

Animal and human faces in natural scenes: How specific to human faces is the N170 ERP component?

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The N170 is an event-related potential component reported to be very sensitive to human face stimuli. This study investigated the specificity of the N170, as well as its sensitivity to inversion and task status when subjects had to categorize either human or animal faces in the context of upright and inverted natural scenes. A conspicuous N170 was recorded for both face categories. Pictures of animal faces were associated with a N170 of similar amplitude compared to pictures of human faces, but with delayed peak latency. Picture inversion enhanced N170 amplitude for human faces and delayed its peak for both human and animal faces. Finally, whether processed as targets or non-targets, depending on the task, both human and animal face N170 were identical. Thus, human faces in natural scenes elicit a clear but non-specific N170 that is not modulated by task status. What appears to be specific to human faces is the strength of the inversion effect.

Keywords: N170, event-related potentials, rapid visual categorization, natural scenes, human faces, animal faces

Introduction

Several studies using event-related potentials (ERPs) have isolated a component, the N170, which appears to reflect a stage of visual processing at which objects are categorized. This component is a negative potential peaking at around 150-170 ms over lateral occipito-temporal electrodes. It is generally larger and peaks earlier in response to human faces compared to many other object categories (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Carmel & Bentin, 2002; George, Evans, Fiori, Davidoff, & Renault, 1996; Rossion et al., 2000; Sagiv & Bentin, 2001; Taylor, Edmonds, McCarthy, & Allison, 2001). The N170 is very sensitive to human faces and some authors have suggested that it reflects their early structural encoding before face recognition processes take place (e.g., Eimer, 1998, 2000a; Sagiv & Bentin, 2001). However, these conclusions are drawn from experiments that have mainly used central presentations of isolated and homogeneous stimuli (with the exception of Eimer, 2000b, e.g., who used peripheral presentations). Here we report the results from an experiment in which we investigated whether a N170 can be found for faces in the more realistic context of natural scenes. To this end, subjects were requested to categorize as fast and as accurately as possible human faces in briefly flashed photographs of natural scenes. For comparison, they performed a control task in which they had to categorize animal faces under the same conditions. According to

previous reports, a N170 of larger amplitude was expected in response to human faces compared to animal faces.

The N170 has also been found to be particularly affected by face inversion, contrary to other object categories. It is delayed for inverted faces compared to upright faces (Bentin et al., 1996; Eimer, 2000c; Itier & Taylor, 2002; Rebai, Poiroux, Bernard, & Lalonde, 2001; Rossion et al., 1999; Rossion et al., 2000). It is also delayed for faces with eyes removed (Eimer, 1998), during the analysis of single face components (Bentin et al., 1996; Jemel, George, Chaby, Fiori, & Renault, 1999), or when attention is directed to alphanumeric strings superimposed on the center of the face (Eimer, 2000c). N170 amplitude has been found to be larger in response to inverted than upright faces (Itier & Taylor, 2002; Rossion et al., 1999, 2000; Sagiv & Bentin, 2001). In relation with the behavioral literature, the effects of inversion on the N170 have been interpreted as reflecting the disruption of processing of the spatial relationships between face components (configural information; see more details in Itier & Taylor, 2002; Maurer, Le Grand, & Mondloch, 2002; Rossion & Gauthier, 2002). Hence, normal face perception would rely on mechanisms dedicated to the processing of upright face configural information. However, an enhancement of N170 amplitude has also been found for inverted houses (Eimer, 2000c), and various categories of real world objects (Itier, Latinus, & Taylor, 2003); and an increase in latency has been reported for inverted cars and words (Rossion, Joyce, Cottrell, & Tarr, 2003), suggesting that the inversion effect

might not be face specific (unlike results found by Rossion et al., 2000). In this study, we wanted to determine whether an inversion effect would occur with human and animal faces in natural scenes. To address this issue, half of the pictures were presented in an upright position, the other half were presented upside-down. According to some previous reports (Bentin et al., 1996; de Haan, Pascalis, & Johnson, 2002; Rebai et al., 2001; Rossion et al., 2000), an inversion effect was expected on the N170 for pictures containing a human face but not for those containing an animal face. However, a small inversion effect in response to animal faces was also possible given those found for various object categories (Eimer, 2000c; Itier et al., 2003; Rossion et al., 2003).

Finally, there is a controversy in the literature about whether the N170 can be modulated by task requirements, for example, when faces are given a target task status versus a non-target task status. Among the few studies that investigated this aspect, some have reported that the N170 does not seem to be modulated by task requirements (Carmel & Bentin, 2002; Séverac-Cauquil, Edmonds, & Taylor, 2000). However, top-down effects have also been reported on the N170, indicating that the neural mechanisms indexed by the N170 are not totally immune from high-level control (Bentin & Golland, 2002; Bentin, Sagiv, Mecklinger, & von Cramon, 2002; Eimer, 2000b, 2000c). To investigate this issue in the present experiment, targets of a given task were used as non-targets in the other task. For example, when subjects performed the human face categorization task, half of the non-targets were pictures of animal faces (and vice versa). We were thus able to compare the N170 elicited by a given category of faces when processed either as target or as non-target.

To summarize, the present study was designed to assess the specificity of the N170 for human faces in natural scenes as well as its sensitivity to inversion and to task status in such a context.

Methods

Participants

Twenty-four participants were tested (12 women and 12 men, mean age 30 years, ranging from 19 to 51 years; 3 of them were left handed). They volunteered in this study and gave their written informed consent. All participants had normal or corrected-to-normal vision.

Experimental procedure

Subjects sat in a dimly lit room at 100 cm from a computer screen (resolution, 800 × 600 pixels, vertical refresh rate, 75 Hz) controlled by a PC computer. To start a block of trials, they had to place their finger on a response pad for 1 s. A trial was organized as follows: a fixation cross (0.1° of visual angle) appeared for a 300-900 ms random duration and was immediately followed by the stimulus

presented for two frames (i.e., about 23 ms in the middle of the screen). Participants had to lift their finger as quickly and as accurately as possible (go response) each time a target was presented. Responses were detected using infrared diodes. Subjects had 1000 ms to lift their finger, after which their response was considered a no-go response. A black screen remained for 300 ms following this maximum response time delay, before the fixation point was presented again for a variable duration, resulting in a random 1600-2200 ms inter-trial interval. When the photographs contained no target, subjects had to keep their finger on the pad for at least 1000 ms (no-go response).

Subjects alternated between two categorization tasks, processing either human faces or animal faces as targets. They were asked to respond as fast as possible while minimizing errors. Each task consisted of one block of four consecutive series of 96 trials each. Half of the subjects performed the human face task first, while the other half started with the animal face task. Before each task, subjects were given a 48-trial training session.

All series of pictures (Figure 1) contained 50% targets and 50% non-targets. Among non-targets, half were neutral non-targets that had to be processed as such in both tasks and half were targets of the other task (i.e., human faces when subjects performed the animal face task and animal faces when they performed the human face task). Moreover, half of the images for each condition were presented upright while the other half were presented upside-down (rotation 180°).

A given subject saw each image only once, with one orientation (upright or inverted) and one status (target or non-target), but the design was counterbalanced for all conditions across the set of subjects to allow all data comparisons without any bias over the group of subjects or the sets of images.

Stimuli

We used photographs of natural scenes taken from a large commercial CD-ROM library (Corel Stock Photo Libraries 1 and 2; e.g., see Figure 1). All photographs were horizontal (768 × 512 pixels, sustaining about 19.8° by 13.5° of visual angle) and chosen to be as varied as possible. Animals included mammals, birds, fish, and reptiles. Human faces included Caucasian and non-Caucasian people. Animal and human faces were shown as close-ups in realistic conditions. The pictures could show more than one face and the faces were not necessarily centered. There was a very wide range of non-target images (neutral non-targets) that included outdoor and indoor scenes, natural landscapes, street scenes, pictures of food, fruits, vegetables, plants, buildings, tools and other man-made objects, as well as some more tricky non-targets (e.g., dolls, sculptures, statues, and a few non-target images containing humans for which the faces were not visible). In a given task, together with non-targets that were targets of the other task, these more ambiguous non-targets were used to assess the sophis-

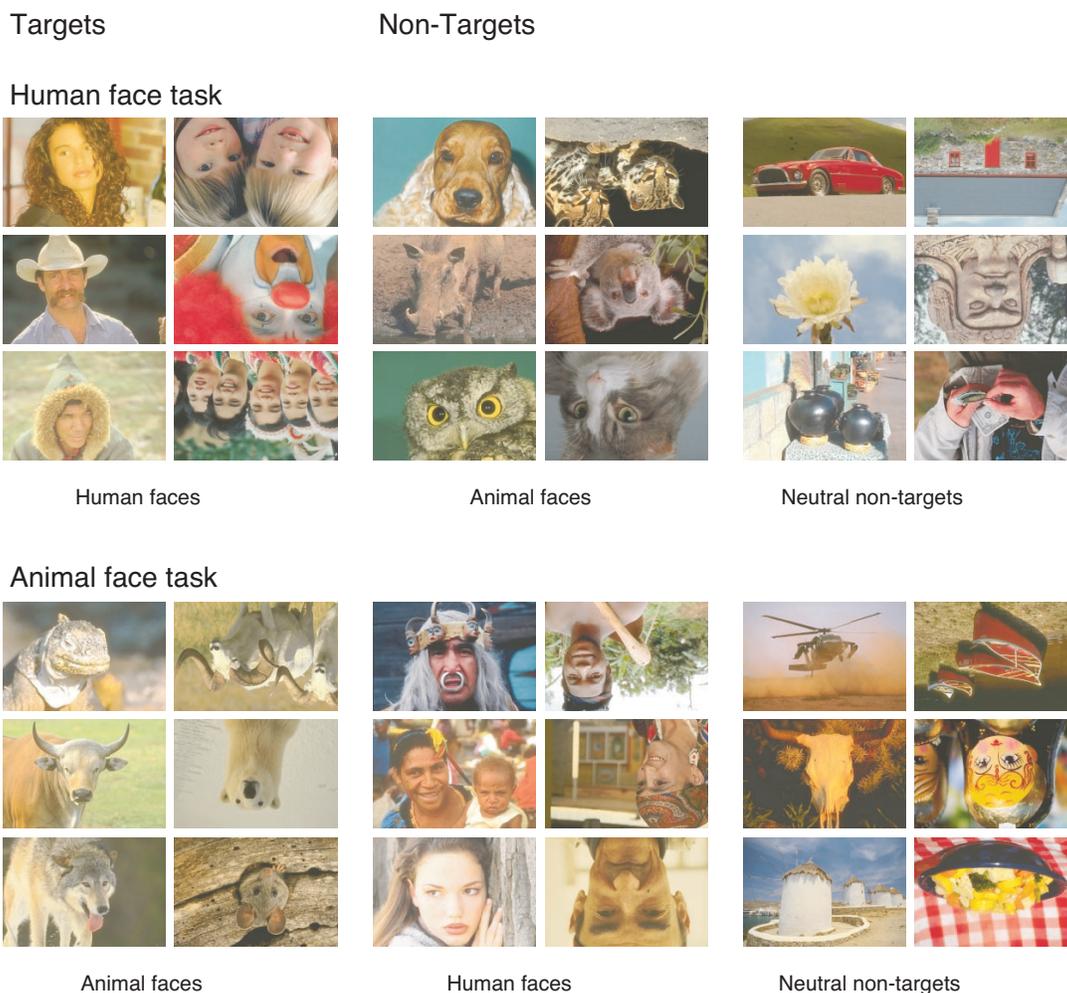


Figure 1. Examples of human, animal, and neutral non-target pictures used in the human face and the animal face categorization tasks.

tication of the behavioral responses triggered in our fast categorization task. See Rousselet, Macé, and Fabre-Thorpe (2003) for further discussion on this point.

Subjects had no a priori information about the presence, the size, the position or the number of targets in an image. Unique image presentation prevented learning.

Evoked-potential recording and analysis

Brain electrical activity was recorded from 32 electrodes mounted in an elastic cap in accordance with the 10-20 system (Oxford Instruments) with the addition of extra occipital electrodes, using a SynAmps amplifier system (Neuroscan). The ground electrode was placed along the midline, ahead of Fz, and impedances were systematically kept below 5 k Ω . Signals were digitized at a sampling rate of 1000 Hz (corresponding to a sample bin of 1 ms) and low-pass filtered at 100 Hz. Potentials were referenced on-line to the Cz electrode and averaged-referenced off-line. Baseline correction was performed using the 100 ms of pre-stimulus activity. Two artifact rejections were applied over the [-100 ms; +400 ms] time period, first on frontal elec-

trodes with a criterion of [-80; +80 μ V] to reject trials with eye movements, and second on parietal electrodes with a criterion of [-40; +40 μ V] to remove trials with excessive activity in the alpha range. Subjects were asked to minimize eye movements. Only correct trials were averaged. ERP components were low-pass filtered at 40 Hz before analysis.

ERPs were computed separately for correct target trials and correct non-target trials. We report results for the N170 at 6 temporo-occipital electrodes where its amplitude was maximal (left hemisphere: T5, O1', CB1; right hemisphere: T6, O2', CB2). Note that CB1-CB2 are referred as PO9-PO10 in the 10-10 system. For each experimental condition and each hemisphere, the peak latency was taken from the electrode that presented the highest peak amplitude. Amplitude was then measured at that latency for the remaining electrodes (Picton et al., 2000). Peak amplitudes and latencies were entered into omnibus ANOVA with task status (target vs. non-target), category (human face vs. animal face), orientation (upright vs. inverted), hemisphere (left vs. right), and electrode (3 levels, only for amplitudes) as within-subject factors. To compare the neutral non-target

N170 to the N170 associated with human and animal faces seen as non-targets, a non-target factor (neutral non-targets vs. non-target faces) was used instead of the task-status factor. Greenhouse-Geisser corrections were applied and post hoc *t*-tests were performed with a Bonferroni correction.

Results

The behavioral results associated with this experiment have been presented in a previous article (Rousselet et al., 2003, Experiment 2). Overall, very good performances were found in the human and in the animal task, which hardly differed from one another. The close similarity of behavioral results makes the ERP for these two categories perfectly comparable.

N170 in natural scenes: specificity and effect of task requirement

The most important result from these analyses is the finding of a large N170 in response to all faces in natural scenes (Figure 2 and Table 1). Its amplitude was much larger than the one recorded for very varied control natural scenes, confirming the sensitivity of the N170 to facial features (Figure 2B). In addition, the N170 was not modulated by task requirement (Figure 3).

A clear N170 was recorded following the presentation of upright human and animal faces when seen as targets

	Amplitude (μ V)		Latency (ms)	
	Left	Right	Left	Right
Up animal faces as targets	-2.3 (0.7)	-4.2 (0.6)	176 (3.3)	174 (2.5)
Inv animal faces as targets	-2.5 (0.6)	-4.3 (0.5)	177 (3.3)	178 (2.4)
Up animal faces as non-targets	-2.2 (0.6)	-4.3 (0.5)	177 (3.2)	176 (2.6)
Inv animal faces as non-targets	-2.4 (0.6)	-4.2 (0.5)	178 (3.2)	180 (2.4)
Up human faces as targets	-1.9 (0.6)	-3.8 (0.5)	168 (3.4)	169 (2.2)
Inv human faces as targets	-3.0 (0.6)	-5.7 (0.5)	173 (3.4)	174 (2.4)
Up human faces as non-targets	-1.7 (0.6)	-3.6 (0.5)	168 (3.0)	169 (2.7)
Inv human faces as non-targets	-2.9 (0.6)	-5.3 (0.5)	176 (3.0)	175 (2.3)
Up neutral non-targets	0.3 (0.6)	-0.6 (0.4)	172 (3.5)	173 (2.7)
Inv neutral non-targets	-0.3 (0.6)	-1.2 (0.5)	173 (3.4)	176 (2.6)

Table 1. Summary of N170 mean peak amplitudes and latencies. Results are reported for each hemisphere separately and values were averaged over the three electrode sites from which the peaks were measured. SE is indicated in brackets. Up = upright, Inv = inverted.

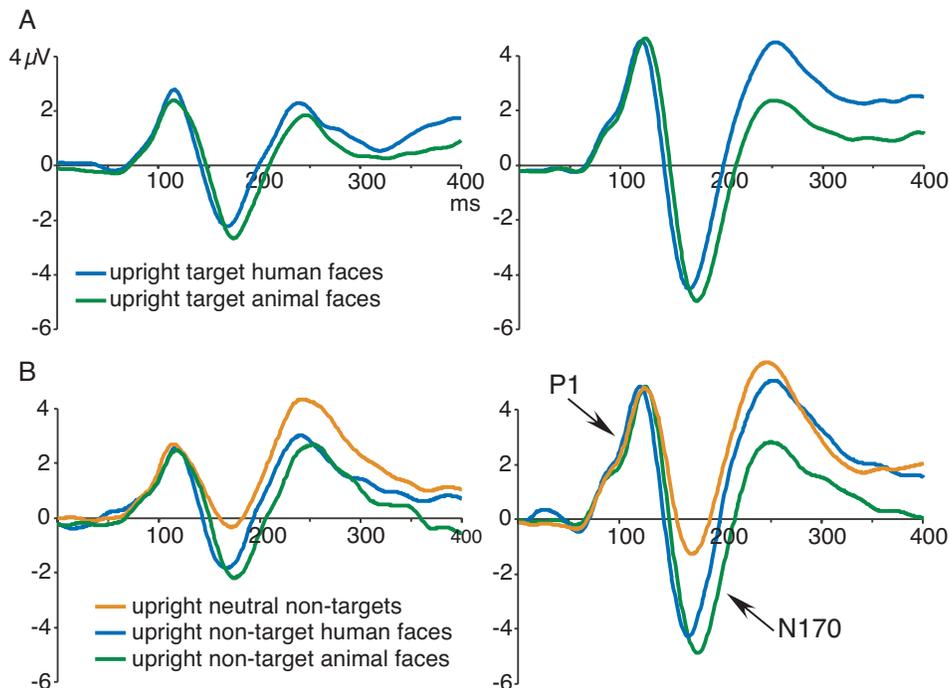


Figure 2. N170 specificity. Grand averages across 24 subjects showing the N170 at electrodes T5 (left) and T6 (right) where it had the largest amplitude. A. N170 associated with the presentation of upright human and animal faces seen as targets. B. N170 associated with the presentation of upright neutral non-targets and upright human and animal faces seen as non-targets. Note that the N170 was preceded by a large P1 component. Results for this component are not reported in this work.

(Figure 2A and Table 1). The N170 amplitudes in these two conditions did not differ significantly from one another ($F(1, 23) = 3.1$, $p = .09$), although the N170 for animal faces was on average $0.4 \mu\text{V} \pm 0.25 \mu\text{V}$ (SE) larger than the N170 for human faces (Figure 2A). The N170 latency was $6 \text{ ms} \pm 1.3 \text{ ms}$ shorter for human than animal upright targets ($F(1, 23) = 23.0$, $p < .0001$). No significant effect of task status was seen on either N170 peak amplitude ($F(1, 23) = 2.9$, $p = .10$) or latency ($F(1, 23) = 2.0$, $p = .17$) (Figure 3). Thus, the same effects reported for upright target faces were also found for upright non-target faces (Figure 2B and Table 1): there was a non-significantly larger N170 amplitude for animal faces compared to human faces seen as non-targets (difference = $0.6 \mu\text{V} \pm 0.3 \mu\text{V}$; $F(1, 23) = 3.3$, $p = .08$; Figure 2B), while N170 latency was $8 \text{ ms} \pm 1.2 \text{ ms}$ shorter for human than for animal pictures ($F(1, 23) = 48.1$, $p < .0001$).

The N170 elicited by human and animal faces when seen as non-targets was $2.9 \mu\text{V} \pm 0.2 \mu\text{V}$ larger than the one recorded in response to neutral non-targets (Figure 2B and Table 1), as shown by a significant amplitude effect between human and animal face N170 and neutral non-target N170 ($F(1, 23) = 211.7$, $p < .0001$). This effect was stronger over right (difference = $3.5 \mu\text{V} \pm 0.3 \mu\text{V}$) than left ($2.3 \mu\text{V} \pm 0.2 \mu\text{V}$) hemisphere electrodes ($F(1, 23) = 9.8$, $p = .005$). The neutral non-target N170 was significantly more prominent at sites T5-T6 (on average $+1.9 \mu\text{V} \pm 0.4 \mu\text{V}$ compared to O1'-O2' and CB1-CB2; $F(2, 46) = 21.0$, $p < .0001$). Upright human and animal faces whether seen as targets or non-targets were associated with

a larger N170 at sites CB1-CB2 and T5-T6 (difference = $2.4 \mu\text{V} \pm 0.3 \mu\text{V}$ compared to O1'-O2'; $F(1.8, 40.3) = 24.7$, $p < .0001$), with a non-significantly larger amplitude observed at T5-T6 relatively to CB1-CB2. In addition, the N170 amplitude in these conditions was larger over right hemisphere electrodes (difference = $2 \mu\text{V} \pm 0.6 \mu\text{V}$; $F(1, 23) = 9.7$, $p = .005$).

Effects of inversion on the N170

The effect of inversion was studied on animal faces and human faces seen both as targets or non-targets and on neutral non-targets that did not contain any face.

When human and animal faces were compared, the N170 amplitude was enhanced by inversion of both targets and non-targets, but this effect was restricted to human pictures as shown by a significant interaction between category and orientation factors ($F(1, 23) = 33.5$, $p < .0001$; target human face difference = $1.6 \mu\text{V} \pm 0.2 \mu\text{V}$, $F(1, 23) = 43.8$, $p < .0001$; non-target human face difference = $1.5 \mu\text{V} \pm 0.3 \mu\text{V}$, $F(1, 23) = 27.0$, $p < .0001$) (Figure 4A). No amplitude effect was observed for animal faces ($F(1, 23) = 0.5$, $p = .5$) (Figure 4B). This interaction also means that the N170 was on average larger in response to inverted human faces than inverted animal faces (difference = $0.9 \mu\text{V} \pm 0.2 \mu\text{V}$).

The latency of the N170 peak was shorter for upright than for inverted faces, a result that again was not affected by task status ($F(1, 23) = 56.3$, $p < .0001$) (Figure 4A and 4B). An interaction between category and orientation factors ($F(1, 23) = 7.2$, $p = .013$) revealed that this effect was

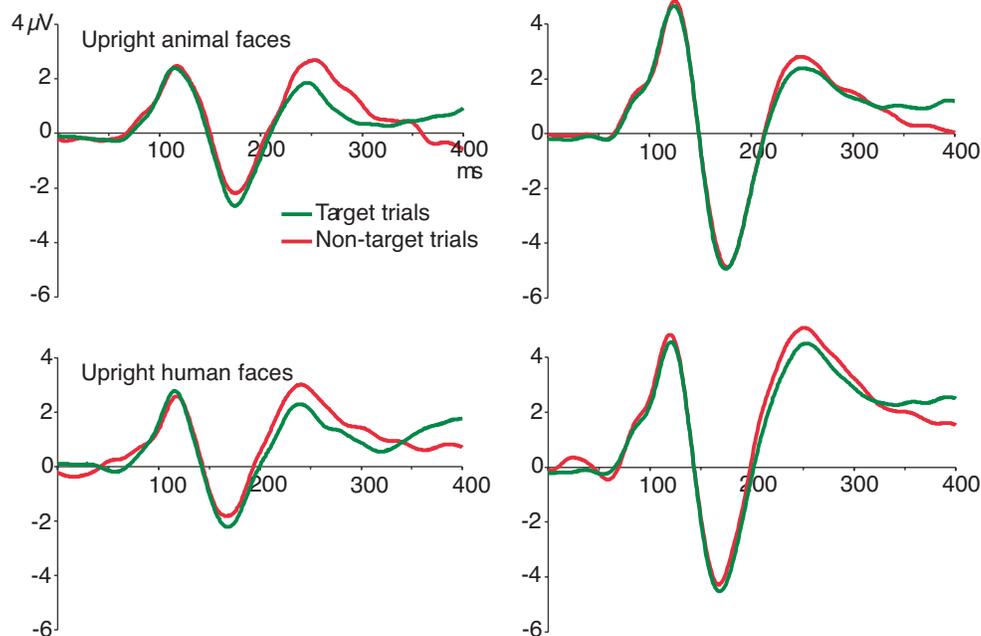


Figure 3. Task status effect. Grand averages across 24 subjects showing the N170 at T5 (left) and T6 (right) sites for correct trials. ERP components following the presentation of a given category with a target and a non-target task status are compared.

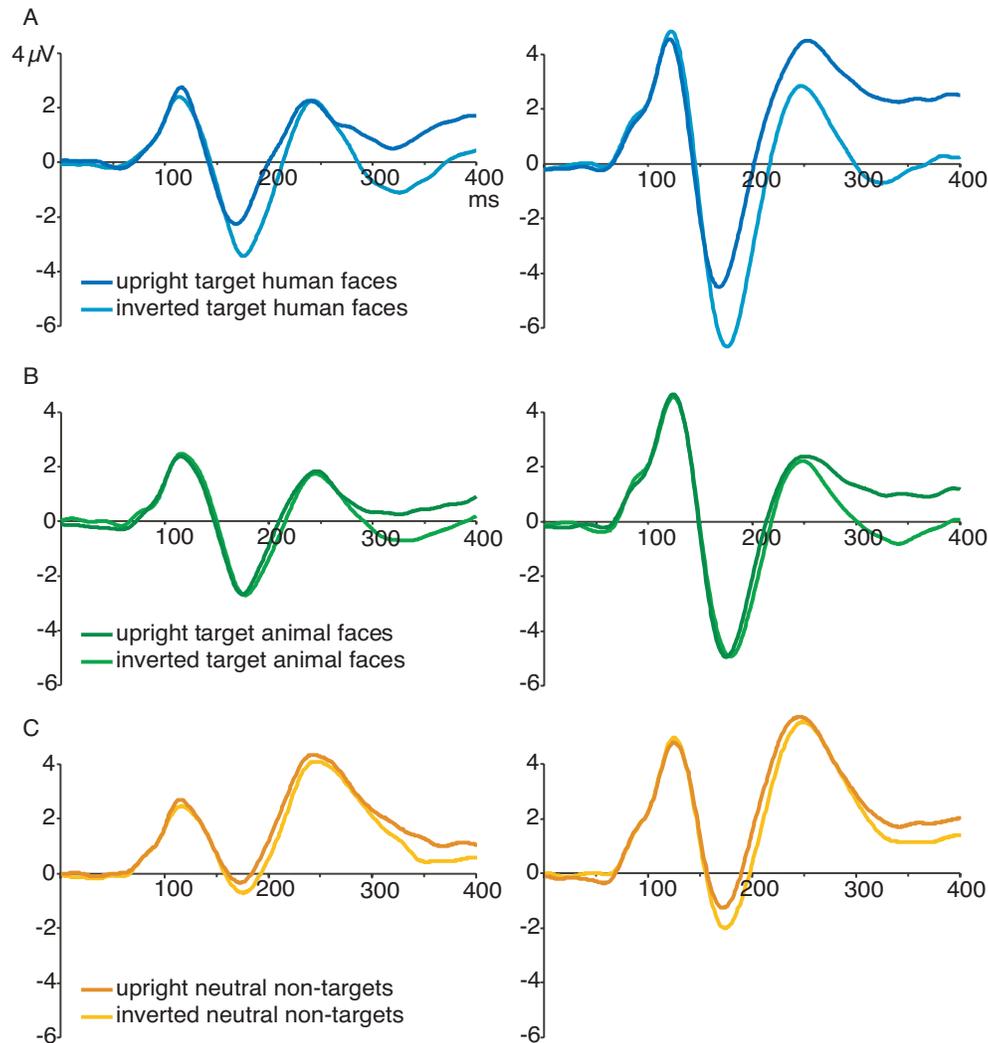


Figure 4. Inversion effect. Grand averages across 24 subjects showing the N170 at T5 (left) and T6 (right) sites for correct trials. ERPs following the presentation of upright and inverted pictures are compared separately for human targets (A), animal targets (B), and neutral non-targets (C). ERPs for human and animal faces processed as non-targets are not shown because they were associated with the same N170 effects.

stronger for human faces (+6 ms \pm 1 ms; target human faces: $F(1, 23) = 16.7, p < .0001$; non-target human faces: $F(1, 23) = 27.3, p < .0001$) than for animals (+3 ms \pm 1 ms; target animal faces: $F(1, 23) = 7.1, p = .01$; non-target animal faces: $F(1, 23) = 6.7, p = .02$) (Figure 4), regardless of whether they were seen as targets or as non-targets.

We also analyzed the N170 for upright and inverted neutral non-targets (Figure 4C). There was no effect of inversion on the latency of the neutral non-target N170 ($F(1, 23) = 1.5, p = .2$). Surprisingly, its amplitude was significantly enhanced by inversion (+0.6 μV \pm 0.2 μV ; $F(1, 23) = 6.3, p = .002$), but to a lesser extent than for the human face N170 (significant interaction between non-target, category, and orientation factors, $F(1, 23) = 15.4, p = .001$).

Discussion

This study was aimed at analyzing the N170 recorded in response to human and animal faces in upright and inverted natural scenes. The main results are the following:

(1) It is shown for the first time that there is a clear N170 component for faces of very different kinds presented in the context of natural scenes.

(2) Extending the results from some previous reports, the N170 does not appear to be specific to human faces, being here of similar amplitude in response to a large set of animal faces.

(3) Strong inversion effect that increased both the N170 latency and its amplitude was seen in response to human faces. With other stimuli the inversion effect was reduced and restricted to the amplitude effect with neutral non-targets and to the latency effect with animal faces.

These two points confirm results from some earlier studies and suggest that what appears to be specific to human faces is not the N170 or the inversion effect, but rather the strength of the inversion effect.

(4) Confirming some previous findings, the N170 recorded in response to human faces does not appear to be affected by task status. This result is here extended to animal faces. Although a definitive conclusion about this null effect is premature, it could reflect the fact that, compared to other objects, faces are processed by default up to a higher level of representation without requiring specific attention.

The presentation of close-up views of human faces in the context of natural scenes was associated with a clear N170. The amplitude of this signal was much larger than the one recorded following the presentation of a large range of control scenes containing various kinds of objects. Thus it appears that there is a “N170 effect” even in the context of natural scenes. This larger amplitude in response to human faces compared to control objects has been used as the hallmark of the N170 face specificity (e.g., Bentin et al., 1996).

However, the N170 recorded in the present experiment did not appear to be specific to human faces. Indeed, its amplitude was not different from the one recorded in response to animal faces. This means that the N170 itself is not specific to human face features as already stated previously by others (Rossion et al., 2000). However, the N170 presented a maximum earlier for human faces compared to animal faces. In previous experiments, the N170 has been reported to be either larger and delayed (de Haan et al., 2002) or just delayed (Carmel & Bentin, 2002) following the presentation of upright monkey and ape faces, respectively. Because delayed and enhanced N170 have been taken as evidence for the disruption of configural mechanisms dedicated to the processing of upright faces (Eimer, 2000a; Itier & Taylor, 2002; Rossion et al., 1999), de Haan et al. (2002) postulated that monkey faces were somehow equivalent to inverted human faces, disturbing the canonical human face configuration. On the other hand, Carmel and Bentin (2002) concluded that the N170 reflects the involvement of a mechanism triggered by every stimulus sharing the same spatial organization as a human face. The results from the present study indicate that this spatial organization might be relatively coarse, including facial characteristics from very various kinds of animals seen from different viewing angles.

The shorter N170 latency in response to human faces might also be taken as evidence for a sensitivity of this component to the precise configuration of the human face (Carmel and Bentin 2002; see also Eimer, 1998, 2000a). In this context, a delayed N170 for animal faces would imply a delayed analysis of their features and their spatial relations. However, the difference in peak latency between the two categories, although highly significant, was very limited (6-8 ms). Furthermore, human and animal faces in this study were processed at the same speed according to behavioral

data (Rousselet et al., 2003). Thus, a very simple explanation cannot be ruled out, namely that this delay would be due to a higher variability in animal pictures (all kinds of vertebrates were used) compared to more homogeneous human pictures. As a result of the averaging process by which ERPs were computed, this might be reflected in a slightly delayed N170 peak latency for animal face pictures compared to human face pictures.

Although the present results do not support the hypothesis that the N170 is specific to human faces, the strength of the inversion effect was quite specific to human face pictures. Indeed, although inversion of animal faces and neutral non-targets increased the latency and the amplitude of the N170, respectively, these effects were of much smaller magnitude than those found for human faces.

Thus, even if there is growing evidence for the existence of N170 inversion effects for stimuli other than human faces (Eimer, 2000c; Itier et al., 2003; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002; Rossion et al., 2003), a systematic inversion effect of large amplitude seems to be the hallmark of human faces.

The larger N170 amplitude with inversion might be due to inverted faces recruiting additional population of neurons with broader selectivity compared to upright faces that would activate only face-selective neurons (Rossion et al., 1999). On the other hand, recent studies by Itier and Taylor (2004) and Watanabe, Kakigi, and Puce (2003) suggest that upright and inverted faces activate the same areas but with a slower time course in the last case. These authors also conclude that areas in the lateral temporal cortex, around the superior temporal sulcus, are important generators of the N170. Furthermore, the location of the electrodes recording maximal N170 (such as T5-T6 in the present experiment) is optimal to capture the activity of those brain areas (Bentin et al., 1996). Given the functional properties of these lateral cortical areas (Allison, Puce, & McCarthy, 2000), the N170 might be linked to the processing of eye gaze, as well as face expression, emotion, and other biological cues. Now, one can hold the plausible assumption that by default this lateral network would find an attractor corresponding to one or a combination of those properties. Thus, from a computational point of view, the larger N170 amplitude with inversion might be due to the massive recruitment of collaterals in an auto-associative network trying to find a stable attractor. The weak inversion effect for objects might be explained by the relative specificity of this network to human faces. One can also advance the hypothesis that the presence of eyes in animal faces might be sufficient to produce a large N170, in keeping with data suggesting that the N170 is in part an automatic response to eyes (Bentin et al., 1996; Schyns, Jentsch, Johnson, Schweinberger, & Gosselin, 2003; but see Eimer, 1998).

Surprisingly, despite a larger inversion effect for human faces compared to animal faces, the behavioral results associated with these two categories revealed a similar drop in

accuracy ($-0.6\%/ -0.3\%$, respectively) and mean reaction times ($+14\text{ms}/+10\text{ms}$, respectively) with inverted stimuli (Rousselet et al., 2003). Further investigations will be necessary to establish the relationship between the N170 and the behavioral performance in face categorization tasks.

Another interesting result reported here is the absence of an effect of task status on the N170 for either human or animal faces. This might be taken as evidence that, by default, faces are processed to a high level of representation whether or not they are pertinent for the ongoing activity (Tanaka, 2001). The absence of task status on the N170 is in keeping with previous reports that explored the effects of top-down processing on face ERP (Carmel & Bentin, 2002; Séverac-Cauquil et al., 2000; and see Puce, Allison & McCarthy, 1999, for intracranial recordings). However, it contradicts other findings showing that task requirements can modulate the N170 (Eimer, 2000b, 2000c; Bentin & Golland, 2002; Bentin et al., 2002). The absence of task-status effect on the N170 in the present study might find its origin in the relative simplicity of the tasks employed. Indeed, behavioral results (Rousselet et al., 2003) indicate that human subjects are fast and especially accurate at categorizing faces and animals in natural scenes. On the contrary, Eimer found effects related to task status when using demanding comparison tasks (Eimer, 2000b) and a difficult detection task of red digits superimposed on black and white faces (Eimer, 2000c). Thus, the N170 modulation linked to the status of faces in various tasks might be correlated to specific requirements and may be observed only when face processing needs to reach a high level of detailed visual analysis.

These results seem to be at odds with previous reports showing that animals and other targets can start to be discriminated at about 150 ms in natural images (Thorpe, Fize, & Marlot, 1996; VanRullen & Thorpe, 2001). In the present experiment, the first task-status effects were found at about 170 ms for human faces and even later, around 230 ms, for animal faces (Rousselet, Macé, Thorpe, & Fabre-Thorpe, 2003). However, when a given category seen as target was compared to the other category seen as non-target, both human and animal faces were associated with early effects with onsets as short as 120-140 ms. Moreover, the onset latencies of these early ERP effects might be related to the subjects' reaction times, contrary to what was reported recently by Johnson and Olshausen (2003). Thus, although the visual system might be able to start to discriminate very early between animal and human faces, faces might be processed by default to a higher level of representation such that the associated ERPs are not modulated easily by task status.

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