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Electrophysiological correlates of facial decision: insights from upright and upside-down

Mooney-face perception

GEORGE Nathalie, JEMEL Boutheina, FIORI Nicole, CHABY Laurence and RENAULT Bernard

Nathalie GEORGE^{CA} and Bernard RENAULT

Unité de Neurosciences Cognitives et Imagerie Cérébrale, CNRS UPR 640 – LENA, Paris and
Université Paris 6, Paris, France

Boutheina JEMEL

Hôpital Rivière des Prairies, Centre de Recherche Fernand Seguin, Université de Montréal,
Montréal, Canada

Laurence CHABY and Nicole FIORI

Unité de Neurosciences Cognitives et Imagerie Cérébrale, CNRS UPR 640 – LENA, Paris and
Université Paris 5, Boulogne-Billancourt, France

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Corresponding author : Nathalie GEORGE

CNRS UPR 640 – LENA

Hôpital de la Salpêtrière

47 bd de l'Hôpital

75651 Paris cedex 13

FRANCE

Tel: +33 1 42 16 11 69, Fax: +33 1 45 86 25 37, E-mail: Nathalie.George@chups.jussieu.fr

Webpage: <http://www.ccr.jussieu.fr/cnrs-upr640-lena/>

ABSTRACT

We investigated the ERP correlates of the subjective perception of upright and upside-down ambiguous pictures as faces using two-tone Mooney stimuli in an explicit facial decision task (deciding whether a face is perceived or not in the display). The difficulty in perceiving upside-down Mooneys as faces was reflected by both lower rates of “face” responses and delayed “face” reaction times for upside-down relative to upright stimuli. The N170 was larger for the stimuli reported as “faces”. It was also larger for the upright than the upside-down stimuli only when they were reported as faces. Furthermore, facial decision as well as stimulus orientation effects spread from 140-190 ms to 390-440 ms. The behavioural delay in ‘face’ responses to upside-down stimuli was reflected in ERPs by later effect of facial decision for upside-down relative to upright Mooneys over occipito-temporal electrodes. Moreover, an orientation effect was observed only for the stimuli reported as faces; it yielded a marked hemispheric asymmetry, lasting from 140-190 ms to 390-440 ms post-stimulus onset in the left hemisphere, and from 340-390 to 390-440 ms only in the right hemisphere. Taken together the results supported a preferential involvement of the right hemisphere in the detection of faces, whatever their orientation. By contrast, the early orientation effect in the left hemisphere suggested that upside-down Mooney stimuli were processed as non face objects until facial decision was reached in this hemisphere. The present data show that face perception involves not only spatially but also temporally distributed activities in occipito-temporal regions.

Classification terms:

Theme I: Neural Basis of Behaviour - Topic: Cognition

Keywords: Faces; Facial decision; Orientation; Perception; Event related potentials

1. INTRODUCTION

In this study we investigated the ERP correlates of the subjective perception of upright and inverted ambiguous pictures as faces. Faces are particularly important stimuli in our visual environment as they convey a wealth of information essential to interindividual interactions [see also 52]. Thus the perception of faces appears as a crucial process in visual cognition, and it seems to involve specific processing mechanisms that are achieved very automatically and efficiently by human subjects. For example, whereas most visual objects are usually processed at a basic categorical level, faces are fundamentally processed at the individual level and this requires very fine discrimination processes; faces constitute a homogeneous category of visual objects – all sharing a common spatial structure (two eyes above a nose itself above a mouth). These processes appear to rely crucially on the extraction of configural and shape-from-shading information [6,10,22,31,43,48,53], and face perception has been shown to involve specialised brain regions within the ventral occipito-temporal cortex, such as the fusiform gyrus [e.g. 18,20,21,29,36,41], as well as within the lateral occipital and temporal cortices [1,11,13,21,29,42].

Using event-related potentials (ERPs), it has been shown that the perception of faces relative to other visual objects is reflected by an early negative component peaking over occipito-temporal regions around 170 ms. The so-called N170 is of maximal amplitude and minimal latency in response to faces relative to non face objects. Its cerebral generators would involve different regions of the ventral and lateral occipito-temporal cortex [15]. Bentin et al. proposed that the N170 may be related to the detection of eye features or to the mere detection of faces based on first-order relations and holistic processing [3,47]. However, other authors provided some evidence that the N170 is related to late stage of face structural encoding [12] and it has been proposed that earlier activities – around 100ms – would be associated to facial

categorisation or perceiving general facial configuration [19,23,32,33]. Moreover, electrophysiological correlates of face perception may well extend beyond the N170 time range. In a previous study using normal and moderately scrambled faces we have shown that the encoding of the latter relative to the former was reflected by sustained occipito-temporal ERP responses from 150 ms until 350 ms after stimulus onset [15]. Although not analysed, sustained responses associated with the perception of natural upright faces relative to inverted and schematic faces can also be observed in Sagiv and Bentin (2001 [47]; see Figure 3 of that paper). Intracerebral recordings have also shown that both early (~200ms) and late (~350 and 700ms) evoked potentials in response to faces can be recorded from discrete regions of the posterior ventral and lateral occipito-temporal cortices [1].

This raises the question of the relationship of the N170 and occipito-temporal responses with the subject's overt perception of a face or facial decision. Using priming paradigms, Bentin and colleagues have recently shown that N170 could be elicited by distorted or very schematic partial patterns following the presentation of the corresponding normal faces [4,5]. However this priming effect was automatic and the subjects' perception was not assessed. Jemel et al. [28] also used degraded faces and showed a proportional increase of the N170 with decreasing noise but their study focused on familiarity recognition. There is also evidence that the N170 may be automatically evoked by faces even when these are not consciously perceived [50]. However, does the subject's overt facial decision (report of a stimulus as a face versus a non face) further modulate the N170 and/or occipito-temporal responses in a different time range? Thus we were interested in the behaviour of the N170 and occipito-temporal responses in an explicit facial decision task using ambiguous pictures yielding variable subject's report of perceiving a face or not.

We used a set of stimuli which are in fact all faces but are more frequently and easily overtly perceived as such or not depending on their orientation [see 2,30]. Mooney stimuli are

two-tone figures constituted only by the shadow (in black) and light (in white) pattern obtained from asymmetrically lighted photographs of faces [38]. Thus they contain few explicit local features of faces (see Figure 1). However, they are usually easily perceived as faces when presented upright, whereas, by contrast, turning them upside-down makes their perception as faces less frequent and much more difficult. This effect was here assessed behaviourally. Our assumption was that the difficulty in perceiving upside-down stimuli as faces would be associated with delayed facial decision (i.e. increased “face” response times). Moreover, in an effort to disentangle the effect related to the subject’s overt facial decision from that related to the stimulus orientation, we analysed separately the ‘yes’ and ‘no’ facial decision responses for upright and upside-down stimuli respectively. Although these responses were unevenly distributed over upright and upside-down Mooneys, the use of a high number of trials allowed us to obtain the Event-Related Potential under these four conditions and therefore to investigate the electrophysiological correlates of the overt perception of upright and upside-down Mooney stimuli as faces or non faces. It is possible that the N170 would be automatically associated with the subject’s report of perceiving a face independently of the “face” response time. However, the delay in face perception for upside-down Mooney stimuli should be reflected by the time course of the occipito-temporal evoked responses related to facial decision (“face versus “no face” responses) for upside-down relative to upright stimuli. As orientation strongly interferes with face perception in Mooneys, we were also interested in stimulus orientation effects. We expected that only stimuli perceived as meaningful (“faces”) would yield orientation effects. The effects obtained are also discussed in terms of the differences in the brain regions involved in the perception of upright versus upside-down Mooneys as faces.

Part of these data have been used for another analysis [16]. This paper focused specifically on repetition effects for upright “faces” and upside-down “non faces” and did not

investigate facial decision and stimulus orientation effects. The eventual relationship between repetition effects [16] and the effects reported here will be addressed in discussion.

2. MATERIALS AND METHOD

Subjects

Thirteen healthy volunteers (7 females; age = 20 to 30 y.o.) participated in this experiment. All subjects were right-handed (according to a card distribution test), had a right predominant eye and normal or corrected-to-normal vision. They were fully informed of the recording technique, methods and proceedings before agreeing to participate in this non-invasive experiment which was approved by the French Comité Opérationnel pour l’Ethique dans les Sciences de la Vie of the Centre National pour la Recherche Scientifique (CNRS).

Stimuli

A hundred sixty upright and the corresponding 160 upside-down stimuli were used (Figure 1). They were constituted of the 40 faces of Mooney (1957 [37]) presented twice in their original way and twice after vertical mirroring. All stimuli were presented on slides back-projected onto a screen in the recording room using a slide projector with an electronic shutter (constant 3-ms opening delay). Visual angles subtended by the stimuli were approximately 7 degrees horizontally and 10 degrees vertically.

Insert Figure 1 about here

Procedure

Subjects sat on a comfortable chair in a dimly lit room. They were instructed to fixate a central point on the screen (distance: 1m30) within each block of successive stimuli and to report whether they perceived a face or not whatever its orientation, with a two-alternative button-press response, for each stimulus. The instruction insisted on responding as quickly as possible and on reporting subjective perception at first glance. Debriefing indicated that face perception was indeed mostly rapid or did not happen. In the rare occasions where subjects changed their mind or pressed the wrong button by mistake, they reported it by pressing the at-first-non-selected button (double response). Half the subjects gave the “face” response with the right forefinger and the “no face” response with the left forefinger; this was reversed for the other half. Each block started by the presence of a 30dB white noise in the headphones which remained during the whole block duration. After a training block, subjects were given 8 experimental blocks of 40 trials. During each block, each of the 40 different Mooney stimuli was presented once (either upright or upside-down, vertically mirrored or not), for 200 msec each, with a random inter-stimulus interval between 2000 and 3500 msec. The first four blocks were constituted of the 40 Mooney stimuli seen once in their original way and once vertically mirrored in the upright and in the upside-down orientation (with a different random order of the 40 different Mooney stimuli within each block), and the last four blocks were the repetition of the first four ones. All subjects saw the same random succession of stimuli.

Data collection

Subjects’ behavioural responses and the electroencephalogram (EEG) were recorded on-line by a PC 386-33MHz. “Face” and “No face” responses were counted separately for upright and upside-down stimuli. Double button press indicating a change in subject’s response were discarded. Only trials with response times (RTs) longer than 200 ms and shorter than 2000 ms were analysed. EEG was recorded from 30 electrodes at standard EEG-placement (Fz, Cz, Pz, Oz, FC1-FC2, FC5-FC6, C3-C4, T7-T8, CP1-CP2, CP5-CP6, P3-P4,

P7-P8, PO3-PO4), including a row of low temporo-occipital electrodes (M1-M2, P9-P10, PO9-PO10, O9-O10), with respect to a nose reference. Eye movements and blinks (EOG) were recorded by two bipolar leads placed above and below the right eye and at the outer canthi of both eyes. The EEG was band-pass filtered between 0.08 and 160Hz and sampled at 500Hz. After removal of EEG artifacts, vertical eye movements and blinks were corrected by an automatic eye-movements correction program [17]. The length of the averaging window was 1200 msec with a 200-msec pre-stimulus baseline. ERPs were computed separately for the “Face” and “No face” responses for the upright and upside-down stimuli respectively (mean number of averaged trials = 119 ± 3 for “Face” / 31 ± 3 for “No face” for upright stimuli, and 36 ± 3 / 114 ± 3 for upside-down stimuli). Despite the uneven number of averaged trials in each condition, the visual inspection of individual waveforms indicated that the ERPs were clearly identifiable and comparable between the four different experimental conditions and the digital filtering of the data allowed to level the signal-to-noise ratio. The data were filtered with a low-pass filter (half-amplitude cut-off = 27.5Hz) and displayed off-line in the form of chronograms and scalp potential (SP) maps. At each time instant SP maps are obtained by a spherical spline interpolation of the ERP value on each electrode site [40]. The grand average of the ERP for the 13 subjects was also calculated.

Data analysis

Regarding behavioural data, the percentage of “Face” responses was submitted to a repeated-measure analysis of variance (ANOVA) with the stimulus orientation (upright / upside-down) as within-subject factor. The RTs were submitted to a two-way ANOVA with the subject’s facial decision (“Face” / “No face”) and the stimulus orientation (upright/upside-down) as factors. Regarding ERP data, we performed measurements of the peak latency and amplitude of early components. The latency and amplitude of the maximum peak of the P1 visual wave were measured between 80 and 140 ms over posterior parieto-occipital regions in

both hemispheres (O9 / PO9 / PO3 on the left; O10 / PO10 / PO4 on the right). These measurements were analysed with a three-way ANOVA including facial decision, stimulus orientation and hemisphere (left/right) as factors. The latency and amplitude of the occipital peak of the visual N1 was measured at Oz between 130 and 180 ms. The latency and amplitude of the maximum temporal peak of the N1 (N170) were measured over the row of low temporo-occipital electrodes in both hemispheres (M1/2-P9/10-PO9/10-O9/10) between 140 and 220 ms. We first analysed the parameters (amplitude and latency respectively) of the occipital and bilateral temporal peaks of the N1 using multivariate analyses of variance (MANOVAs) with facial decision, stimulus orientation, and electrodes (Oz / Left temporal / Right temporal) as factors in order to test for systematic differences between the amplitude (respectively the latency) of the occipital and temporal peaks of the N1. Then, the effect of facial decision and stimulus orientation were analysed separately for the occipital N1 and the temporal N170 waves using ANOVAs. For the latter component, the hemisphere was also introduced as a within-subject factor. The peak amplitude and latency of the Vertex Positive Potential (VPP) and of the occipital P2 were also measured. The maximum peak of the VPP was picked over the vertex region (C3-Cz-C4) between 170 and 240ms whereas that of the occipital P2 was measured over PO3-Oz-PO4 between 200 and 300ms. These components' parameters were analysed using ANOVAs with facial decision and stimulus orientation as within-subject factors. For the P2, we computed also the correlation between its amplitude and the mean amplitude of occipito-temporal responses (over P9/10-PO9/10) between 240-290ms. Moreover, mean ERP amplitude measurements were performed over P9-PO9 and P10-PO10 in six successive 50-ms time windows: 140-190 ms, 190-240 ms, 240-290 ms, 290-340 ms, 340-390 ms, 390-440 ms. These were analysed using a MANOVA with facial decision, stimulus orientation, hemisphere and time window as factors followed by planned

comparisons (ANOVAs) in each time window and hemisphere with facial decision and stimulus orientation as factors. Mean values \pm standard errors (SE) are reported.

3. RESULTS

Behavioural results

As expected, upright Mooney stimuli were most often perceived as faces while reciprocally upside-down stimuli were predominantly perceived as non faces ($F_{[1,12]}=531.6$, $p<10^{-6}$; Table 1). Most importantly, stimulus orientation affected facial decision times: “Face” responses were given much faster for upright than upside-down Mooneys ($F_{[1,12]}=126.8$, $p<.0001$). There was no such effect when the stimuli were reported as non faces ($F<1$; Table 1) and the interaction between Facial decision and Stimulus orientation was highly significant ($F_{[1,12]}=199.7$, $p<.0001$).

Insert Table 1 about here

Electrophysiological results :

Peak measurements: P1, N1/N170, VPP, P2

The ERPs to upright and upside-down stimuli reported or not as faces showed the well-known succession of early visual evoked potentials with an occipital P1 followed by the N1 component which emerged occipitally and spread laterally yielding the bilateral temporal peaks of the so-called N170 (Figure 2).

Insert Figure 2 about here

As there has been recent reports of facial configuration effect on P1 [19,23,24], we first measured P1 peak latency and amplitude over bilateral occipito-parietal regions. This showed that the P1 culminated globally at $7.06 \pm 0.82 \mu\text{V}$ around 114 ± 3 ms in both hemispheres. Its amplitude was modulated neither by face (relative to no face) perception nor by stimulus orientation nor as a function of hemisphere (all $p > .05$) and its latency was similar in every condition (Table 2a).

We then turned to the analysis of the N1/N170 occipital and temporal peaks. In order to spatio-temporally characterise the onset of facial decision and stimulus orientation effects, we measured the amplitude and latency of the occipital peak of N1 on Oz as well as that of the bilateral temporal peak of the N170 picked on the row of inferior occipito-temporal electrodes (M1/2, P9/10, PO9/10, O9/10). The occipital peak of N1 was observed around 164 ms while the temporal peak of the N170 culminated on P9-PO9 (left) and P10-PO10 (right) around 183 ms (see Table 2). A MANOVA with electrodes (Oz, right occipito-temporal, left occipito-temporal) as within-subjects factor confirmed that the temporal N170 peaked significantly later than the occipital N1 ($F_{[2,11]}=10.96$, $p < .003$). Moreover the occipital peak of N1 was significantly smaller (mean effect = $4.20 \pm 1.02 \mu\text{V}$) than the temporal peaks of the N170 ($F_{[2,11]}=9.33$, $p < .005$). Importantly, the ANOVAs performed on the amplitude and latency of the N1 peak on Oz yielded no effect of facial decision nor of stimulus orientation as well as no interaction between these factors (all $p > .10$; Table 2b). By contrast, the temporal peaks of the N170 were larger when the stimuli were reported as faces than when they were not reported as such ($F_{[1,12]}=4.80$, $p < .05$; Fig. 3 and Table 2c). There was also a close-to-significance interaction between facial decision and orientation on N170 peak amplitude ($F_{[1,12]}=4.51$, $p = .055$). It reflected that the N170 was larger in response to upright than to upside-down stimuli only when stimuli were perceived as significant (“Face” responses: $F_{[1,12]}=18.39$,

$p < .002$, whereas $F_{[1,12]} < 1$ for the “No face” responses). Also the effect of facial decision reached in fact significance only for upright stimuli ($F_{[1,12]} = 6.05$, $p < .04$). Finally although the N170 was larger on the right than the left hemisphere in every experimental condition (Table 2c), the lateralization effect was not significant and there was no significant interaction between hemisphere, stimulus orientation and/or facial decision on N170 amplitude. The latency and scalp distribution (measured as a relative distance over the row of low occipito-temporal leads – M1/2, P9/10, PO9/10, O9/10 – in each hemisphere) of the N170 did not vary significantly with any of the experimental factors either.

Insert Figure 3 about here

The Vertex Positive Potential (VPP) was best identified on Cz. Its mean peak amplitude and latency were $6.09\mu\text{V}$ and 211ms respectively. There was no significant effect of facial decision, stimulus orientation nor interaction between these factors on the VPP parameters (all $p > .10$; Table 2d).

Following the N170 and VPP, an occipital P2 was observed with a mean latency of 247ms (Figure 2 and Table 2e). Its peak amplitude was significantly smaller for ‘faces’ than ‘non faces’ ($F_{[1,12]} = 10.5$, $p = .007$). There was no other effect on P2 peak amplitude nor any significant effect on its latency.

Insert Table 2 about here

Thus it appeared that the overt perception of upright Mooney stimuli as faces (relative to their report as *non faces* as well as relative to the perception of *upside-down*

Mooneys as faces) was reflected by a modulation of the amplitude of the bilateral temporal peaks of the N170. Moreover, the subsequent occipital P2 was reduced for faces relative to non faces. Closer examination of the ERPs (Fig. 2) further indicated that this latter effect resulted from a sustained enhanced occipito-temporal response to the stimuli reported as faces. Indeed the amplitude of the P2 was positively correlated with the mean amplitude of occipito-temporal responses between 240-290 ms ($r=0,70$; $p<.05$), and the modulation of evoked responses by facial decision and face orientation culminated over occipito-temporal regions beyond the N170 time range. These latter effects were analysed by measuring the mean EP amplitude on low occipito-temporal electrodes (P9-PO9 and P10-PO10) in six consecutive 50-msec time windows from 140 to 440 ms.

Mean amplitude measurements

A global MANOVA with facial decision, stimulus orientation, hemisphere and time windows as within-subjects factors yielded a main effect of facial decision with more negative occipito-temporal potentials for the stimuli reported as faces than for that not reported as such ($F_{[1,12]}=25.41$, $p<.0004$). An interaction between facial decision and orientation ($F_{[1,12]}=7.85$, $p<.02$) also revealed that occipito-temporal potentials were modulated by stimulus orientation only in the case of meaningful perception (“Face” responses) with more negative potentials in response to upright than to upside-down “Face” stimuli ($F_{[1,12]}=15,39$, $p<0,003$). However, these effects were accompanied by significant interactions between facial decision and time window ($F_{[5,8]}=4.25$, $p<.04$) as well as between facial decision, orientation and time window ($F_{[5,8]}=6.13$, $p<.02$), and between facial decision, orientation and hemisphere ($F_{[1,12]}=4.90$, $p<.05$). Consequently, the effects of facial decision and stimulus orientation were further analysed by ANOVAs in each time window and planned comparisons were run in each hemisphere.

These analyses showed first that the facial decision effect appeared delayed for upside-down relative to upright stimuli, paralleling the delay in ‘face’ responses for upside-down relative to upright stimuli observed on RT data (Fig. 4). More precisely, between 140-190 ms, occipito-temporal responses were larger for stimuli perceived as faces than for that not perceived as such for upright stimuli only ($F_{[1,12]}=5.41$, $p<.04$); this effect was significant in the left hemisphere ($F_{[1,12]}=6.97$, $p<.03$) whereas it showed a trend to significance in the right hemisphere ($F_{[1,12]}=3.38$, $p=.09$). Between 190-240ms, 240-290 ms, and 290-340 ms, the effect of facial decision was again observed for upright stimuli only and this effect was significant in both the left and right hemisphere (all $F_{[1,12]}>8.57$, $p<.02$). Then, between 340-390 ms, the effect of facial decision was still observed in both the right ($F_{[1,12]}=33.50$, $p<.0001$) and left ($F_{[1,12]}=31.16$, $p<.0002$) hemisphere for upright stimuli and it reached significance in the right hemisphere for upside-down stimuli ($F_{[1,12]}=5.23$, $p<.05$). Finally, between 390-440ms, occipito-temporal responses were larger for ‘faces’ than ‘non faces’ for both upright and upside-down stimuli in the left as well as in the right hemisphere (all $F_{[1,12]}>4.76$, $p<.05$).

Moreover, a significant interaction between facial decision and stimulus orientation was observed in every time window (all $F_{[1,12]}>5.23$, $p<.05$) but the last one on the left hemisphere. By contrast this interaction reached significance between 290-340 ($F_{[1,12]}=9.96$, $p<.01$) and 340-390 ms ($F_{[1,12]}=12.93$, $p<.004$) only on the right hemisphere. This reflected that the orientation of the stimuli reported as faces yielded significant effects predominantly in the left hemisphere (Fig. 4). More precisely, between 140-190 ms, 190-240ms, 290-340 ms, 340-390ms and 390-440ms, occipito-temporal responses were significantly larger for upright than upside-down stimuli perceived as faces in the left hemisphere (all $F_{[1,12]}>8.10$, $p<.02$). By contrast, in the right hemisphere, the effect of ‘face’ orientation showed a trend to significance between 290-340 ms ($F_{[1,12]}=4.19$, $p<.07$) and occipito-temporal responses were significantly

larger to upright than upside-down stimuli perceived as faces between 340-390ms and 390-440ms only (all $F_{[1,12]} > 5.13$, $p < .05$).

Finally, ERPs were found to be significantly more negative on the right (P10-PO10) than on the left (P9-PO9) occipito-temporal electrodes between 190 and 240msec (effect= $-1.89 \pm 0.62 \mu\text{V}$, $F_{[1,12]} = 9.34$, $p < .01$) and between 390 and 440msec (effect= $-1.28 \pm .49 \mu\text{V}$, $F_{[1,12]} = 6.96$, $p < .03$).

Insert Figure 4 about here

4. DISCUSSION

This study aimed at investigating the electrophysiological correlates of the overt perception of upright and upside-down Mooney stimuli as faces or non faces. We show N170 modulation by the subject's perception of a face but also by the orientation of the stimuli reported as faces. Moreover, occipito-temporal responses beyond the N170 time range reflect the behavioural delay in face perception for upright relative to upside-down stimuli.

First, behaviourally, we found that the difficulty in perceiving upside-down Mooney stimuli as faces was reflected by both lower rates of "face" responses and delayed "face" RTs for upside-down relative to upright stimuli. This confirms that while upright Mooney stimuli are easily perceived as faces, they are mostly perceived as non faces when turning them upside-down. However, it was not an all-or-nothing phenomenon, thus allowing us to analyse 'yes' and 'no' facial decision responses for both upright and upside-down stimuli, at the behavioural and electrophysiological levels. Moreover, the fact that there was a delay in facial

decision for upside-down relative to upright Mooney stimuli perceived as faces can be related to the extensive binding and contour-reconstruction processes required for Mooneys perception as faces. Such processes appear to be performed rather automatically for upright stimuli, which - despite being impoverished representation of faces - contain preserved 3D shape-from-shading information that is crucial for face perception and recognition [31]. However, this information is greatly affected by turning the stimuli upside-down, and this yielded to slower 'face' responses for upside-down Mooney stimuli. This notwithstanding, it is noteworthy that stimulus orientation had no effect on RT for the stimuli reported as non faces while the RT remained relatively fast. This first suggests that orientation processing was not performed independently of facial decision processes. Second it supports that the stimuli categorised as non faces were indeed perceived as meaningless and therefore non oriented stimuli. The concomitant recording of ERPs allowed us to examine the electrophysiological correlates of facial decision and stimulus orientation effects.

As a preliminary, might the uneven distribution of 'yes'/'no' facial decision responses over upright and upside-down stimuli have impacted on the observed effects? This seems unlikely in regard to the main effects of facial decision as the total number of trials was similar for 'faces' and 'non faces'. Moreover, the unequal repartition of trials impacted similarly on all simple main effects of facial decision and stimulus orientation. Therefore it cannot account for the differential effect of facial decision for upright versus upside-down stimuli, nor for the differential effect of stimulus orientation for 'faces' versus 'non faces'. Thus we examined the effects of overt facial decision ('yes' vs. 'no' responses) independent of stimulus orientation (upright / upside-down) vs. those which depended on it.

We found that these effects emerged on the temporal N170. This component was larger to stimuli perceived as faces than to those not perceived as such. This confirms the numerous previous results reporting larger N170 to faces than to other non face (meaningful

or meaningless) objects [3,5,9,47,49]. It further shows that low-level physical properties are very unlikely to account for this effect as in the present study the very same stimuli were presented upright and upside-down and yielded face and non face responses. This underlines the importance of the subject's overt perception of a face in the N170 generation process. It is in line with recent findings of Bentin's group showing that priming the perception of a stimulus as either a distorted face or a pair of eyes yields the elicitation of a normal N170 component, whereas the same stimuli when unprimed and perceived as meaningless geometrical shapes elicit no or very little N170 [4,5]. However it is interesting to note that in the present study the N170 was reduced but present for the stimuli not reported as faces. This may be due to the task as the subjects were engaged in a facial decision task throughout the entire stream of stimuli, and may then reflect top-down pre-activation or attentional selection of brain regions responsible for face detection. It may also reflect that non reported face perception took place to a certain extent. This may be first associated to some level of non conscious face perception. Vuilleumier et al. [50] have shown that the N170 can be elicited by neglected (non reported) faces in a patient with visual extinction. It could also reflect some subject's attempt to process the stimulus as a face even when finally reporting it as a non face. Note however that the instruction insisted on discarding this strategy and debriefing confirmed that the subjects conformed to it. Furthermore, if anything, this may have weakened our results rather than biased them. Thus, although the N170 may be automatically evoked in response to faces, our study shows that this early ERP component is further modulated by the subject's overt facial decision.

The effect of facial decision on the N170 was also qualified by an interaction between facial decision and stimulus orientation. This showed that the N170 was sensitive to the stimulus orientation but only when the stimulus was reported as a face. Face inversion effect has already been observed on N170. This component is usually delayed and sometimes

enhanced in response to upside-down relative to upright faces [3,45,46]. However, a noticeable exception to this enhancement effect has been provided by Sagiv and Bentin [47] who showed that while inverting photographs of faces yielded the “classical” face inversion effect on N170, inverting schematic – impoverished – representations of faces yielded a decrease in N170 amplitude. They interpret this dissociable effect of face inversion as reflecting the dual-process system – holistic (whole-based) and analytic – that is involved in face encoding: The N170 would be more sensitive to the face component processor and only the inversion of schematic faces that recruit solely holistic processing when upright would result in decreased N170 [47]. Thus, in the present study, the decrease of the N170 for upside-down Mooneys reported as faces leads to several conclusions. First, it is likely that upside-down Mooneys reported as faces yield an impoverished percept of face as compared to upright Mooney stimuli, thus evoking a smaller N170. Second, conforming to Sagiv and Bentin model, it confirms that upright Mooney faces yield holistic perception of face Gestalts. This face Gestalt is here provided by information restricted to shape-from-shading rather than by first-order relation information [two eyes above a nose above a mouth, 34,47]. Thus the N170 appears to be sensitive to these two types of information [see also 47], and rather than reflecting mainly the analytical face component sub-processor, it would be modulated by the multiple subsystems involved in the face encoding system: the holistic subsystem which extracts the face gestalt based on first-order spatial arrangement of features and/or shape-from-shading information, and the analytic subsystem which relies on the processing of face components. This is in agreement with the involvement of different regions of the ventral and lateral occipito-temporal cortex in the N170 activity which may also depend on task [1,15,25] and may explain why somewhat discrepant results have sometimes been obtained regarding the precise N170 functional properties.

By contrast with the results obtained on N170 peak amplitude, there was no effect of facial decision nor of stimulus orientation on the VPP. The VPP was first described as face-responsive, but primarily in studies where a mastoid reference was used [7,8,26]. Jeffreys [26] was the first to note that this component yielded negative temporal counterpart when re-referenced to the nose. Several studies have then suggested that the N170 generators would be at least partly distinct from that of the VPP [3,9,14,15]. This is confirmed in the present study as the VPP did not vary as a function of overt face perception and/or orientation whereas the temporal N170 did. The lack of a significant VPP responsiveness to faces has also been observed by George et al. [14] and by Bötzel et al. [8]. The latter authors noted that when the data are recomputed with respect to a mastoid reference the VPP was found to be face responsive again. Jemel et al. [28] also found a close relationship between the N170 and VPP using an average reference. Taken together with the present results, this supports that while the VPP involves generators distinct from that of the temporal negativities, its responsiveness to faces observed in previous studies using mastoid or average reference could largely be accounted for by temporal generators. The VPP was also of particularly late latency in the present study. Such a delayed latency of the VPP in response to Mooney faces (as compared to realistic drawings of faces) was also observed by Jeffreys [27] in a naive subject. It may be related to the use of Mooney stimuli which are very specific impoverished stimuli and may also be explained by the spatio-temporal overlap of the VPP wave with the large temporal N170 component evoked in the present study.

Following the N170 and VPP, an occipital P2 was observed which has already been described in various tasks involving faces [19,23]. Although this component has been shown to be sensitive to some manipulations of faces, the processes that it may index are unclear. While Halit et al. [19] found that the P2 was decreased by stretching the position of internal face features, Itier and Taylor [23] found that it was on contrary increased by the contrast

reversal of faces and Rossion et al. [45] found that its negative fronto-central counterpart was unaffected by face inversion. In the present study the occipital P2 was smaller for the stimuli reported as faces than for that not reported as such. This effect appeared to be due to the spatio-temporal overlap between the P2 and the sustained occipito-temporal negative responses related to facial decision and stimulus orientation. Thus in the present study, it was not possible to attribute a specific functional significance to the P2 in relation to face processing. This is consistent with the fact that the P2 component has been associated to the processing of face identity rather than to the 'mere' perception of faces [19].

The behavioural delay in facial decision for upside-down stimuli was reflected by the time course of the electrophysiological occipito-temporal responses beyond the N170 time range. We found that the report of upright Mooneys as faces (relative to non faces) was accompanied by increased occipito-temporal responses from 140-190 ms until 390-440 ms, whereas the effect of facial decision for upside-down stimuli was significant only from 340-390 ms on the right hemisphere and from 390-440 ms on the left hemisphere. These effects cannot be related to motor processes as the response hands for 'Face' / 'No face' responses were counterbalanced across subjects and there was no effect of response hand nor interaction between hemisphere and response hand when this factor was introduced in the analyses. Thus upside-down stimuli yielded delayed occipito-temporal activities related to facial decision (the perception of a face in the display yielding to 'Face' response). This is in close parallel with the longer RT observed for 'Face' responses to upside-down (relative to upright) stimuli. These results support that there is a slower perceptual encoding of upside-down relative to upright stimuli and that facial decision requires more time for upside-down Mooneys consistently with Perrett et al.'s account for delayed processing of rotated figures [39]. It is also possible that the delay in 'Face' responses and electrophysiological facial decision effects for upside-down relative to upright Mooney stimuli reflects some sequential strategy of the

subjects who may have automatically ‘searched’ first for an upright face, and then, if this failed, for an upside-down face. In this case, the difficulty of the mental rotation of complex stimuli [44] may have also contributed to these delayed responses. However, whereas occipito-temporal activities related to facial decision were delayed by about 200 ms for upside-down relative to upright stimuli, the corresponding ‘Face’ responses were delayed by 100 ms only. This supports a contingent-parallel processing model. In other terms, it shows that the processes involved in facial decision, response selection and outputting motor response are not strictly sequential but rather proceed in cascade with each processing stage starting before the previous stage is totally completed [37].

Moreover, facial decision effects need to be discussed in relation with stimulus orientation effects. First, note again that there was no effect of orientation for the stimuli reported as meaningless (‘Non faces’). By contrast, for the stimuli reported as faces, occipito-temporal responses were larger for upright than upside-down stimuli. Moreover, and most importantly, such stimulus orientation effects for ‘faces’ were observed as soon as 140-190 ms post-stimulus onset and sustained between 140 and 440 ms in the left hemisphere, whereas they were significant only ~200 ms later (between 340 and 440 ms) in the right hemisphere. This suggests that the orientation effect may be associated to different processes in the left and right hemisphere. Taken together with the differential time course of facial decision effects for upright and upside-down stimuli, it also suggests different interpretations for the early and late parts of the orientation effects. The early orientation effect observed for ‘face’ responses on the left occipito-temporal electrodes only can be attributed to the delayed facial decision for upside-down relative to upright stimuli. In other words, only upright ‘faces’ were already categorised as faces, therefore yielding greater occipito-temporal responses, in the early time range. There was no such early orientation effect for the stimuli reported as faces on the right occipito-temporal electrodes. Indeed, as can be seen on Fig. 4, brain responses on P10-PO10

were relatively close – and not significantly different – for upside-down and upright subsequently-reported-as-face stimuli from early on. Thus, despite the lack of a significant early facial decision effect for upside-down stimuli, it suggests that in the right hemisphere, the perceptual processes related to subsequent overt facial decision take place from early on whatever the ‘face’ orientation. By contrast, the left hemisphere would be more sensitive to stimulus orientation and process upside-down stimuli as non face objects until facial decision is reached. Such interpretation may appear to contradict somewhat with the finding of greater sensitivity to face orientation for the right than the left intracerebral N200 [35], and that of earlier responses to inverted relative to upright faces in the left hemisphere whereas the reverse is observed in the right hemisphere [35,51]. However, it is important to keep in mind that as we used Mooney stimuli, stimulus orientation interfered strongly with face perception in our paradigm. This limits the comparison of our result with the ones derived from the inversion of normal faces – still quite easily perceived as faces. Moreover, the late orientation effects (between 390-440 ms on left hemisphere and between 340-440 ms on right hemisphere, where facial decision effects were observed for both upright and upside-down stimuli) yield a different interpretation. They may reflect ‘face’ inversion effect. Indeed, even when “faces” and “non faces” yielded distinct occipito-temporal responses whatever the stimulus orientation, upright and upside-down stimuli reported as faces involved different electrophysiological responses over the occipito-temporal regions. This is reminiscent of Haxby et al. [21] who have shown that the face inversion effect is associated with differential activity in infero-temporal regions distinct from nearby face-selective fusiform regions and it suggests that these activities may take place over a late time range, in parallel with facial decision processes.

In total, facial decision effects and ‘face’ orientation effects were observed in a long-lasting time window on occipito-temporal electrodes. This is consistent with the observation

of face-specific intracerebral ERPs at various latencies (N200, P350, N700) in the ventral occipitotemporal cortex [1]. In line with these studies, it suggests that facial decision or face categorisation involves not only spatially distributed occipital and temporal regions [2,13,42] but also temporally distributed and sustained activities within these regions.

Finally, could any of the observed effects be related to repetition effects previously described on part of these data (Upright “Faces” and Upside-down “Non faces”; [15])? This appears very unlikely first because repetition did not interact with facial decision differentially for upright and upside-down stimuli: it increased the rate of “face” responses for upright as well as upside-down Mooneys. Second, the effects of facial decision and of “face” orientation described here were observed over inferior occipito-temporal regions whereas repetition effects selective to upright “faces” were observed over parietal regions, as well as only within a very limited time range centred around 300 ms.

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Table 1 – Percentage of ‘Face’ and ‘No face’ responses and corresponding response time (\pm SE) for upright and upside-down stimuli

	“Face” responses	“No face” responses
Upright stimuli	79.4 \pm 1.7 % 645 \pm 20 ms	20.6 \pm 1.7 % 768 \pm 20 ms
Upside-Down stimuli	24.4 \pm 1.9 % 766 \pm 22 ms	75.6 \pm 1.9 % 765 \pm 21 ms

Table 2 – Peak amplitude, latency (and topography* for the N170) of early ERP components in response to upright and upside-down stimuli perceived as ‘Faces’ and ‘Non faces’.

	Upright stimuli		Upside-down stimuli	
	« Face »	« No face »	« Face »	« No face »
<i>a) P1 Left occ.</i>	6.46 \pm 1.10 μ V 115 \pm 4ms	7.68 \pm 1.30 μ V 113 \pm 4ms	7.51 \pm 1.10 μ V 117 \pm 3ms	7.03 \pm 1.00 μ V 111 \pm 3ms
<i>Right occ.</i>	6.26 \pm 0.69 μ V 114 \pm 3ms	7.73 \pm 0.82 μ V 116 \pm 3ms	6.89 \pm 0.94 μ V 113 \pm 2ms	6.66 \pm 0.59 μ V 112 \pm 3ms
<i>b) Occip. N1</i>	-5.71 \pm 1.19 μ V 164 \pm 6ms	-4.61 \pm 1.35 μ V 159 \pm 5ms	-5.10 \pm 0.98 μ V 168 \pm 7ms	-5.01 \pm 0.95 μ V 165 \pm 4ms
<i>c) Left N170</i>	-10.48 \pm 0.89 μ V 183 \pm 6ms 56 \pm 7%*	-8.47 \pm 0.91 μ V 179 \pm 6ms 59 \pm 9%	-8.22 \pm 0.88 μ V 181 \pm 6ms 56 \pm 7%	-8.64 \pm 0.92 μ V 181 \pm 5ms 50 \pm 7%
<i>Right N170</i>	-11.07 \pm 0.97 μ V 188 \pm 5ms 58 \pm 4%	-9.25 \pm 0.84 μ V 182 \pm 6ms 62 \pm 7%	-9.16 \pm 1.09 μ V 187 \pm 5ms 55 \pm 3%	-9.17 \pm 0.94 μ V 183 \pm 5ms 58 \pm 3%
<i>d) VPP</i>	5.42 \pm 0.92 μ V 209 \pm 6 ms	6.93 \pm 0.93 μ V 211 \pm 5 ms	6.10 \pm 0.68 μ V 214 \pm 7 ms	5.94 \pm 0.80 μ V 212 \pm 5 ms
<i>e) Occip. P2</i>	7.81 \pm 1.23 μ V 248 \pm 5 ms	11.09 \pm 1.48 μ V 246 \pm 6 ms	8.54 \pm 1.03 μ V 250 \pm 6 ms	9.75 \pm 1.12 μ V 243 \pm 5 ms

* Peak topography is measured as a relative distance – expressed in percentage – over the row of left and right low occipito-temporal electrodes, with M1/2, P9/10, PO9/10, O9/10 corresponding to 0, 33, 66, and 100% respectively.

FIGURE LEGENDS

Figure 1 – Example of upright (on the left) and upside-down (on the right) Mooney stimuli

Figure 2 – Timecourse of evoked potentials in response to upright and upside-down stimuli perceived as faces or not. The temporal course (in ms) of the grand mean evoked potentials (in μV) is represented on a subset of electrodes where measurements were done, under each experimental condition: upright (in black) and upside-down (in gray) stimuli perceived as faces (bold line) or not (thin line). The P1, occipital N1 (Occ.N1), temporal N170 (Temp. N170), VPP and occipital P2 components are indicated by arrows.

Figure 3 – Scalp potential maps at the time of the N170 peak for upright and upside-down stimuli perceived as faces or not. In each experimental condition, the scalp potential maps averaged across the 13 subjects are represented at 184 ms, on left and right three-quarter back side views of the head. Red and blue colours represent respectively positive and negative values of the potential (in μV), and black represents the zero value. The green crosses represent electrode locations and the front part of the head anterior to the electrode coverage is shaded in gray.

Figure 4 – Temporal course of the facial decision and orientation effects on occipito-temporal electrodes. *Upper part*: The temporal course (in ms) of the grand mean evoked potentials (in μV) averaged over P10-PO10 on the right hemisphere (upper row), and over P9-PO9 on the left hemisphere (middle row) is plotted for the upright (in black) and upside-down (in gray) stimuli perceived as faces (bold line) or not (thin line). *Lower part*: The time windows where the facial decision and orientation effects (measured in 50-ms windows from 140-190 ms to 390-440 ms) were significant are represented in black and gray for the right (P10-PO10) and left (P9-PO9) hemispheres respectively. The facial decision effect is

represented for upright and upside-down stimuli respectively. The orientation effect is represented only for the stimuli perceived as faces as it was non significant for the stimuli perceived as meaningless (non faces).

Figure 1
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Figure 2
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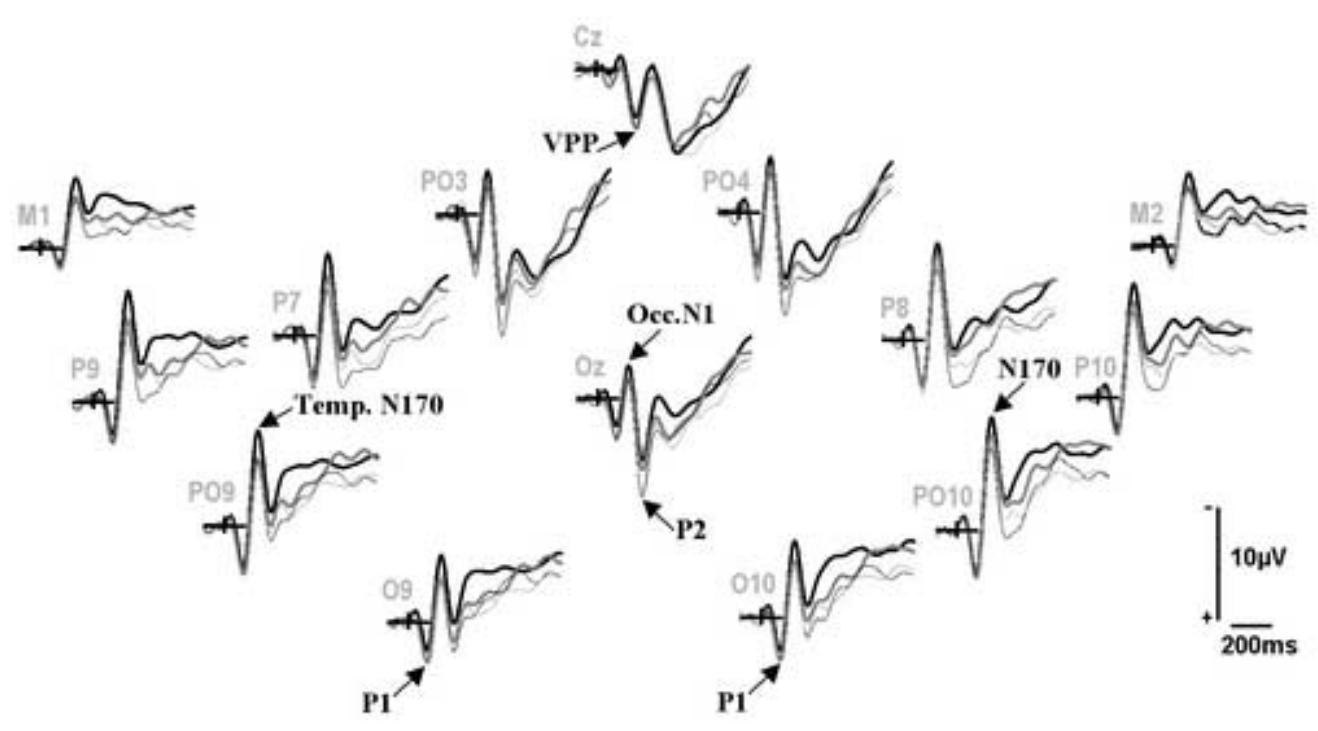


Figure 3
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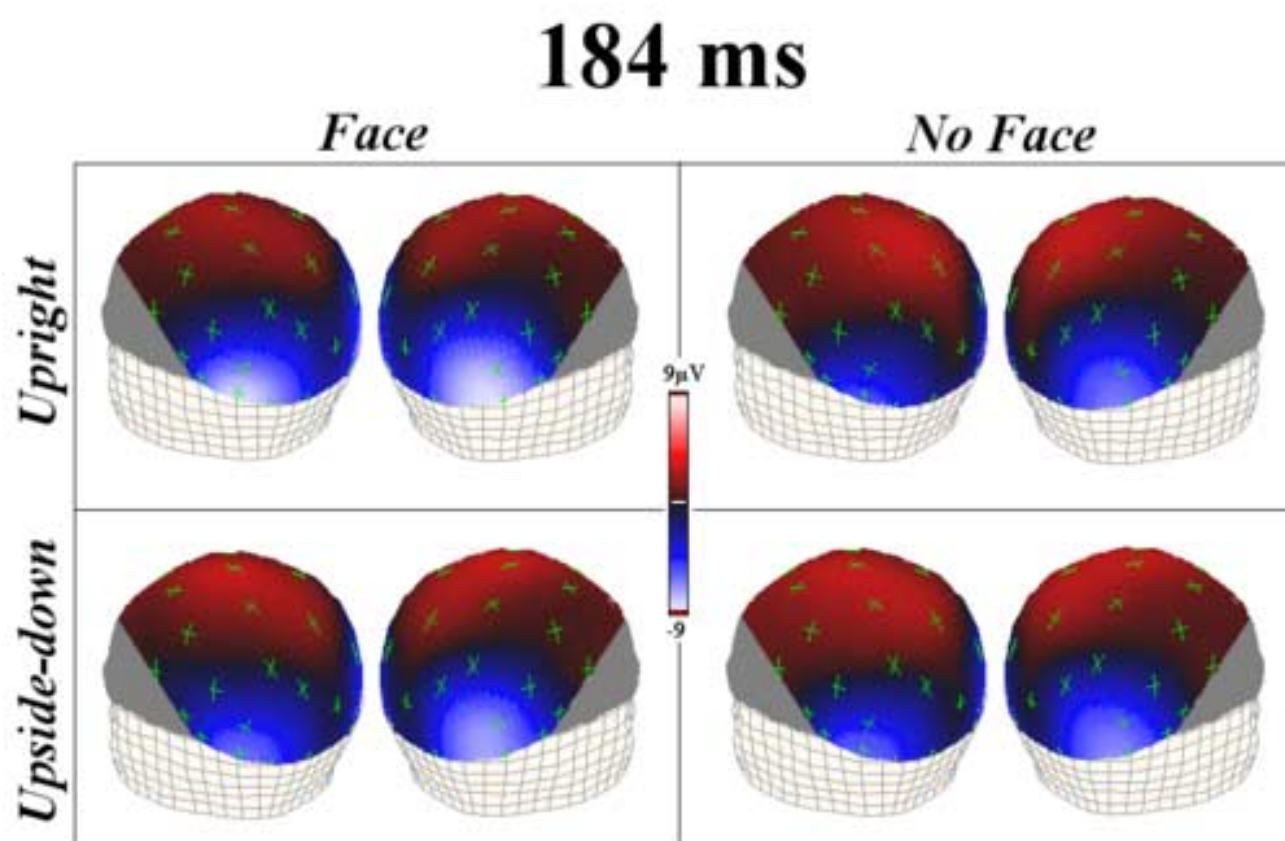
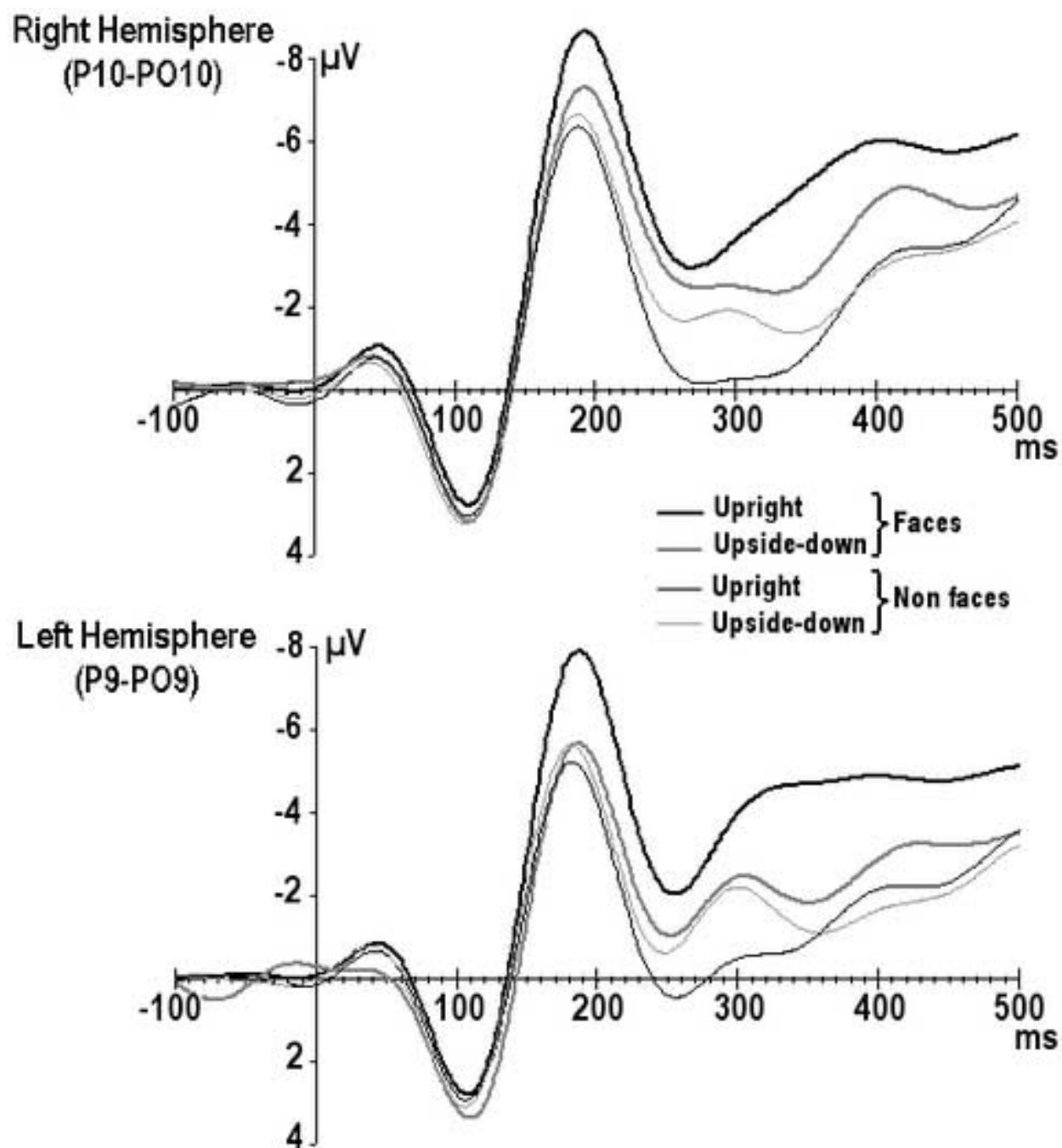


Figure 4
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Timecourse of effects

