

The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain

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Behavioral studies have shown that picture-plane inversion impacts face and object recognition differently, thereby suggesting face-specific processing mechanisms in the human brain. Here we used event-related potentials to investigate the time course of this behavioral inversion effect in both faces and novel objects. ERPs were recorded for 14 subjects presented with upright and inverted visual categories, including human faces and novel objects (Greebles). A N170 was obtained for all categories of stimuli, including Greebles. However, only inverted faces delayed and enhanced N170 (bilaterally). These

observations indicate that the N170 is not specific to faces, as has been previously claimed. In addition, the amplitude difference between faces and objects does not reflect face-specific mechanisms since it can be smaller than between non-face object categories. There do exist some early differences in the time-course of categorization for faces and non-faces across inversion. This may be attributed either to stimulus category per se (e.g. face-specific mechanisms) or to differences in the level of expertise between these categories. *NeuroReport* 11:69–74 © 2000 Lippincott Williams & Wilkins.

Key words: Event-related potentials; Face inversion effect; Face processing; Greebles; N170

INTRODUCTION

It is often stated that human face recognition is subserved by specific processes within specific neural structures. Behavioral evidence supporting face-specific mechanisms has been provided by studies showing that stimulus inversion disrupts the processing of faces more than other objects (the face inversion effect) [1], and that individual feature recognition in faces is particularly dependent upon the relationships between features (the face superiority effect) [2]. The evidence for neuroanatomical specialization has been provided both by neuropsychological patient studies and neuroimaging. Studies of brain injuries have provided cases of impaired of face processing, usually following bilateral occipito-temporal damage [3], with intact visual object processing, as well as the opposite deficit, spared face processing with impaired object processing [4]. More recently, PET and fMRI studies have provided additional evidence that face processing in nor-

mal subjects may involve specific neural regions distinct from those regions support general object recognition [5]. This hypothesis should be evaluated in terms of all factors that play some role in determining visual recognition behavior [6]. Specifically, stimulus class membership (face *vs* non-face), categorization level (placing objects in basic level categories such as chair, dog and car or in subordinate level categories, such as dalmatian, beagle and bloodhound), and level of expertise are all critical to understanding some of the observed differences between object and face processing. First, behaviorally, it has been demonstrated that visual expertise with a given dog breed [7] or with synthetic nonsense objects (Greebles) [8], can lead to inversion and/or superiority effects similar to those obtained for faces. Second, recent case descriptions have also shown that prosopagnosics are more affected by manipulations of the level of categorization than normal controls [9]. This finding suggests that prosopagnosics

apparently disproportionate impairment for faces than for non-face objects may be partly explained by the fact that faces are usually recognized at the subordinate level, while non-face objects are typically recognized at the basic level. Third, recent fMRI studies suggest that the so-called face fusiform area (FFA) [5] is more strongly activated when objects are categorized at the subordinate level than at the basic level [10] and that expertise training with non-face objects (Greebles) may also recruit the FFA to the same degree as faces [11].

Of particular interest to the present study, scalp electrophysiological recordings in humans have revealed early face-specific mechanisms which could not have been found using behavioral, neuropsychological, or brain imaging methodologies. Using ERPs, it has been demonstrated that face processing differs from visual object processing 170 ms following stimulus onset [12–14]. This dissociation takes place at the level of the visual N170 component in occipito-temporal regions [13–16] and is characterized by a larger amplitude in the component for faces [14] or an absence of N170 for non-faces objects [13,17].

One unresolved issue with these ERP studies is that they generally compared faces to a single mono-oriented object category, e.g. cars [13] or houses [14]. To be able to strongly argue that faces are special one not only has to show specific processes for faces but also that most other object classes are processed the same way, by a generic object recognition [18]. For example, differences in level of activity have also been obtained between different non-face object categories in both electrophysiological [12] and neuroimaging studies [19]. It is unlikely that anyone would seriously interpret such results as evidence for separable neural mechanisms between such categories, for instance, chairs and houses. In other words, comparing faces with a single category is not sufficient for claiming a dissociation and one has to be careful to show specific effects for faces that are not observed for the majority of non-face categories. A second weakness of previous ERP studies is that the differential amplitude of the N170 for faces and objects might have been obtained due to potential confounds such as differences in the low-level visual features between faces and objects [5], higher visual familiarity for faces (as a class) than for objects [20] and different levels of expertise [8].

In light of these concerns, the aim of the present study is to establish a framework in which the modularity of face processing can be better evaluated through ERPs. More precisely, we tested whether the N170 component might really reflect face-specific neural mechanisms occurring early in visual categorization by comparing faces to a variety of non-face mono-oriented stimuli. To avoid the potential confound of differential low-level visual features between faces and objects, these stimuli were not compared directly but were compared relative to their respective picture-plane inverted presentations. While inversion of a face (or an object) preserves the low-level visual features, inverted faces are not believed to involve configural processing [2,4] which is considered to be the hallmark of the face-specific processing as compared to non-face object processing.

We also took advantage of the recent evidence that the N170 is strongly influenced by face inversion [21]. When

faces are presented upside-down, the N170 latency is significantly delayed (around 10 ms) and may also be larger when subjects are engaged in a face discrimination task [21]. The latency delay, which is fairly robust and has been found in several ERP studies [13,14,21] has been proposed to reflect the loss of configural information with inversion [16,21].

The specificity of the electrophysiological correlate of the inversion effect to faces was tested by presenting subjects with faces and various non-face categories of mono-oriented objects such as houses, chairs, shoes, cars and Greebles [8], in upright and inverted presentations.

According to the face-specific processing hypothesis, which argues for differential neural coding for faces and objects, a latency delay and an increase of activity is expected when faces are inverted but not when inverted non-face objects are presented. The alternative view, a general object-recognition system shared by faces and objects, predicts that the latency delay and the higher activity of the N170 potential reflects generic object rotation effects that should be observed for any mono-oriented object [22].

MATERIALS AND METHODS

Fourteen subjects (seven females; three left-handed) with normal or corrected vision participated in this experiment (mean age 25 years). Eight different images of six categories of stimuli were used: photographs of faces, full front cars, shoes, chairs, houses and Greebles. The corresponding inverted stimuli were also presented. All stimuli subtended a visual angle of $\sim 2.5^\circ$. The height of the stimuli was slightly different between categories but identical for upright and inverted versions of the images. Subjects sat on a comfortable chair in a dimly lit room. They were instructed to visually fixate the center of the screen (distance 1.2 m) during each experimental block. After a short training block of 20 stimuli, subjects received 12 experimental blocks of 120 trials (10 images \times 6 categories \times 2 orientations). Each stimulus was presented for 500 ms; the inter-stimulus interval was randomized between 1500 and 2000 ms. All of the stimuli were randomized within a block but all subjects viewed the same succession of stimuli. The subject's task was to press a key if the stimulus was upright and another key if the stimulus was inverted. The upright and inverted orientations of Greebles were shown on the screen to the subjects before the experiment, although without exposure to upright Greebles, they still tend to orient to this particular viewpoint because of their flat base, their bilateral symmetry axis and their rotational axis. All responses were made with the right hand. Subjects were instructed to respond as accurately and as quickly as possible. Responses < 200 ms or > 1250 ms were discarded in the behavioral and ERPs analyses ($< 2\%$ of trials).

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 (electrocap, Neuroscan Lab) with respect to a left mastoid reference. EEG was amplified with a gain of 30 K and bandpass filtered at 0.15–70 Hz. Electrode impedance was kept below 5 k Ω . EEG and EOG were continuously acquired at

a rate of 500 Hz. After automatic removal of EEG and EOG artifacts, epochs beginning 200 ms prior to stimulus onset and continuing for 800 ms were made. They were referenced off-line to a common average reference. The average waveforms computed for the different categories (6×2 averages for each subject) were low pass filtered at 30 Hz. Peak amplitude and latencies of the N170 at occipito-temporal sites (T5 and T6) electrodes were measured relative to a 200 ms pre-stimulus baseline on a computed grand average waveform and in each subject individually, for the 12 types of stimuli used in the experiment. Topographic maps were also computed for the various categories of stimuli presented.

Behavioral (accuracy rates and correct RTs) and electrophysiological (latencies and amplitudes of components) measures on these different electrodes were analyzed by means of repeated-measures analyses of variance (ANOVA) with orientation (two levels), visual category (six levels) and, when relevant, hemispheric lateralization (two levels) as factors. *Post-hoc* paired *t*-tests were also performed.

RESULTS

Behavioral data: The overall accuracy in the detection task for the categories ranged between 92% (shoes) and 96% (faces and houses); mean reaction times ranged between 556 ms (upright houses) and 615 ms (inverted shoes). The 2×6 ANOVA on reaction times revealed significant main effects of orientation ($F_{1,13} = 9.27$; $p = 0.009$), the inverted stimuli being detected more slowly (603 ms *vs* 579 ms), and of category ($F_{1,13} = 8.13$; $p < 0.001$), cars being the fastest stimuli for the orientation decision (576 ms on average) and Greebles being the slowest (613 ms). There was also a significant interaction ($F_{1,13} = 3.25$; $p = 0.01$), mainly due to the absence of any difference between orientation for Greebles and shoes.

ERPs: All subjects elicited an occipito-temporal N170 for all the visual categories tested, including Greebles. The topography of this N170 was very similar for all object categories. Table 1 shows the latencies of the N170 for the various categories tested. Amplitudes are shown in Table 2. On average, the N170 component to faces peaked at 165 ms at T6 and at 163 ms at T5, with similar latencies for objects (see Table 1), except for houses which elicited a slightly later N170. Three main results were observed: (1) the N170 was larger for faces than for all other visual

Table 1. Mean latencies of the N170 to the different visual categories presented, for the two orientations and at the two hemispheres

	T6 (right hemisphere)		T5 (left hemisphere)	
	Upright	Inverted	Upright	Inverted
Faces	165	173	163	170
Greebles	165	164	162	165
Cars	165	167	164	164
Chairs	170	170	167	169
Houses	174	170	172	174
Shoes	165	166	165	165

The latency delay for faces is 8 ms on average at T6 and 7 ms at T5 while there was no such delay for all other objects tested.

categories (Table 1; Fig. 1); (2) the N170 was delayed and larger for inverted faces than for upright faces at both hemispheres (Fig. 1; Tables 1, Table 2); (3) there was no effect of orientation for all the non-face categories tested (Table 1; Fig. 2).

Statistical analyses largely confirmed these observations. The ANOVA (category \times orientation \times hemisphere) on N170 latencies showed a significant interaction between category and orientation ($F_{5,65} = 10.022$; $p < 0.001$). There was also a main effect of category ($F_{5,65} = 6.476$, $p < 0.001$), due to the larger latencies for houses, and a main effect for orientation ($F_{1,13} = 8.086$; $p = 0.014$). When faces were not included in the analysis (ANOVA $2 \times 2 \times 5$), there was no main effect of orientation ($F_{1,13} = 0.263$; $p = 0.617$) nor any significant interaction between orientation and category ($F_{4,52} = 1.070$; $p = 0.381$) but still a main effect of category ($F_{4,52} = 9.09$, $p < 0.001$). *Post-hoc t*-tests conducted on each category showed a significant delay for inverted faces only ($p < 0.0001$). For all non-face categories, there was no effect of orientation (cars: $p = 0.314$; Greebles: $p = 0.502$; shoes: $p = 0.869$; chairs: $p = 0.364$; houses: $p = 0.065$). The non-significant trend for houses was actually due to an increase in latencies for upright houses. Finally, *post-hoc t*-tests revealed that the N170 to Greebles and cars peaked earlier than for other categories ($p = 0.001$ and $p = 0.01$, respectively) but did not differ from one another ($p = 0.13$) while N170 to shoes and houses was significantly delayed compared with all other categories, including faces ($p = 0.026$ and $p = 0.01$, respectively). All other comparisons between categories were non-significant (p between 0.194 and 0.462). It is worth noting that all of the 14 subjects tested exhibited a delayed (> 6 ms) N170 to inverted faces at least at one hemisphere. Eight subjects showed the effect (> 6 ms) in both hemispheres.

The ANOVA on N170 amplitudes also revealed a main effect of visual category ($F_{5,65} = 10.647$; $p < 0.001$) and a significant interaction between orientation and category ($F_{5,65} = 4.942$; $p < 0.001$). The first effect reflected the larger amplitude of the N170 to faces (Fig. 1) but also differences between object categories (see *post-hoc t*-tests). The interaction in this ANOVA was due to the specific increase of voltage amplitude for inverted faces as compared to upright faces (Fig. 1; Table 2). *Post-hoc t*-tests confirmed the larger amplitude for faces than for all other objects ($p = 0.003$) although the N170 to faces was not significantly larger than for cars ($p = 0.059$). There was also significant differences between categories of objects (e.g. cars *vs* others: $p = 0.025$; chairs *vs* others: $p < 0.001$; see Table 2). *Post hoc t*-tests conducted for each category showed a main effect of orientation for faces ($p = 0.014$) and the absence of any such effect for all other visual categories (cars: $p = 0.780$; shoes: $p = 0.159$; chairs: $p = 0.605$; houses: $p = 0.130$), except that the N170 was actually larger for upright than inverted Greebles (see Table 2; $p < 0.001$).

DISCUSSION

The first observation of our study is that the N170 is not at all specific to faces, as it has been claimed in previous reports [13,17]. This component is actually observed for completely novel objects such as Greebles. This result demonstrates that long-term familiarity with a category is not a prerequisite to trigger a N170 potential. The fact that

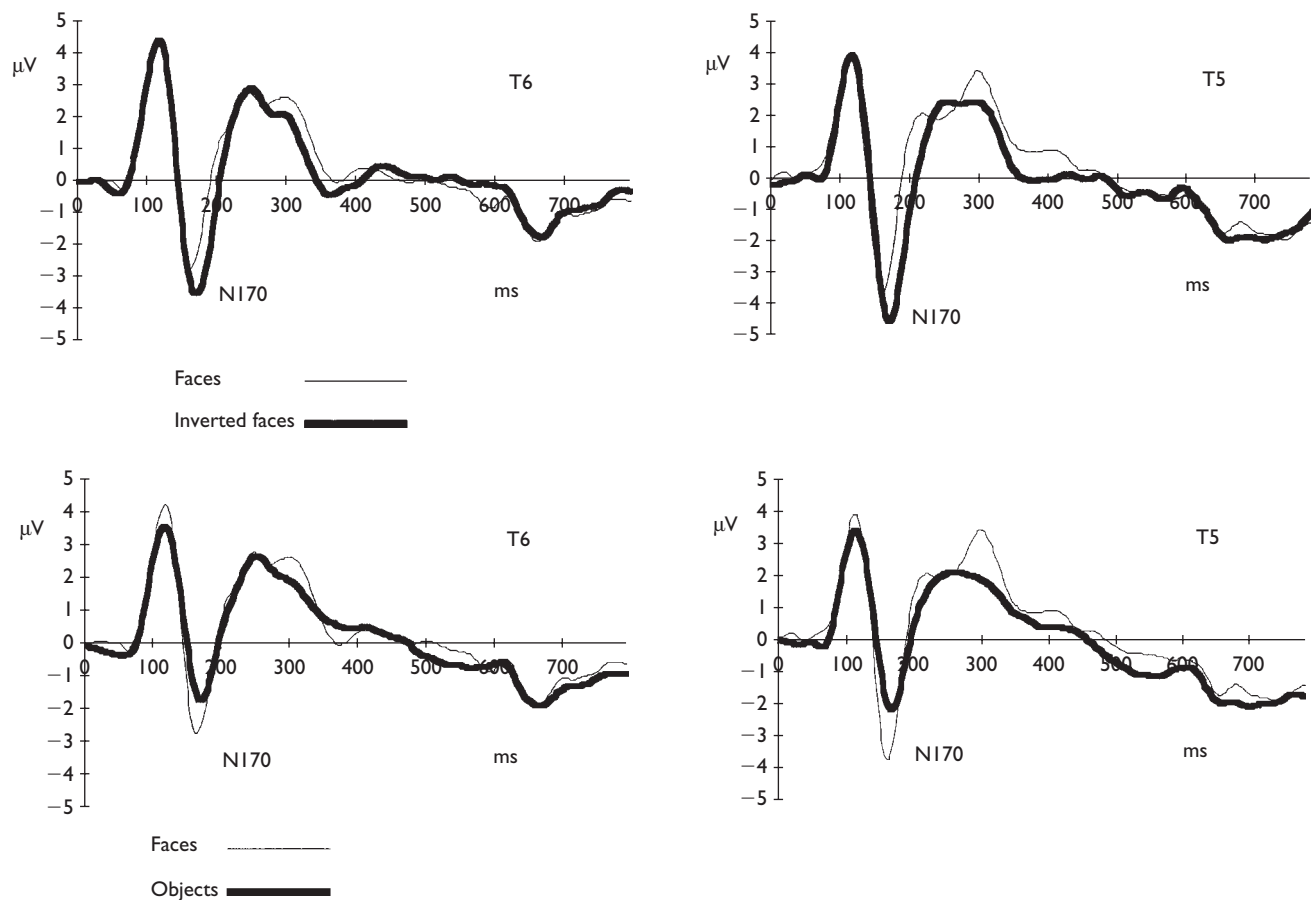


Fig. 1. Above. Grand average waveforms obtained for normal and inverted faces at T6 (right occipito-temporal site) and T5. The N170 is larger and delayed for inverted faces as compared to normal faces at both sites. Below. Grand average waveforms obtained for faces and for all other objects categories. Overall, the N170 is significantly larger for faces than for objects at both occipito-temporal sites.

Table 2. Mean amplitudes of the N170 to the different visual categories presented, for the two orientations and at the two hemispheres

	T6 (right hemisphere)		T5 (left hemisphere)	
	Upright	Inverted	Upright	Inverted
Faces	-3.18	-4.13	-4.33	-5.21
Greebles	-2.28	-1.96	-3.55	-2.74
Cars	-3.09	-3.01	-3.69	-3.59
Chairs	-1.85	-2.07	-1.66	-1.73
Houses	-2.89	-2.58	-3.07	-2.72
Shoes	-1.62	-1.80	-2.36	-2.81

The amplitude of the component is significantly larger for faces than for all other categories. The increase for inverted faces is 0.95 µV on average at T6 and 0.92 µV at T5 while there was no evidence of such increase for all other objects tested.

the N170 amplitude is even larger for Greebles than for some common familiar objects (e.g. chairs and shoes) is not as surprising as it might seem at first glance: Greebles share more physical properties with faces (smooth surfaces, bilateral symmetry, homogeneity of the class, configuration of individual features, organic appearance) than

many other objects. A second observation is that the N170 observed for faces is larger than for the other objects tested here. This confirms previous reports [14,23], even though neither these studies nor the present study definitively rule out the possibility that these amplitude differences are due to the low-level visual properties differing between faces and objects. Moreover, when compared only to cars, faces failed to elicit a significantly larger N170. More to the point, our results demonstrate that the amplitude differences in the N170 component can be as large between different categories of non-face objects (e.g. cars and shoes) as between faces and some object categories. In our view, a difference between faces and non-face objects is not sufficient to argue for face-specific processes in the human brain. However, a stronger claim for face-specific processes in early visual categorization can be made on the basis of the main finding of this study, namely the observation of a specific latency shift of the N170, as well as an increase in amplitude, for faces when they are inverted. This result confirms and extends our previous findings [21] as none of the other visual categories tested in the present study showed a similar effect when inverted stimuli were presented. To our knowledge, the specificity of this N170 latency delay for inverted faces has not been previously

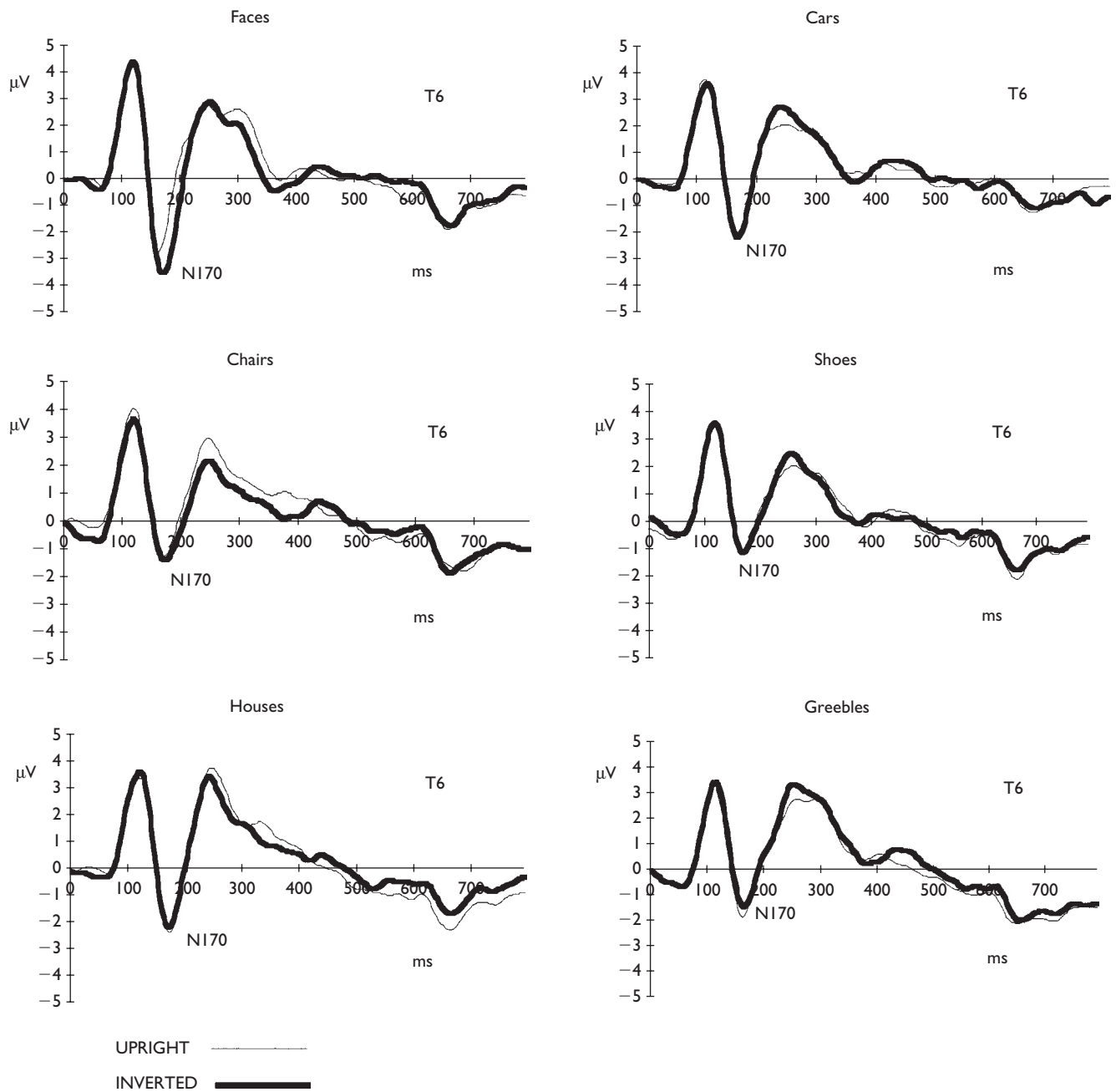


Fig. 2. Comparison of waveforms obtained at T6 (right occipito-temporal electrode site) for normal and inverted stimuli for all the visual categories tested in this study. A larger and delayed N170 to inverted stimuli is observed only for faces.

established. The neural correlates of the behavioral face inversion effect have been examined in several recent fMRI studies [11,24,25], but the timing effect observed here are undetectable by these techniques. As we have suggested previously [21], the effect observed with inverted faces is compatible with both behavioral studies and neurophysiological findings in monkeys. According to behavioral experiments, face inversion disrupts the configural information (i.e. the spatial relationships between parts) that is used by default and accessed more quickly than individual

parts during face recognition [2,26]. The loss of configural information through inversion may thus slow down early face processing. Support for the view that the loss of configural information is intimately linked to the latency delay observed for inverted faces is provided by other ERP studies that have observed similar delays for isolated eyes [13], or faces with the eyes removed [14,16]. A shift in the latency of the N170 has also been observed when subjects are engaged in analytical processing of faces (i.e. focusing on the eyes [16]).

The latency delay observed for inverted faces is also compatible with neurophysiological recordings in the monkey temporal lobe. The onset of activity for individual face-selective cells is roughly equivalent for normal and inverted faces [27]. However, differential proportions of cells coding normal and inverted faces cause differential rates of activity accumulation in the cell population as a whole and, thus, may lead to timing differences, that is, delays for uncommon view of faces, in subsequent processing stages [27].

The larger N170 observed for inverted faces than for upright faces provides further evidence for a face-specific effect in early visual categorization. Two explanations for this increased amplitude for inverted faces have been suggested [21]. First, inverted faces are more difficult to process than normal faces and this may increase the component's amplitude due to the superimposition of a long-lasting temporal negativity associated with difficulty [15]. The second explanation rests on a recent fMRI study indicating that inverted faces recruit both the regions involved in face and object processing whereas normal faces or normal objects recruit only face-specific substrates or object processing substrates [25]. The larger amplitude of the N170 observed for inverted faces than for upright faces may thus be due to inverted faces recruiting brain areas specifically sensitive to faces and those areas more generally involved in object recognition. At the same time, the fact that general object recognition usually operates by default at the basic level may account for why an N170 latency delay and increase of activity is not observed in early visual categorization when objects are inverted. Supporting this conjecture, basic level recognition is only slightly disrupted by inversion.

According to the face-specific processing hypothesis, the result of a specific increase and delay of the N170 to faces is indicative of a process dedicated to face recognition [2,28]. An alternative hypothesis emphasizes the recognition processes rather than the object category differences. According to this subordinate level expertise model, it is the experience of solving the problem of face recognition that tunes our visual recognition system so that it treats faces differently than other object classes. Whereas we recognize most objects at a basic level level (e.g. chair, car or bird) we recognize faces at the individual level (e.g. Charlie or Lucy). The subordinate level expertise hypothesis states that when an observer acquires experience discriminating between objects that share a similar configuration of parts (members of a homogeneous object class), the particular recognition processes that are recruited, as well as their corresponding neural substrates, will be the same as those used for face recognition, because the constraints are the same. For instance, previous behavioral studies [8] as well as fMRI studies [11] have used the same novel stimuli as used here (Greebles) and found that effects which appeared face-specific for Greeble novices were also obtained for upright but not inverted Greebles for Greeble

experts (trained with upright Greebles; see also [7] for an inversion effect found in dog experts). Since our present results provide evidence for face-specific differences in the early processing of faces and objects which are not due to low-level visual differences, further studies should build on this finding, testing whether these face-specific effects may be observed in experts for non-face objects belonging to their domain of expertise, e.g. Greebles.

CONCLUSION

Using event-related potentials, we have demonstrated that the N170 potential is not specific to faces *per se*, as has been previously claimed [13,17]. Moreover, our observations show that the N170 difference between non-face categories can be as large as between faces and these non-face categories. Thus such differences are not diagnostics for face-specific mechanisms. In order to claim face-specific mechanisms on the basis of electrophysiological data, one would need to present results revealing other face-specific effects. Our study provides one such result, showing that the N170 is enhanced and delayed only to face stimuli.

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