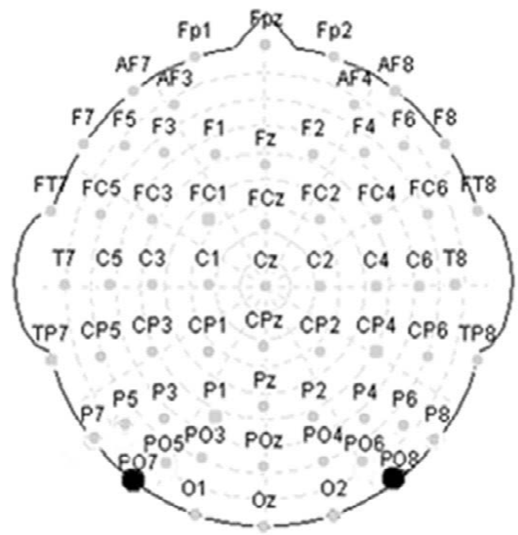

Fig. 2. Scalp locations of the 64 EEG electrodes distributed at the standard 10–20 system locations and additional intermediate positions. Amplitude and latency of P100 and N170 were measured at occipito-temporal electrodes on left and right hemispheres (PO8 and PO7, large black dots).

3. Results

3.1. Behavioral data

Table 1 summarizes the mean accuracy and response times (and standard deviations) in all experimental conditions.

The orientation judgment was an easy task as evidenced by near ceiling performance (mean 96.6±1.1%). The three-way Category×Spatial frequency×Orientation interaction was significant, $F(1.9;20.74) = 5.9$, $P < 0.01$. Better

Table 1
Mean (±standard deviation) accuracy and response times across experimental conditions

		Accuracy (%)		Response times (ms)	
		Upright	Inverted	Upright	Inverted
Cars	Normal	97.1±2.3	98±2.3	551.7±53	628.3±62
	LSF	95.8±3.3	96.1±5	585.1±67	583.4±36
	HSF	97.1±2.6	95.8±4.7	638.2±52	591.3±45
Faces	Normal	97.1±2.7	97.6±1.4	551.9±42	626.9±78
	LSF	98.3±1.9	96.4±3.2	574.2±58	600.3±40
	HSF	94.5±3.5	96.9±2.6	650.2±54	603.7±52

accuracy was observed for inverted than upright HSF faces, $P<0.034$. Cars were significantly better processed than faces in the HSF condition, $P<0.02$. Neither inversion nor category differences were significant in broad-pass and LSF conditions, $P>0.08$. HSF and LSF stimulus conditions led to overall similar accuracy rates, $P=0.37$.

When computed on response times, the three-way ANOVA showed main effects of Spatial frequency, $F(1.9;22.4)=16.9$, $P<0.001$, and Orientation, $F(1;12)=9.7$, $P<0.01$. The interaction between the two factors was significant, $F(1.7;20.4)=26.1$, $P<0.001$. Upside-down inversion delayed the responses in the broad-pass condition, $P<0.001$, while it led to faster responses in the HSF condition, $P<0.001$. In the LSF condition, upside-down inversion did not significantly affect the response times, $P=0.2$ ($P=0.06$ for faces).

3.2. Electrophysiological results

In the broad-pass condition, the presentation of both faces and cars elicited a N170, which was maximal on PO7 and PO8, peaking at 184 ms (broad-pass faces) and 179 ms (broad-pass cars) post-stimulus onset (when PO7 and PO8 are collapsed, see Fig. 3). Inspection of N170 recorded in

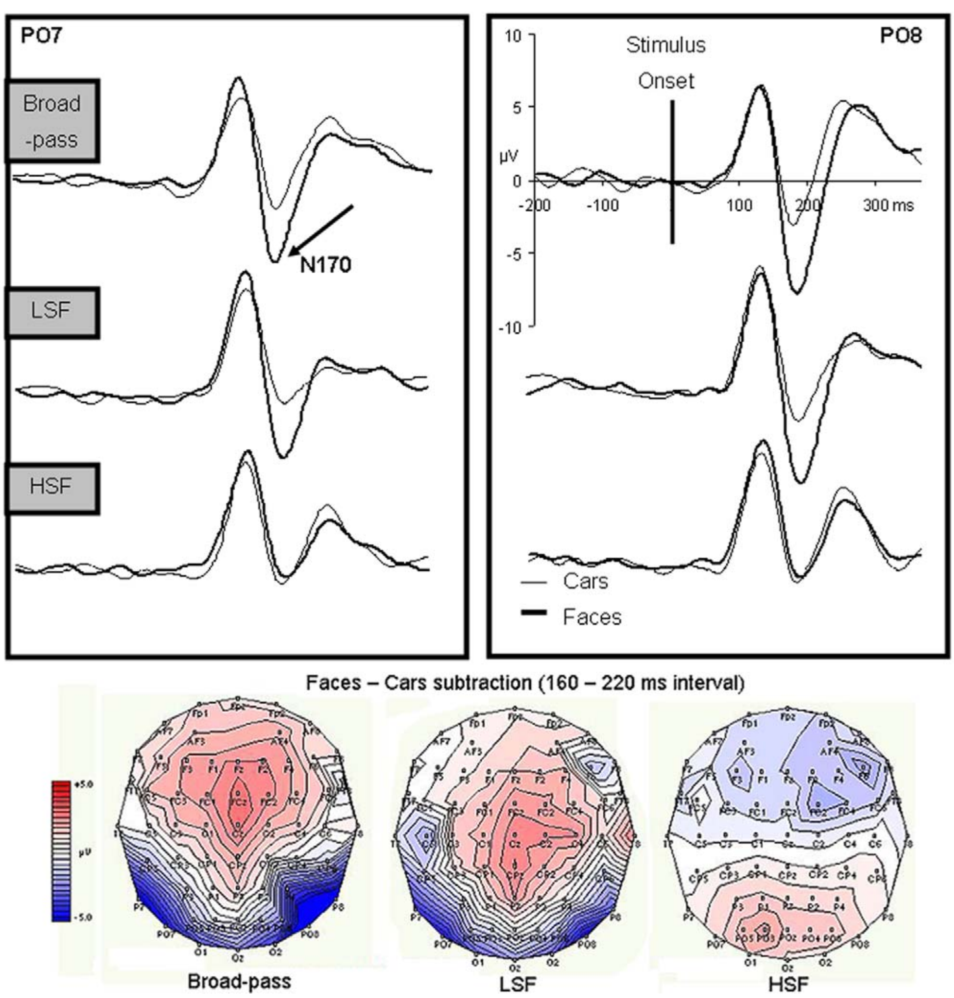

Fig. 3. Top panel: Grand-average ($n=13$) waveforms recorded for faces (thick line) and cars (thin line) on left (PO7, left panel) and right hemispheres (PO8, right panel) in the broad-pass, LSF and HSF conditions separately. Around 170 ms post-stimulus onset, a large negative N170 component (indicated by the arrow) was observed. Note the large N170 amplitude difference between cars and faces observed for the broad-pass and LSF conditions on both hemispheres. In the HSF condition, this difference is greatly reduced. Bottom panel: Scalp topography of faces−cars subtraction curve in a time interval ranging from 160 to 220 ms after onset of stimulation.

the broad-pass condition revealed the kinds of face-specific effects previously reported: a larger N170 amplitude for faces as compared to cars (Fig. 3) and a N170 latency delay with face inversion (mainly on PO7), but no inversion effect for cars (Fig. 4). Overall, these effects were still present in the LSF condition (Figs. 3 and 4). However, a completely opposite pattern was revealed in the HSF condition: (1) a slightly larger N170 amplitude for cars as compared to faces and (2) a reduced latency for inverted faces on PO7. Thus, the HSF condition abolished the face-specific N170 effects.

3.2.1. N170 amplitude

The overall four-way ANOVA revealed significant effects of Spatial frequency, $F(1.5;17.5) = 44.33$, $P <$ 0.0001, and Category, $F(1;12) = 50.8$, $P < 0.001$. These factors interacted significantly, $F(1.6;19.9) = 43.43$, $P <$ 0.001, since the N170 amplitude was larger for faces than cars in broad-pass, $P < 0.001$, and LSF conditions, $P <$ 0.001, but not in the HSF condition in which the N170 amplitude was significantly larger for cars, $P < 0.05$. The effect of Spatial frequency was significant for both faces, $F(1.4;17) = 68.52$, $P < 0.001$, and cars, $F(1.5;18.6) = 5.29$,

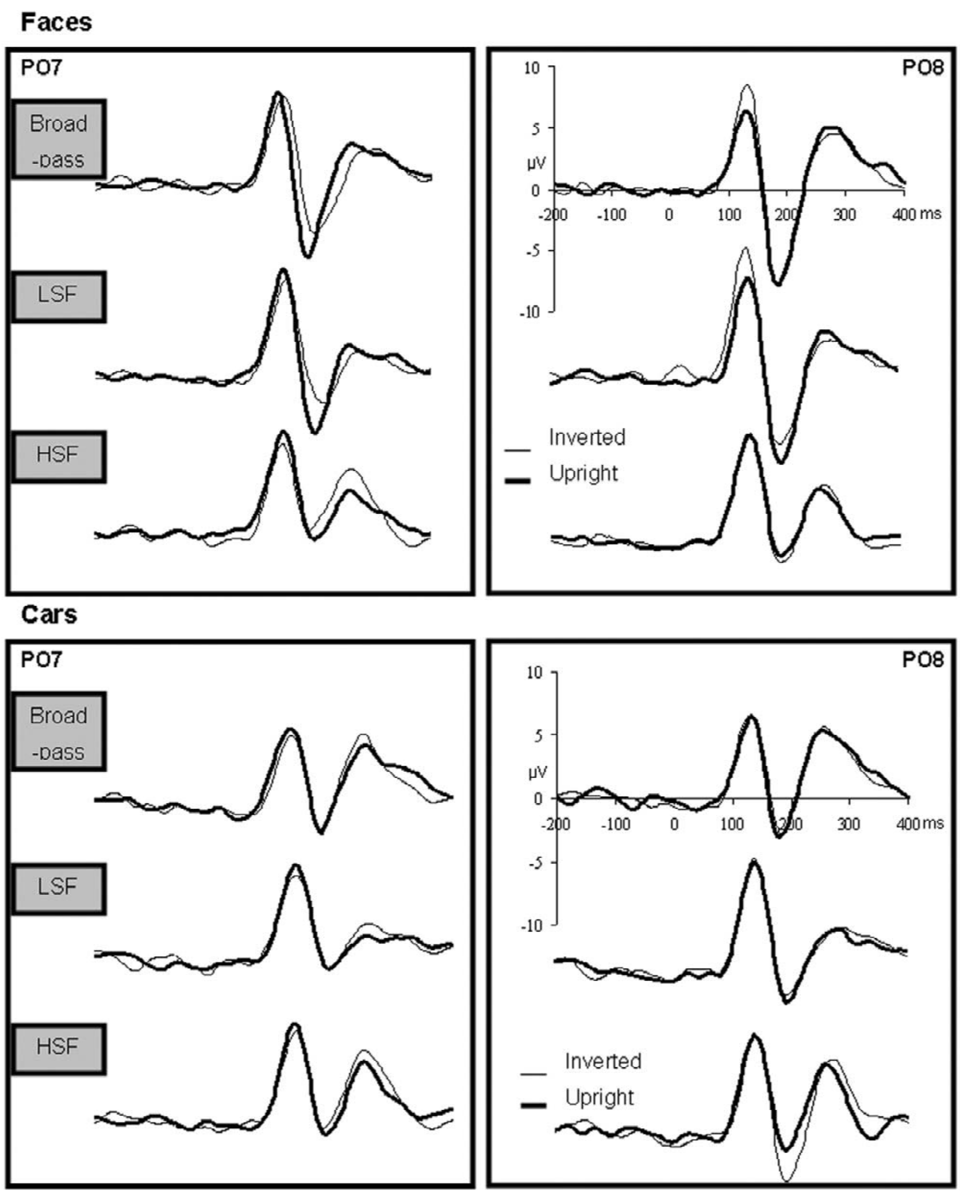

Fig. 4. Top panel: Grand-average waveforms recorded in response to upright (thick line) and inverted (thin line) faces on left (PO7, left panel) and right hemispheres (PO8, right panel) are presented for the broad-pass, LSF and HSF conditions. Note the N170 latency delay and amplitude reduction for inverted faces in the broad-pass and LSF conditions on PO7. In HSF, we observed a latency decrease in response to face inversion on PO7. Bottom panel: Grand-average waveforms recorded in response to upright (thick line) and inverted (thin line) cars on left (PO7, left panel) and right hemispheres (PO8, right panel) are presented for the broad-pass, LSF and HSF conditions. No inversion effect characterized this category. However, in the HSF condition, inverted cars induced significantly larger N170 amplitudes on the right hemisphere.

$P<0.012$. However, for faces, the N170 amplitude significantly decreased from broad-pass to LSF, $P<0.001$, and from the LSF to the HSF conditions, $P<0.001$, whereas the amplitude of N170 to cars slightly decreased from broad-pass to LSF conditions, $P<0.023$, but did not decrease further for the HSF condition, $P=0.55$. The effects of Laterality, $F(1;12)=5.04$, $P<0.04$, and the Category × Laterality interaction, $F(1;12)=6.67$, $P<0.02$, were significant but were qualified by a significant three-way Category × Spatial frequency × Laterality interaction, $F(1.5;18.3)=15.4$, $P<0.001$. The N170 amplitude to faces was larger than cars on both hemispheres in broad-pass (PO8, $P<0.001$; PO7, $P<0.001$) and LSF (PO8, $P<0.001$; PO7, $P<0.001$) conditions. In the HSF condition, however, cars and faces elicited similar N170 amplitudes on PO7, $P=0.68$, whereas the N170 to cars was larger than faces on PO8, $P<0.006$. The N170 recorded for faces was largest on the right hemisphere in broad-pass, $P<0.011$, and LSF conditions, $P<0.012$, but not in the HSF condition, $P=0.293$. For cars, there was no significant difference between PO7 and PO8 electrodes, $P=0.096$. Finally, the three-way Spatial frequency × Orientation × Laterality interaction was significant, $F(1.4,16.5)=4.95$, $P<0.03$. Stimulus inversion decreased the N170 amplitude marginally in the broad-pass condition, $P<0.058$, and significantly in the LSF condition, $P<0.028$; in the HSF condition, the N170 amplitude was larger for inverted stimuli, but only on the right PO8, $P<0.007$ (PO7, $P=0.27$).

3.2.2. N170 latency

The four-way ANOVA performed on N170 latencies revealed significant main effects of Spatial frequency, $F(1.2;14.3)=18.1$, $P<0.0001$, Category, $F(1;12)=10.1$, $P<0.008$, and Orientation, $F(1;12)=11.6$, $P<0.005$. The two-way interactions of Category × Orientation, $F(1;12)=5$, $P<0.04$, and Spatial frequency × Orientation, $F(1.2;14.9)=8.11$, $P<0.01$, were significant, but were qualified by a three-way interaction between Category, Spatial frequency and Orientation, $F(1.8;21.1)=7.31$, $P<0.005$. In the broad-pass condition, upside-down inversion delayed the N170 latency for faces only, $P<0.0001$ (cars, $P=0.112$), thus confirming the face-specificity of the N170 inversion effect. In the LSF condition, the inversion effect was again restricted to faces, $P<0.026$ (cars, $P=0.25$). No significant inversion effect emerged from the HSF condition, nor for faces, $P=0.077$, nor for cars, $P=0.57$. The effects of Laterality, $F(1;12)=6.05$, $P<0.03$, and the Spatial frequency × Laterality interaction, $F(1.5;18.1)=5.28$, $P<0.02$, were significant, as was the Orientation × Laterality interaction. However, these effects were qualified by a three-way interaction between Category × Orientation × Laterality, $F(1;12)=11.6$, $P<0.005$. For cars, a slight (1 ms) but significant latency delay was observed on the right PO8, $P<0.049$, but not on the left PO7, $P=0.17$. For faces, upside-down inversion caused a mean 15.6 ms latency delay on the left PO7, $P<0.001$, but not on the right PO8, $P=0.57$.

P100 analyses did not reveal any of the critical effects observed on N170, i.e. abolition of the faces–cars amplitude difference in the HSF condition and absence of the inversion effect on the latency of N170 to HSF faces. In contrast, these critical effects emerged from analyses performed on relative N170 latency and amplitude, confirming the N170 as the functional locus of the observed modulations of the differences between faces and cars across SF.

4. Discussion

Do the so-called face-specific effects typically observed on the N170 amplitude (larger for faces) and latency (delayed by face inversion) automatically arise once a face picture is provided to the visual system? Here we tested the hypothesis that these effects are highly dependent on the type of low-level visual information that is provided to the visual system. In broad-pass images, we replicated typical face-specific N170 markers: the N170 amplitude was larger for faces than for cars and the N170 latency was delayed for inverted faces but not for inverted cars[2]. Interestingly, SF filtering greatly modulated these N170 face-specific effects (Figs. 3 and 4). On the one hand, the LSF condition produced the typical pattern obtained for faces, as the N170 to LSF faces was larger than to LSF cars, and inversion delayed the N170 latency for LSF faces, but not for LSF cars. On the other hand, the HSF condition revealed a completely different pattern: the N170 amplitude was similar for HSF cars as compared to HSF faces and no latency delay was observed for inverted HSF faces. For broad-pass and LSF faces, the N170 amplitude was larger on the right as compared to the left occipito-temporal hemisphere, replicating previous observations (e.g. Ref. [2]), whereas no right hemisphere advantage was found for N170 amplitude to cars. This category by laterality interaction was not observed in the HSF condition where faces and cars no longer differed in terms of their lateralization patterns.

The modulations caused by SF filtering cannot be accounted for by differences in the mere presence of energy in a particular band of spatial frequencies, since LSF and HSF stimuli covered an identical SF spectrum.

[2] To our knowledge, all ERP investigations of the N170 face inversion effect report bilateral effects [2,10,15,23,26–28,30]. In the present study, however, the face inversion effect on N170 latency was only observed on the left PO7 electrode. Our use of 3/4 views of faces and cars could have led to a slight bias of salient information being more abundant in the right visual field, and might account for the larger effect in the left hemisphere. Other data from our group favor this view [25,29]. Nevertheless, the bias related to the use of 3/4 views was comparable for both categories and identical for all spatial frequencies. Thus, it did not interfere with the SF modulations observed on the N170 differences between faces and cars.

Nor can these effects be reduced to differences in overall visibility between LSF and HSF; as indicated by similar and good performance levels, both LSF and HSF stimuli were effortlessly processed. Moreover, if the modulations of the difference between faces and cars in N170 amplitude and inversion delay were to reflect differences in the basic physical properties of LSF and HSF stimuli, these should arise at earlier processing steps than the N170 component. However, the absence of these effects on the P100 (see Appendix A)—a component which is sensitive to the low-level visual properties determining the overall stimulus visibility—rather supports that they reveal differences in how different scales of information are used by observers looking at faces and cars.

It has been argued that the mere presentation of a face is sufficient to trigger a normal N170, whether or not the face contains a lot of detailed textural information, for instance [1–3,20,30]. Consequently, some authors have proposed that the N170 represents the occurrence of a face processing module, the function of which is to detect the presence of a face [3,6,30] (but see Ref. [26]). However, the present evidence supports the idea that the dissociation between face and object processing at this early stage of processing strongly relies on the differential perceptual extraction of LSF and HSF cues. More precisely, our results show that the visual information leading to a N170 difference between faces and objects is mostly contained in the LSF.

In the present study, several facts pinpointed LSF as playing a dominant role in early visual face processing, in contrast to object processing. First, the N170 amplitude was larger for faces than for cars as long as subjects were provided with LSF (in broad-pass and LSF conditions). Second, another interesting finding is that the typical inversion effect on N170 latency was obtained with LSF, but not with HSF faces. As upside-down inversion is known to disrupt configural processing [7,8,11,19,24], the LSF face inversion effect confirms that this scale conveys configural cues crucial to face perception, in contrast to HSF information. Third, the observation of a larger N170 amplitude for LSF faces as compared to HSF faces, whereas no such difference was observed for cars, indicates LSF/configural tuning of face processing.

The prevalence of LSF in face configural processing is consistent with the behavioral literature. For example, Leder [18] observed that the use of line drawings, known to alter coarse cue representation [4,18,32], impairs configural encoding of faces. Sagiv and Bentin [30] also reported a small reduction of N170 amplitude for schematic faces and a reduction of the inversion delay of the N170. Line drawings are a special case of stimuli, mainly characterized by HSF at a particularly high level of contrast (higher than photographs). On the contrary, our study controlled the basic visual properties of the signal provided in the different SF conditions, the difference being about the SF band that conveyed face or car information. More comparable to our HSF condition is the use by Sagiv and Bentin [30] of less contrasted sketches of faces, which contained far more edges and details than schematic stimuli. When compared to the natural face condition, sketched faces led to significant N170 amplitude reduction and a latency increase, mimicking the N170 response to HSF faces. It thus seems that removal of LSF, either by filtering or line drawing, causes a decrease in N170 amplitude. Evidence from developmental research also confirms the close relation existing between LSF, configuration and face processing. Indeed, Le Grand and colleagues [17] observed that visual deprivation during the very first months of life prevents normal exposure to LSF and results in permanent deficits in face configural processing. Moreover, several studies have demonstrated that a bandwidth of relatively low SF (centered around 11 cycles per face) is important for conveying face identity (reviewed in Ref. [22]).

Nevertheless, the small decrease of N170 amplitude to LSF compared to broad-pass faces also supports a role of HSF information in triggering the N170 response to faces. This observation is in agreement with a previous behavioral study showing that face recognition performance benefits from the presence of both analytical and configural cues [7]. In addition, the LSF versus HSF contribution to early face processing might depend on the context of the specific task to be solved [14,31]. For example, a recent ERP study demonstrated that the task to perform on faces (gender versus familiarity categorization) modulates the N170 amplitude to LSF faces [13]. The task used in the present experiment did not require the extraction of fine stimulus details. A task requiring a more detailed analysis of the stimulus, such as individual face identification, might reduce the LSF prevalence over HSF observed for face processing in the present study.

In summary, we found that early processing differences between faces and objects are highly dependent on the LSF processing of faces. The sources of differences between faces and other categories at this early processing stage remain to be clarified, but our study suggests that most may be contained in LSF, which, among other information, support configural cues. Our results thus corroborate the view that LSF are important for face perception because their early processing provides configural cues to the perceptual system. Overall, our work emphasizes the importance of considering the observer's processing biases, which may develop through experience, in order to gain understanding of category-specific effects. Future studies should examine if LSF tuning of face processing originates from the extensive expertise we develop for the fine and fast inter-individual discrimination of faces.

Acknowledgements

The authors are grateful to Celine Cornet and Corentin Jacques for their help during EEG data acquisition and processing. IG is supported by grants from the National Science Foundation, the National Eye Institute and the James S. McDonnell Foundation. VG and BR are supported by the Belgian Fund for Scientific Research (FNRS). This study was supported by grant ARC 01/06-267 (Communauté Française de Belgique—Actions de Recherche Concertées).

Appendix A

P100 analyses

P100 amplitude

When computed on P100 amplitude values, the four-way ANOVA revealed a significant effect of Category, $F(1;12) = 19.7$, $P<0.001$. The Category×Orientation, $F(1;12) = 5$, $P<0.045$, as well as the Category×Spatial frequency×Orientation, $F(1.8;22.1) = 4.8$, $P<0.02$, interactions were significant. In broad-pass and LSF conditions, faces produced larger P100 amplitude as compared to cars, but only in the inverted condition, $P<0.001$ and $P<0.045$, respectively. In HSF, P100 to faces was larger in amplitude than cars independent of orientation, $P<0.01$. Inversion of faces increased P100 amplitude in broad-pass and LSF conditions, $P<0.01$ and $P<0.039$, respectively, but not in the HSF condition, $P=0.46$. Cars did not display any significant inversion effect on P100 amplitude. Orientation and Laterality factors interacted significantly, $F(1;12) = 31.8$, $P<0.001$, but were qualified by a significant three-way Category×Orientation×Laterality interaction, $F(1;12) = 7.14$, $P<0.02$. Inversion of faces increased the P100 amplitude on the right PO8 electrode only, $P<0.001$, whereas inversion of cars decreased the P100 amplitude on the left PO7 electrode, $P<0.011$.

P100 latency

Spatial frequency significantly modulated P100 latency, $F(1.7;20.8) = 16.6$, $P<0.001$. LSF and HSF stimuli led to a similar P100 latency, $P=0.48$, but delayed P100 latency as compared to broad-pass stimuli ($P<0.002$ in both cases). The Laterality×Category interaction was significant, $F(1;12) = 4.9$, $P<0.048$. For faces, P100 latency was longer at the right PO8 as compared to the left PO7, $P<0.01$. No difference across hemispheres was observed for the latency of P100 to cars, $P=0.242$.

Analyses of relative N170 values (P100 as baseline)

Relative N170 amplitude

The overall four-way ANOVA revealed significant effects of Spatial frequency, $F(1.6;19.3) = 24.97$, $P<0.0001$, and Category, $F(1;12) = 41$, $P<0.001$, and an interaction between these two factors, $F(1.9;23.02) = 41.89$, $P<0.001$. The N170 amplitude was larger for faces than for cars in broad-pass, $P<0.001$, and LSF conditions, $P<0.001$, but not in the HSF condition, $P<0.26$. The three-way Spatial frequency×Category×Orientation interaction was also significant, $F(1.9;23.1) = 4.7$, $P<0.02$. The effect of Spatial frequency was significant for faces, $F(1.8;21.7) = 48.7$, $P<0.001$, N170 amplitude significantly decreased from broad-pass to the LSF face condition, $P<0.003$, and from the LSF to the HSF condition, $P<0.0001$. For cars, there was no significant effect of Spatial frequency, $P=0.4$, but there was a significant interaction between Spatial frequency and Orientation, $F(1.7;20.9) = 3.65$, $P<0.05$. In the upright condition, the amplitude of the N170 to broad-pass cars was marginally larger than for LSF and HSF cars, $P=0.06$. The effects of Laterality, $F(1;12) = 12.7$, $P<0.004$, the Category×Laterality interaction, $F(1;12) = 5.7$, $P<0.034$, and the Orientation×Laterality interaction, $F(1;12) = 25.4$, $P<0.001$, were significant and qualified by a three-way Category×Orientation×Laterality interaction, $F(1;12) = 11$, $P<0.006$. On the right PO8, inverted faces elicited a larger N170 amplitude than upright faces, $P<0.003$, whereas the largest amplitude was observed for upright faces on the left PO7, $P<0.005$. Inversion of cars only affected the N170 amplitude on the left PO7, which showed a larger amplitude for upright cars, $P<0.008$. The two-way Spatial frequency×Laterality interaction was also significant, $F(1.9;23.4) = 5.5$, $P<0.011$. N170 was larger on the right as compared to the left hemisphere for each spatial frequency condition, but mostly for broad-pass and LSF stimuli.

Relative N170 latency

The four-way ANOVA performed on relative N170 latencies revealed significant main effects of Category, $F(1;12) = 6.1$, $P<0.03$, and Orientation, $F(1;12) = 6$, $P<0.03$. The two-way interaction between Spatial frequency and Orientation was significant, $F(1.7;20.5) = 4.53$, $P<0.03$. It was qualified by a marginal three-way interaction between Category, Spatial frequency and Orientation, $F(1.8;21.9) = 2.9$, $P<0.07$. In the broad-pass condition, upside-down inversion significantly delayed the N170 latency for faces only, $P<0.02$ (cars, $P=0.75$), thus confirming the face-specificity of the N170 inversion effect. In the LSF condition, the inversion effect was again restricted to faces, $P<0.02$ (cars, $P=0.29$). No significant inversion effect emerged from the HSF condition for faces, $P=0.16$, or for cars, $P=0.75$. The Spatial frequency×Laterality interaction was significant, $F(1.8;22.1) = 3.8$, $P<0.042$. Spatial frequency affected N170 latency on the left PO7 electrode, $F(1.7;20.1) = 4$, $P<0.041$, but not on the right PO8 electrode, $P=0.25$. On PO7, LSF stimuli significantly increased the N170 latency as compared to broad-pass, $P<0.013$, and HSF stimuli, $P<0.029$, whereas no latency difference was found across broad-pass and HSF conditions, $P=0.99$.

References

[1] S. Bentin, L. Deouell, Structural encoding and identification in face processing: ERP evidence for separate mechanisms, Cogn. Neuropsychol. 17 (2000) 35–54.

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

[3] S. Bentin, L.Y. Deouell, N. Soroker, Selective visual streaming in face recognition: evidence from developmental prosopagnosia, Neuroreport 10 (1999) 823–827.

[4] I. Biederman, G. Ju, Surface versus edge-based determinants of visual recognition, Philos. Trans. R. Soc. Lond. B: Biol. Sci. 29 (335) (1988) 121–127, discussion 127–128.

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

[6] D. Carmel, S. Bentin, Domain specificity versus expertise: factors influencing distinct processing of faces, Cognition 83 (2002) 1–29.

[7] S.M. Collishaw, G.J. Hole, Featural and configurational processes in the recognition of faces of different familiarity, Perception 29 (2000) 893–909.

[8] S.M. Collishaw, G.J. Hole, Is there a linear or a nonlinear relationship between rotation and configural processing of faces?, Perception 31 (2002) 287–296.

[9] R. Diamond, S. Carey, Why faces are and are not special: an effect of expertise, J. Exp. Psychol. Gen. 115 (1986) 107–117.

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

[11] A. Freire, K. Lee, L.A. Symons, The face-inversion effect as a deficit in the encoding of configural information: direct evidence, Perception 29 (2000) 159–170.

[12] I. Gauthier, M.J. Tarr, Becoming a ‘Greeble’ expert: exploring the face recognition mechanism, Vis. Res. 37 (1997) 1673–1682.

[13] V. Goffaux, B. Jemel, C. Jacques, P.G. Schyns, ERP evidence of task modulations on the perceptual processing of faces at different spatial scales, Cogn. Sci. (in press).

[14] F. Gosselin, P.G. Schyns, Bubbles: a technique to reveal the use of information in recognition tasks, Vis. Res. 41 (2001) 2261–2271.

[15] R.J. Itier, M.J. Taylor, Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs, NeuroImage 15 (2002) 353–372.

[16] N. Kanwisher, Domain specificity in face perception, Nat. Neurosci. 3 (2000) 759–763.

[17] R. Le Grand, C.J. Mondloch, D. Maurer, H.P. Brent, Early visual experience and face processing, Nature 410 (2001) 890.

[18] H. Leder, Line drawings of faces reduce relational processing, Perception 25 (1996) 355–366.

[19] H. Leder, V. Bruce, When inverted faces are recognized: the role of configural information in face recognition, Q. J. Exp. Psychol. A 53 (2000) 513–536.

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

[21] D.J. Morrison, P.G. Schyns, Usage of spatial scales for the categorization of faces, object and scenes, Psychon. Bull. Rev. 8 (2001) 454–469.

[22] D.M. Parker, N.P. Costen, One extreme or the other or perhaps the golden mean? Issues of spatial resolution in face processing, Curr. Psychol. 18 (1999) 118–127.

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

[24] G. Rhodes, S. Brake, A.P. Atkinson, What’s lost in inverted faces?, Cognition 47 (1993) 25–57.

[25] B. Rossion, Vuong, M.J. Tarr (manuscript in preparation).

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

[27] B. Rossion, I. Gauthier, M.J. Tarr, P.A. Despland, R. Bruyer, S. Linotte, M. Crommelinck, 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 (2000) 69–74.

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

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

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

[31] P.G. Schyns, A. Oliva, Dr Angry and Mr Smile: when categorization flexibly modifies the perception of faces in rapid visual presentations, Cognition 69 (1999) 243–265.

[32] J. Sergent, Microgenesis of face perception, in: H.D. Ellis, M.A. Jeeves, F. Newcombe, A.M. Young (Eds.), Aspects of Face Processing, Martinus Nijhoff, Dordrecht, 1986.

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

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

[35] M.W. Vasey, J.F. Thayer, The continuing problem of false positives in repeated measures ANOVA in psychophysiology: a multivariate solution, Psychophysiology 24 (1987) 479–486.