# Modulation of Face-sensitive Event-related Potentials by Canonical and Distorted Human Faces: The Role of Vertical Symmetry and Up–Down Featural Arrangement

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## Abstract

■ This study examined the sensitivity of early face-sensitive event-related potential (ERP) components to the disruption of two structural properties embedded in faces, namely, ''up–down featural arrangement'' and ''vertical symmetry.'' Behavioral measures and ERPs were recorded as adults made an orientation judgment for canonical faces and distorted faces that had been manipulated for either or both of the mentioned properties. The P1, the N170, and the vertex positive potential (VPP) exhibited a similar gradient in sensitivity to the two investigated properties, in that they all showed a linear increase in amplitude or latency as the properties were selectively disrupted in the order of (1) up–down featural arrangement, (2) vertical symmetry, and (3) both up–down featural arrangement *and* vertical symmetry. Exceptions to this finding were seen for the amplitudes of the N170 and VPP, which were largest for the stimulus in which solely vertical symmetry was disrupted. Interestingly, the enhanced amplitudes of the N170 and VPP are consistent with a drop in behavioral performance on the orientation judgment for this stimulus. ■

## INTRODUCTION

Human faces form a class of complex, visually homogeneous stimuli, all sharing a basic structure; the same set of features arranged in the same fixed layout (i.e., two horizontal eyes above a centrally located vertical nose and horizontal mouth). Over the past 20 years, a great deal of research has been focused on attempting to identify the neurocognitive operations involved in the sophisticated human ability of detecting such a unique layout within the visual world.

Event-related potential (ERP) studies have identified three visual components related to the early encoding stages of face processing: the P1 (Taylor, 2002), the N170 (after Bentin, Allison, Puce, Perez, & McCarthy, 1996), and the vertex positive potential (VPP; after Jeffreys, 1989). The P1 is a visual positive component generated from the striate and extrastriate cortex (Gonzales, Clark, Fan, Luck, & Hillyard, 1994) and appears at occipital leads around 100–120 msec following stimulus onset. Albeit scarcely investigated in studies on face processing, the P1 has recently been found to be significantly larger to faces than to other object categories (Itier & Taylor, 2004a). These findings led to the claim that the P1 may reflect an early global response to faces, perhaps representing a holistic processing stage enabling the perception/detection of first-order properties, those which define a face as a face (Itier & Taylor, 2002, 2004b). Nevertheless, the contribution of low-level visual properties (see discussion in Itier & Taylor, 2004a) or attentional, task-dependent factors (see Taylor, 2002) to the observed differences between faces and other visual objects at the P1 still remains controversial.

Much more frequently measured and consistently observed, the N170, a negative component occurring between 140 and 200 msec over occipito-temporal regions, is widely considered to be the earliest reliable marker of a processing difference between faces and objects, being systematically larger and often faster to faces than to a variety of other object categories (Itier & Taylor, 2004a; Rossion, Gauthier, et al., 2000; Bentin et al., 1996; Botzel, Schulze, & Stodieck, 1995). Although the degree to which the N170 response may be penetrable by top-down effects due to face familiarity (e.g., Bentin & Deouell, 2000; but also Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003) or attentional and conceptual processes (Cauquil, Edmonds, & Taylor, 2000; but also Bentin & Golland, 2002) is still debated, this component is almost unanimously considered as reflecting the initial structural encoding stage of face processing (Bruce & Young, 1986; after Bentin et al., 1996).

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The VPP, a large positive potential appearing at centrofrontal sites over the same time frame as the N170, also appears to respond differentially to faces, being larger and sometimes faster to faces than nonface visual objects (Rossion, Joyce, Cottrell, & Tarr, 2003; Jeffreys, 1996; Botzel et al., 1995). Because of its temporal synchronicity with the N170, its opposite polarity and surface localization, and its remarkable functional similarity (e.g., Itier & Taylor, 2002, 2004b; Rossion, Delvenne, et al., 1999), some authors have argued that the VPP is the positive counterpart to the N170, the two components being part of the same dipolar complex (Joyce & Rossion, in press; Rossion, Joyce, et al., 2003). Even so, N170 and VPP results from studies which have analyzed both components do not always replicate (Itier & Taylor, 2004a; Itier & Taylor, 2002; George, Evan, Fiori, Davidoff, & Renault, 1996; Botzel et al., 1995). Unfortunately, discrepancies of these types are not often elaborated in the discussion of results, usually taken solely as evidence that further investigation is needed to conclude if the N170 and VPP originate from the same source. Alternatively, it has been suggested that the spatial location of each component on the scalp in relation to the reference location, instead of different sources, may be the cause of these discrepancies. In particular, using an average reference, Joyce and Rossion (in press) observed amplified differences between conditions at the N170 compared to the differences at the VPP.

The demonstration that the N170 and the VPP, and according to some authors also the P1 (Itier & Taylor, 2004a), discriminate between faces and nonface objects led to the description of these components as ''face-sensitive.'' Nevertheless, their specificity to faces continues to be debated. For example, little is known about the extent to which these early components are tuned to the specific geometry of the face, specifically, the typical spatial arrangement of the inner facial features.

A possible way to investigate this issue is that of testing the impact of configural changes on early face-sensitive ERP components. Configural changes could include any modification that may change the specific spatial relationship among the internal facial features (Rhodes, Brake, & Atkinson, 1993). The most consistent evidence concerning the impact of such changes comes from studies looking at face inversion. Much behavioral evidence is available showing that stimulus inversion interferes with the processing of the configural properties of the face, that is, the ''face inversion effect'' (e.g., Leder & Bruce, 2000; Bartlett & Searcy, 1993). Face inversion, however, also consistently and reliably delays the latency of the N170 (Itier & Taylor, 2002, 2004a, 2004b; Rossion, Joyce et al., 2003; de Haan, Pascalis, & Johnson, 2002; Sagiv & Bentin, 2001; Eimer, 2000a; Rossion, Gauthier, et al., 2000; Rossion, Delvenne, et al., 1999; Linkenkaer-Hansen et al., 1998; Bentin et al., 1996), the VPP (Joyce & Rossion, 2005; Itier & Taylor, 2002, 2004a; Rossion, Joyce, et al., 2003; Rossion,

Delvenne, et al., 1999; Jeffreys, 1993), and the P1 (Itier & Taylor, 2002, 2004a, 2004b; Taylor, 2002; Taylor, Edmonds, McCarthy, & Allison, 2001; Linkenkaer-Hansen et al., 1998). Much less consistently found is an increase in amplitude of these three components produced by face inversion (Itier & Taylor, 2002, 2004a, 2004b; de Haan et al., 2002; Sagiv & Bentin, 2001; Eimer, 2000a; Rossion, Gauthier, et al., 2000; Rossion, Delvenne, et al., 1999 for the N170; Rossion, Delvenne, et al., 1999 for the VPP; Itier & Taylor, 2004a, 2004b; Linkenkaer-Hansen et al., 1998 for the P1). The effects produced by face inversion have been tentatively interpreted as reflecting a slower and longer-lasting neuronal response associated with the increased difficulty in facial encoding due to inversion, or as a consequence of inverted faces recruiting more general brain areas involved in object recognition in addition to the typical face-sensitive areas (see Rossion & Gauthier, 2002).

Nevertheless, it is important to highlight the fact that the type of configural change investigated in face-inversion ERP studies does not directly disrupt the facial configuration, but rather changes the overall orientation of the entire face stimulus. In all of these ERP studies on face inversion, pictures of canonical upright faces were compared with upside-down images created simply by a 180° rotation (or a vertical flipping) of the whole face, including the inner, as well as the outer features (i.e., the external contour, the neck, and the hair). Therefore, ERP studies on face inversion provide limited evidence on the extent to which the observed electrophysiological face-sensitive responses at the level of the P1, N170, and VPP are tuned to the specific visual geometry of the human face, that is, to the specific internal organization of the features within a face.

The first studies looking at the effects of spatial rearrangement of the facial features focused primarily on understanding under what circumstances the N170 or VPP responses may be elicited. For example, Jeffreys and Tukmachi (1992) demonstrated that objects (e.g., fruit), which on their own do not resemble facial features, could induce a VPP only when arranged in a face-like configuration. These same non-face-related objects, when not arranged in a facial configuration, did not evoke a VPP response. On the other hand, it has been shown that stimuli containing real facial features, dislocated within the outer facial contour, are enough to produce a robust N170 (Bentin et al., 1996, Experiment 5). Together, these data demonstrated that either a face-like configuration or the presence of facial features alone is sufficient to induce an ERP face-sensitive response. The limitation of these early studies is that because no direct comparisons were made to undistorted, canonical faces containing real facial features, no conclusions can be drawn about the role played by the specific configural properties of the face-like configuration in modulating the N170 or VPP responses.

To our knowledge, only three studies (Gliga & Dehaene-Lambertz, 2005; Yamamoto & Kashikura, 1999;

George et al., 1996) have directly investigated the effects produced by disruption of the spatial integrity of the inner facial features on the early face-sensitive responses typically observed at the level of the N170 and/or VPP, and none have tested the effects of such manipulations on the earlier P1. These studies compared schematic (Yamamoto & Kashikura, 1999) or real images (Gliga & Dehaene-Lambertz, 2005; George et al., 1996) of canonical faces to distorted, scrambled faces created by displacing and rearranging the internal facial features while keeping the outline in its canonical orientation. Using schematic face-like configurations, Yamamoto and Kashikura (1999) found a larger VPP response to canonical compared to scrambled configurations, replicating the qualitative observations previously reported by Jeffreys (1996), who, however, also observed a latency shift of the VPP for the most distorted of the scrambled faces used in the study. These findings were interpreted by the authors as reflecting the importance of the overall face-like spatial configuration of constituent features in evoking the VPP. Of the two studies in which stimuli derived from real face images were used (Gliga & Dehaene-Lambertz, 2005; George et al., 1996), only the study by George et al. (1996) found that scrambled faces evoked a later and larger N170, whereas no differentiation between intact and distorted faces was found by Gliga and Dehaene-Lambertz (2005). The results obtained by George et al. were interpreted by the authors as the result of the "extra processing" required to produce a "structural code" for unfamiliar scrambled faces. More recently, these data have been submitted to the same explanation used to interpret the effects produced by inversion or feature removal, in that the disruption of the relational information may activate a broader range of neurons, perhaps firing at different rates, thus producing the enhanced and delayed effects observed at the N170 and/or the VPP (see Rossion & Gauthier, 2002). In addition to the paucity of direct evidence that the abovementioned studies provide on the effects produced by featural displacement, it should be noted that they did not systematically investigate the effects produced by the selective disruption of specific aspects of the face geometry. More precisely, in these studies, the rearrangement of the internal features in the scrambled versions of the face was done without reference to any specific criterion. For example, in the study by George et al., scrambling was obtained by reversing the position but not the local orientation of the eyes and nose, retaining vertical symmetry. However, no comment was made as to which specific aspects of the face geometry this rearrangement disrupts, or how the effects of this rearrangement would differ from those produced by other types of featural scrambling. These limits render unclear the interpretation of the observed effects.

A stricter control of these variables is present in a recent series of studies reported in the developmental literature, which were aimed at investigating the specificity of the well-known newborns' face-preference phenomenon. This phenomenon is based on the observation that both realistic (Macchi Cassia, Turati, & Simion, 2004) and highly schematized face-like configurations (Valenza, Simion, Macchi Cassia, & Umiltà, 1996; Johnson & Morton, 1991; Goren, Sarty, & Wu, 1975) spontaneously capture newborns' visual attention more than other, equally complex, visual objects. These observations have been classically taken as evidence that faces, already at birth, represent a special class of stimuli because humans are born with a specific, "innate" mechanism selectively tuned to the face geometry (Johnson & Morton, 1991). Yet more recently, the newborn face preference has been related to a number of nonspecific attentional biases toward a set of general structural properties embedded in faces, one of which is for visual configurations presenting more patterning in their upper as compared to their lower part (i.e., top-heavy patterns; Simion, Macchi Cassia, Turati, & Valenza, 2001, 2003). Recent research suggests that this structural property (i.e., up–down asymmetry) that faces may share with nonface stimuli, rather than "facedness" per se, plays a crucial role in attracting newborns' attention toward schematic (Turati, Simion, Milani, & Umiltà, 2002), as well as veridical, face images (Macchi Cassia, Turati, et al., 2004).

The rationale upon which this conclusion was drawn was that of altering the spatial integrity of inner facial features so as to selectively break one of the structural rules embedded in faces, and testing the effect of such manipulation on newborns' face-specific attentional response. We believe that an identical, systematic approach of decomposing the structural properties of face stimuli would also be valuable to the understanding of what factors drive the latency and amplitude modulations found at the level of the early face-sensitive ERP components when disrupting the facial organization of the features.

It is important to stress that the visual geometry of the human face is the product of the co-occurrence of a number of general visual structural properties, only one of which is the up–down arrangement of the inner features. In fact, faces can be described as top-heavy, congruent, vertically symmetrical stimuli delimited by a curvilinear contour. In addition to having a larger proportion of high-contrast features in the upper (eyes, eyebrows) compared to the lower part (mouth) (i.e., up–down featural arrangement), faces also have rounded edges and a congruent relation between the position of the inner features and the shape of the outer frame, in that the greater number of features (i.e., eyes) are located in the widest, upper portion of the face, and only one feature (i.e., mouth) is located in the narrowest bottom part of the face (i.e., congruency; see Simion, Macchi Cassia, Turati, & Valenza, 2003). Moreover, faces are bilaterally symmetrical with reference to their vertical axis, in that the left and right halves of the face contain the same number and

type of elements, which are normally equidistant from the axis (i.e., vertical symmetry). Very little is known about the contribution provided by each of these visual structural properties to the observed neurocognitive face-sensitive responses in adults.

The goal of our study was to examine this issue by testing the effects produced by the disruption of the up-down featural arrangement and the vertical symmetry of the human face on the three early face-sensitive ERP components: P1, N170, and VPP. We compared normal upright faces, which in reference to the two studied properties are "symmetrical top-heavy canonical faces" (ST), to three different types of distorted, scrambled faces, each created by selectively breaking one or both of the two selected visual structural rules. The selective violation of the first rule (up–down featural arrangement) led to the creation of "symmetrical bottom-heavy scrambled faces" (SB). The SB faces can also be thought of as an inversion of the internal facial features within the normal upright contour of a face. The selective violation of the second rule (symmetry in the vertical axis) led to the creation of "asymmetrical top-heavy scrambled faces" (AT). Finally, the contemporary violation of the two rules led to the creation of "asymmetrical bottom-heavy scrambled faces" (AB) (see Figure 1). Note that because we wanted to treat stimulus inversion as one possible type of featural displacement, we kept the outline of the face in its canonical upright orientation for all three of the distorted faces and manipulated exclusively the arrangement of the internal features. Thus, the symmetrical bottom-heavy (SB) scrambled faces that we used differ from the inverted faces employed in studies on face inversion in that, in the current study, inversion relates exclusively to the inner features and not to the outline of the face. Moreover, to eliminate possible intervening effects induced by the local facial features, we altered their orientation in all three distorted faces so that the eyes and the nose were rotated by 90° in the AT and AB stimuli and by 180° in the SB stimulus.

Through the comparison of the ERP responses elicited by canonical faces and the three types of distorted faces, we intended to shed light on the roles played by two of the general structural properties embedded in faces in the mature adult face recognition system. If both of these properties play a role in tuning the neurocognitive operations involved in face detection, their disruption should have an "additive" effect on the latency and/or amplitude of the analyzed ERP components. Based on the limited available evidence reported in the literature (Yamamoto & Kashikura, 1999; George et al., 1996), we expected to find progressive latency and/or amplitude increases of the examined early face-sensitive components, varying as a result of an increase in the perceptual distance from the canonical face geometry. That is, there should be a gradient of sensitivity at the P1, the N170, and/or the VPP to the four stimuli
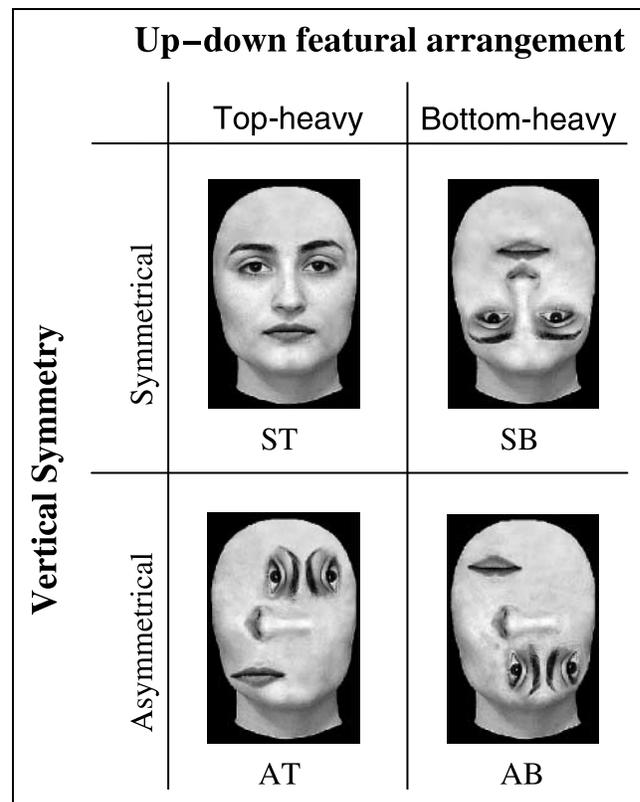


**Figure 1.** Examples of stimuli from the four categories used in the study. From the canonical face, the other three stimulus categories were created by selectively disrupting either one or both of the two visual structural properties manipulated in the study (up–down featural arrangement and vertical symmetry). ST = symmetrical top-heavy canonical face; SB = symmetrical bottom-heavy scrambled face; AT = asymmetrical top-heavy face; AB = asymmetrical bottom-heavy face.

we used, with ST faces being at one end of a continuum, AB scrambled faces being at the other end, and SB and AT scrambled faces lying along the continuum between the two extremes. Alternatively, because no evidence currently exists for the effects of featural scrambling on the P1, and the existing evidence for the N170 and VPP does not replicate (Yamamoto & Kashikura, 1999; George et al., 1996), the hypothesis could be raised that the violation of the two structural rules manipulated in the present study may differentially modulate the P1, the N170, and the VPP, each component being more sensitive to one property or the other, or the co-occurrence of the two. In particular, we were interested in verifying if a concordance exists between the N170 and the VPP, which, if present, could provide further evidence for recently proposed functional similarity between the two components (Joyce & Rossion, 2005; Rossion, Joyce, et al., 2003).

Finally, it could also be hypothesized that electrophysiological face-sensitive responses are driven by the unique face geometry rather than by the visual general structural properties that faces encapsulate. Accord-

ing to this view, the prediction would be that any of the three scrambled stimuli not presenting the typical geometry of the face are differentiated in the same way when compared to canonical faces, thus modulating latency and/or amplitude of the P1, the N170, and/or the VPP in the same way. If this were the case, we would expect to find canonical faces evoking P1, N170 and/or VPP responses of shorter latency and/or smaller amplitude than all three of the distorted faces, which in turn should not be differentiated from each other.

## METHODS

### Participants

The final sample consisted of 29 subjects (16 women), ranging in age from 18 to 29 years (mean age = 20.8 years). Eighteen of these subjects took part in both the behavioral and ERP aspects of the study. The remaining 11 participated only in the behavioral aspect of the study. Subjects were healthy, right-handed students recruited from an undergraduate population at the University of Minnesota and were either paid or received course credit for their participation. Subjects had normal or corrected-to-normal vision and reported taking no medication and having no history of neurological, ophthalmological, or systemic disease. Informed written consent was obtained from all participants in accordance with the Institutional Review Board of the University of Minnesota. Twelve additional subjects were tested but excluded from the analyses because of eye movements that resulted in too many electrooculogram (EOG) artifact ($n = 5$), behavioral performance below 25% accuracy resulting from a failure to understand the task instructions ($n = 4$), or experimenter error/equipment failure ($n = 3$).

### Stimuli

Twenty-five high-quality gray-scale photographs of young female faces were digitally modified so as to create four versions of each face differing exclusively in the spatial positioning of the inner features, the outline contour being equal, for a total of 100 stimuli. The original photographs served as one of the four versions of the stimuli, namely, the "symmetrical top-heavy" canonical face (ST). From ST, the other three versions of the stimuli were created by disrupting either one or both visual structural properties manipulated in the study, namely, "up–down featural arrangement" (top-heavy vs. bottom-heavy) and "vertical symmetry" (symmetrical vs. asymmetrical). These manipulations resulted in the generation of a "symmetrical bottom-heavy" scrambled face (SB), an "asymmetrical top-heavy" scrambled face (AT), and an "asymmetrical bottom-heavy" scrambled face (AB; see Figure 1). The models were photographed in a frontal pose with a neutral expression. The faces

were cropped right below the neck, and the hair and ears were removed. Stimuli were presented on a black background centered on a computer screen, and subtended a visual angle of approximately $11° \times 15°$.

### Apparatus and Task Procedure

Following electrode application, subjects were seated on a comfortable chair in a dimly lit room, approximately 75 cm from a computer screen, and were tested in an active discrimination task involving an orientation judgment. Subjects were instructed to visually fixate the center of the screen during the presentation of two consecutive blocks of 100 trials each (25 images × 2 vertical symmetry × 2 up–down featural arrangement), with about a 1-minute pause between blocks. Each trial consisted of a 100-msec baseline, a 500-msec stimulus presentation, and a poststimulus recording of 1100 msec, resulting in a total trial length of 1700 msec. The interstimulus interval was randomized between 1000 and 1500 msec. All of the stimuli were randomized within a block with the constraints that each unique image in the set appeared once before any was repeated and that the same up–down featural arrangement (top-heavy or bottom-heavy) was not repeated more than three times in succession. All subjects viewed the same succession of stimuli. The subject's task was to provide an orientation judgment by pressing a key if the stimulus was "upright" and another key if the stimulus was "inverted," basing their discriminative response on the up–down arrangement of the inner facial features. Thus, the correct response for the ST and AT stimuli was "upright" and the correct response for the SB and AB stimuli was "inverted." Normally, subjects reported using the height of the eyes or mouth within the contour as a basis for their orientation judgments. All subjects reporting the use of a different judgment criterion (i.e., "normal" upright face vs. all other distorted faces; $n = 4$) produced an accuracy rate below 25% and were removed from the study. The side of the response was balanced across subjects. Subjects were instructed to respond as accurately and as quickly as possible; accuracy rate and response times (RTs) for correct responses were recorded.

### Electrophysiological Recording and Data Reduction

Event-related potentials were recorded from 31 scalp electrodes mounted in a close-fitting cap (Electro-Cap International, Eaton, OH) using a modified 10-20 system. The electrodes comprised Fz, Pz, T3, T4, T5, T6, C3, C4, F3, F4, F7, F8, O1, O2, FC1, FC2, FC5, FC6, CP1, CP2, CP5, CP6, P3, P4, PO3, PO4, PO7, PO8, plus the left and right mastoids (A1, A2) and a ground electrode. Cz was the reference lead during acquisition. EOG was recorded from bipolar miniature electrodes placed vertically above and below the right eye for the purpose of artifact detection.

Impedance for all scalp and EOG electrodes was kept below 5 kΩ. Electroencephalogram (EEG) and EOG were acquired using a Grass Neurodata Acquisition System and amplified using Model 12A5 amplifiers with a gain of 50,000 for scalp leads and 5000 for EOG. The bandpass was 0.1–30 Hz, and a 60-Hz notch filter was engaged. Data were sampled every 5 msec (200 Hz). ERP data were digitized on-line and then edited by computer algorithm. Prior to averaging, trials with excessive artifact (i.e., EEG > ±100 mV) were rejected. Data were then re-referenced to an average reference, and eye movement-related artifact was corrected (Gratton, Coles, & Donchin, 1983). Using 100 msec prior to stimulus onset as the baseline, individual trials were baseline-corrected and then averaged for each participant within each stimulus type. Each subject contributed an average of 41 trials per lead in each condition.

After visual inspection of the grand average in all conditions, peak latency and amplitude values of the P1, N170, and VPP were automatically extracted. For the P1, these values were extracted at the maximum (positive) amplitude point between 75 and 150 msec at a single occipital electrode site in the left and right hemispheres (O1 and O2; see Figure 3). For the N170, latency and amplitude values were measured at the most negative point between 120 and 270 msec at the mastoid and temporal sites in the two hemispheres (A1/T5 and A2/T6; see Figure 4). The VPP measurements were made on the maximum positivity occurring within the same time window at the left, medial, and right central leads (C3, Cz, C4; see Figure 5).

## RESULTS

Behavioral (accuracy rates, correct RTs, and inverse efficiency scores [IESs]) and electrophysiological (peak latencies and amplitudes of components) measures were analyzed by means of $2 \times 2$ repeated-measures analyses of variance (ANOVA) using Greenhouse–Geisser adjusted degrees of freedom. Within-subjects factors were ''vertical symmetry'' (two levels) and ''up–down featural arrangement'' (two levels). For electrophysiological analyses, ''hemisphere'' (two levels) was added to within-subjects factors for the P1 and the N170, and ''electrode'' was added for the N170 (two levels) and the VPP (three levels). Additionally, planned pairwise comparisons were carried out between the four stimuli in an effort to determine whether the systematic disruption of one property has the same effect as the disruption of the other, or both properties.

### Behavioral Data

The mean overall accuracy in the detection task ranged from 97% (ST canonical faces) to 90% (AT scrambled faces); mean RTs ranged between 546 msec (ST canonical

faces) and 639 msec (AT scrambled faces). The $2 \times 2$ ANOVA was performed on the accuracy rates, correct RTs, and IESs (Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Akhtar & Enns 1989; Townsend & Ashby, 1983). The IESs (expressed in milliseconds) were computed separately for each condition and each subject by dividing the mean RTs for each condition by the proportion of correct responses for that same condition, so that lower values on this measure indicate better performance on the orientation judgment task. This measure was used to compensate for possible criterion shifts across conditions or speed–accuracy tradeoffs in performance.

The ANOVAs performed on the 18 subjects who also provided ERP data revealed a significant main effect of vertical symmetry for accuracy rates [$F(1,17) = 5.06$, $p < .05$] and RTs [$F(1,17) = 60.74$, $p < .001$] due to lower accuracy rates and slower RTs for vertically asymmetrical as compared to symmetrical faces. For RTs, there was also a main effect of up–down featural arrangement [$F(1,17) = 9.82$, $p < .01$], with orientation judgments being slower for bottom-heavy as compared to top-heavy faces. Interestingly, the interaction between vertical symmetry and up–down featural arrangement was significant for RTs [$F(1,17) = 30.57$, $p < .001$] and marginal for accuracy rates [$F(1,17) = 3.79$, $p = .07$]. These interactions qualify the main effects reported above. Planned comparisons showed that the ST canonical faces induced the fastest and most accurate response in the orientation judgment task, in that RTs were faster and accuracy rates were higher to the ST faces as compared to both the SB (RTs: $p < .001$; accuracy rates: $p < .01$) and the AT scrambled faces (RTs: $p < .001$; accuracy rates: $p < .01$). Additionally, a final comparison between the ST and AB faces was made (RTs: $p < .001$; accuracy rates: $p < .02$), confirming that the ST canonical faces indeed induced faster and more accurate responses than all of the other three stimulus types, which did not differ significantly among each other ($p > .1$ for all comparisons).

A more complex pattern of results emerged from the ANOVA performed on the IESs, which revealed a main effect of vertical symmetry [$F(1,17) = 20.38, p < .001$] and up–down featural arrangement [$F(1,17) = 8.59, p < .01$], as well as a significant interaction between these two factors [$F(1,17) = 15.91, p < .001$]. Planned comparisons showed that, analogous to the pattern of results observed for RT and accuracy data, performance on the orientation judgment was best (i.e., lowest IES) for the ST canonical faces (ST vs. SB, ST vs. AT, and ST vs. AB; $p < .001$). However, the IES data no longer demonstrated null differences between the other three stimuli, showing a marginal trend toward performance being worst (i.e., highest IES) for the AT scrambled faces (AT vs. ST: $p < .001$; AT vs. SB: $p = .07$; and AT vs. AB: $p = .14$).

In order to verify if this trend holds true with a larger sample size, three ANOVAs were performed on accuracy, RTs, and IES data provided by an additional 11 subjects, for a total sample size of 29 subjects. These analyses rep-

licated the finding that the ST stimulus produced the most efficient [$F(1,28) = 28.89, p < .001$; ST vs. SB, ST vs. AT, and ST vs. AB: $p < .001$], the most accurate [$F(1,28) = 10.84, p < .005$; ST vs. SB and ST vs. AT: $p < .001$; ST vs. AB: $p < .01$], and the fastest response [$F(1,28) = 32.62, p < .001$; ST vs. SB, ST vs. AT, and ST vs. AB: $p < .001$] compared to the other three stimulus types. More crucially, the analyses confirmed and extended the trend found with the smaller sample for the AT stimulus to produce the worst performance. The orientation judgment performance for the AT stimulus was the least efficient (IES: AT vs. ST, $p < .001$: AT vs. SB, $p < .01$; and AT vs. AB, $p < .02$) and the most difficult (accuracy: AT vs. ST, $p < .001$; AT vs. SB, $p < .05$; and AT vs. AB, $p = .059$), although not the slowest (RTs: AT vs. ST, $p < .001$; AT vs. SB, $p < .01$; but AT vs. AB, $p = .12$) (see Figure 2).

## Electrophysiological Data

### P1

No effect of hemisphere, vertical symmetry, or up–down featural arrangement was found for P1 latency (see Figure 3), which was maximal around 135 msec.

For P1 amplitude, there was a main effect of vertical symmetry [$F(1,13) = 12.66, p < .005$],[1] qualified by a significant interaction between this factor and the factor hemisphere [$F(1,13) = 5.06, p < .05$]. Asymmetrical faces elicited a larger P1 than symmetrical faces at both left ($p < .02$) and right ($p < .005$) electrode sites. There was also a main effect of up–down featural

arrangement [$F(1,13) = 10.32, p < .05$] due to an overall larger amplitude of the P1 to bottom-heavy as compared to top-heavy faces (see Figure 3). Moreover, a three-way interaction between the factors vertical symmetry, up–down featural arrangement, and hemisphere approached significance [$F(1,13) = 3.46, p = .09$], showing that the difference between symmetrical and asymmetrical faces on the right hemisphere was driven mainly by the AB stimulus (see Figure 3A), which elicited a larger P1 as compared to both symmetrical stimuli (AB vs. ST: $p < .002$; AB vs. SB: $p < .02$), whereas the AT stimulus elicited larger amplitude only in comparison to the canonical ST face (AT vs. ST: $p < .05$; AT vs. SB: $p = .74$).

To further explore whether the above reported findings may be a reflection of a gradient of sensitivity of the P1 to the four stimuli used, we performed a test of within-subjects contrasts within each hemisphere. Results indicated significant linear increases in P1 amplitudes for the four stimuli within both hemispheres, with ST canonical faces at one end of the linear trend, AB scrambled faces at the other end, and SB and AT scrambled faces in between [left hemisphere: $F(1,13) = 10.62, p < .01$; right hemisphere: $F(1,13) = 17.64, p < .002$] (see Figure 3). Finally, as previous studies on face inversion have found larger P1 amplitudes for inverted (i.e., bottom-heavy) than upright (i.e., top-heavy) faces (Itier & Taylor, 2004a, 2004b; Linkenkaer-Hansen et al., 1998), we performed a pairwise comparison within each hemisphere with only symmetrical faces to verify if the found main effect of up–down featural arrangement holds true when

**Figure 2.** Mean accuracy rates (A), RTs (B), and inverse efficiency scores (C) for the four stimuli ($n = 29$). Error bars represent standard errors of the means.
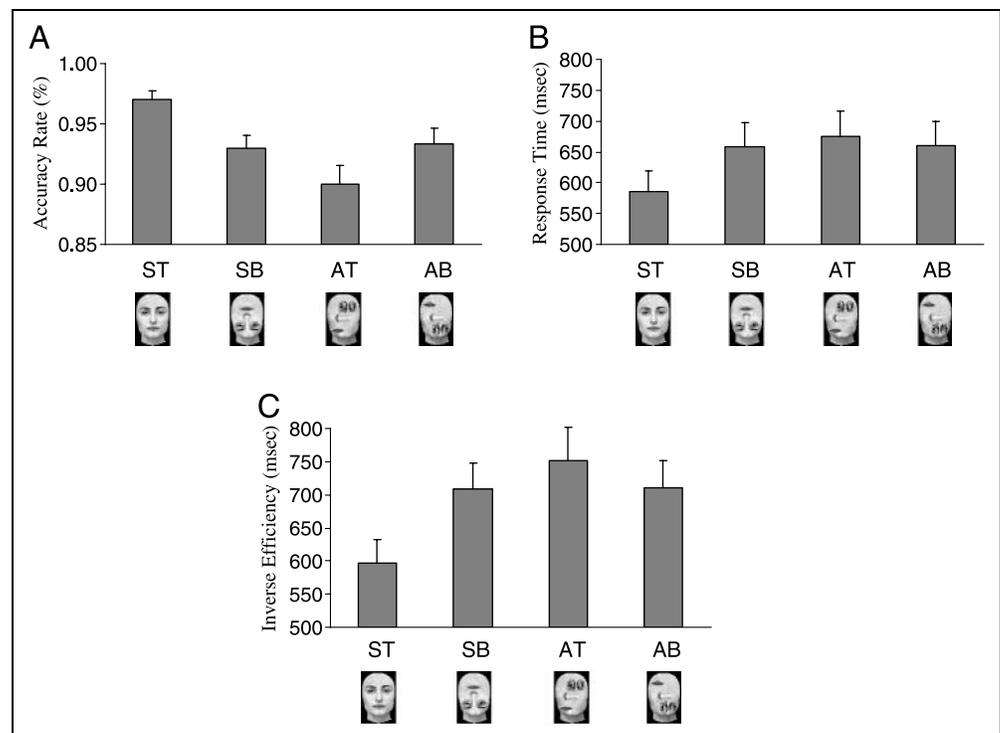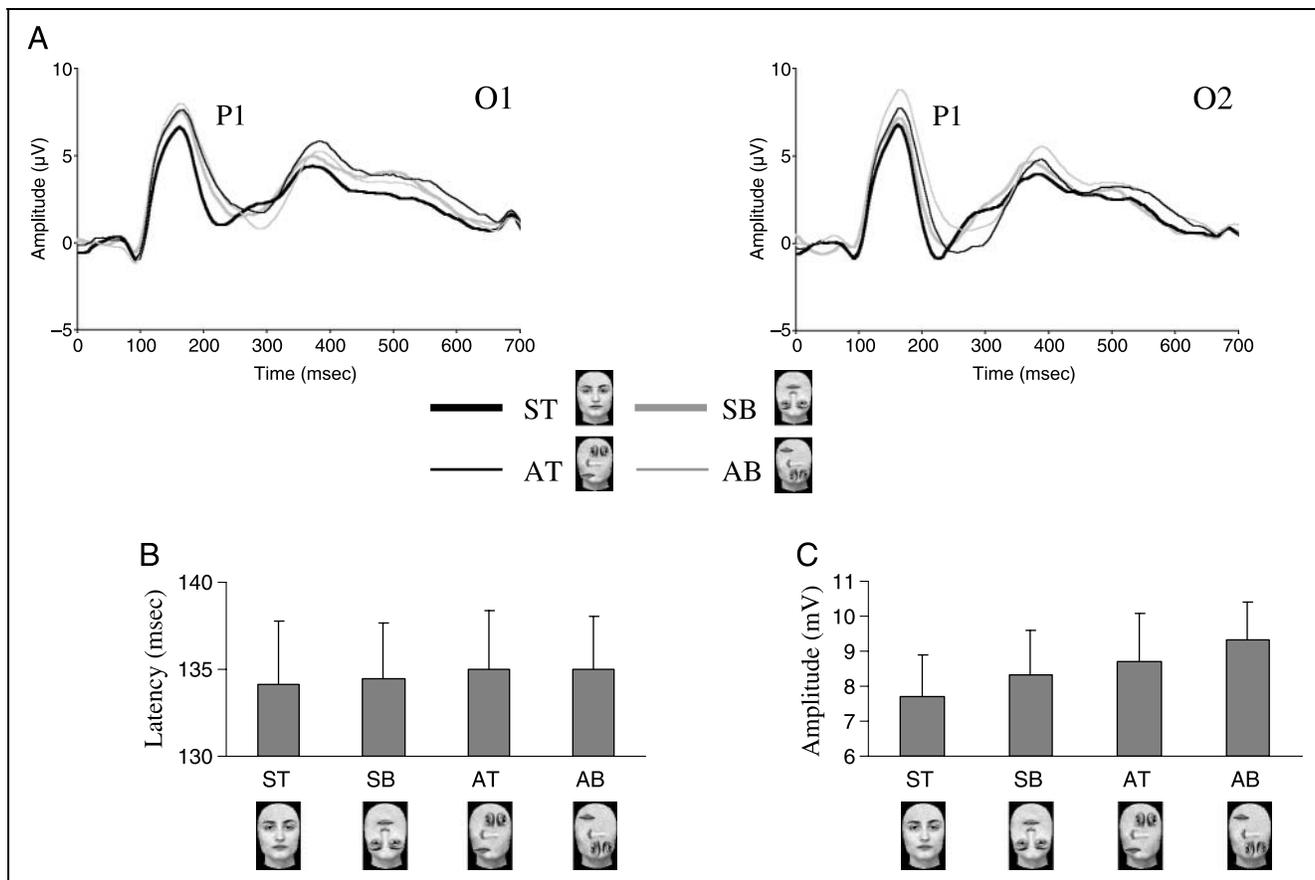
**Figure 3.** (A) Grand-averaged ERPs showing the P1 component at the left (O1) and right (O2) occipital electrodes for ST canonical faces and SB, AT, AB scrambled faces. Bar graphs display the overall mean latencies (B) and amplitudes (C) of the P1 component for the four stimulus categories at O1 and O2. Note the linear increase in the voltage amplitude of the component for SB, AT, and AB scrambled faces as compared to ST canonical faces.

only the ST and SB faces are compared. These comparisons failed to show significant differences between these two stimuli, although there was a marginal trend in both hemispheres [left hemisphere: $t(13) = 1.86, p = .08$; right hemisphere: $t(13) = 1.88, p = .08$].

### N170

The 2 (vertical symmetry) × 2 (up–down featural arrangement) × 2 (hemisphere) × 2 (electrode) ANOVA performed on N170 latency showed a main effect of vertical symmetry [$F(1,17) = 48.98, p < .001$], with symmetrical faces peaking sooner than asymmetrical faces, and a main effect of up–down featural arrangement [$F(1,17) = 7.80, p < .02$], due to the component peaking sooner for top-heavy faces than for bottom-heavy faces. There was also a main effect of electrode [$F(1,17) = 4.78, p < .05$], resulting from a faster latency to peak at temporal (T5 and T6) as compared to mastoid electrodes (A1 and A2) (see Figure 4). Again, we ran a pairwise comparison on the N170 latency including only top-heavy and bottom-heavy symmetrical faces. In line with numerous findings reported in the literature on

face inversion (e.g., Rossion, Joyce, et al., 2003; Bentin et al., 1996), we found that SB scrambled faces elicited longer N170s than ST canonical faces [$t(17) = 2.51, p < .05$]. A test of within-subjects contrasts revealed a significant linear change in N170 latencies, with ST canonical faces and AB scrambled faces at the two extremes of the continuum, and SB and AT scrambled faces lying in between [$F(1,17) = 58.94, p < .001$], as shown in Figure 4.

For the N170 amplitude, a main affect of electrode [$F(1,17) = 4.79, p < .05$] was due to the component being most prominent at mastoid as compared to temporal electrodes. A main effect of vertical symmetry [$F(1,17) = 8.03, p < .02$] showed that asymmetrical faces elicited larger amplitude than symmetrical faces, and a marginal interaction between electrode and up–down featural arrangement [$F(1,17) = 4.13, p = .058$] showed that, at mastoid electrodes, top-heavy faces evoked a larger N170 than bottom-heavy faces ($p < .05$). Finally, a three-way interaction involving the two factors vertical symmetry and up–down featural arrangement and the factor hemisphere [$F(1,17) = 6.63, p < .05$] showed that, over the right hemisphere, the AT
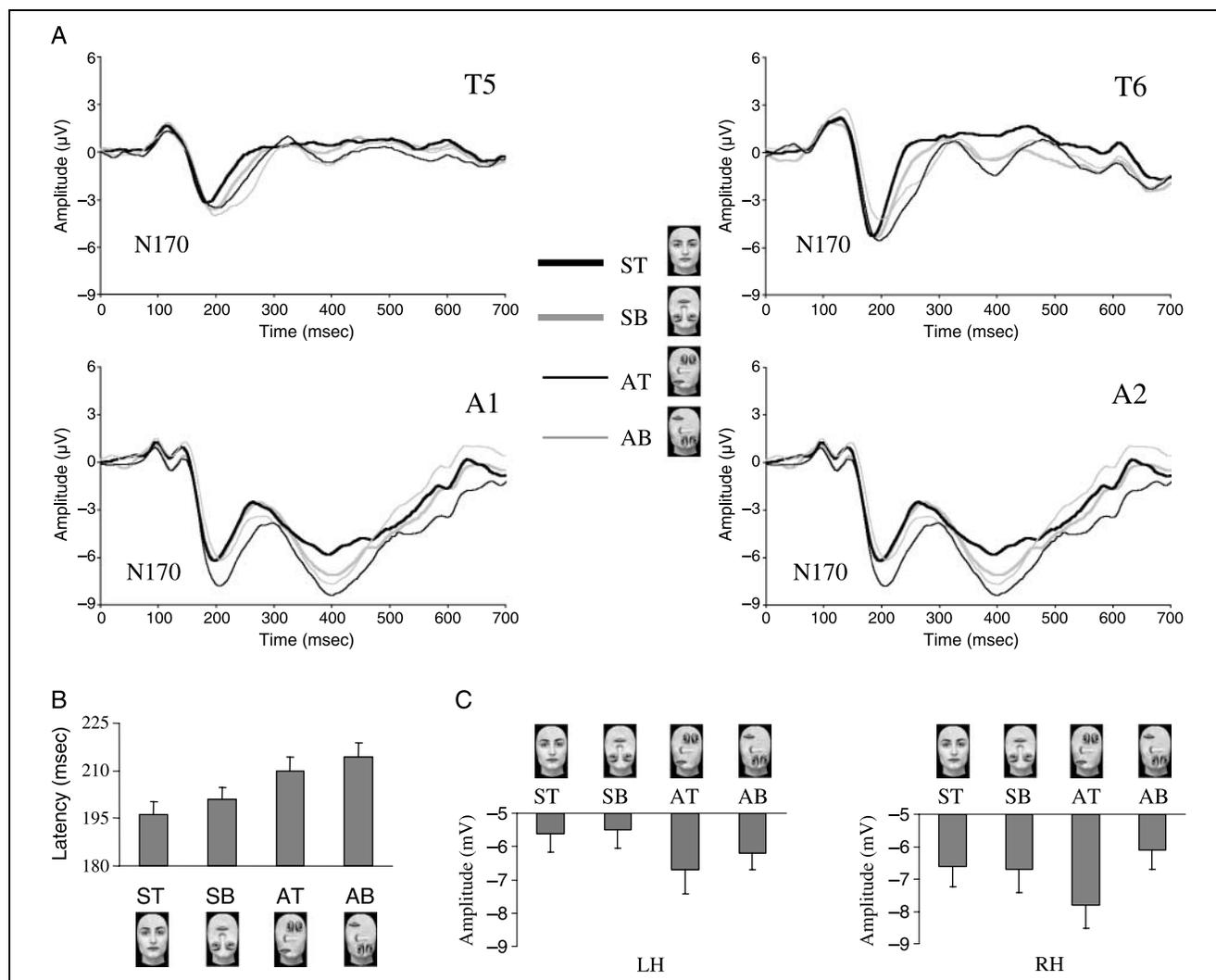
**Figure 4.** (A) The N170 obtained in response to ST canonical faces, SB, AT, and AB scrambled faces at mastoid and temporal electrodes on left (A1 and T5) and right (A2 and T6) hemispheres. (B) The overall mean latencies of the N170 for the four stimulus categories at the four electrodes. Note the linear increase in the latency of the component for SB, AT, and AB scrambled faces as compared to ST canonical faces. (C) The mean amplitudes of the N170 at the mastoid and temporal electrodes over the left (LH) and the right hemispheres (RH). Note the larger N170 component for AT scrambled faces compared to the other three stimuli over the right leads.

scrambled faces produced the largest N170 response in comparison to the other three stimuli (AT vs. AB: $p < .005$; AT vs. ST: $p < .05$; AT vs. SB: $p < .005$), which did not differ among each other ($p > .12$ for all comparisons), as shown in Figure 4. Instead, over the left hemisphere, there was a main effect of vertical symmetry [$F(1,17) = 9.44$, $p < .01$], due to asymmetrical faces producing larger amplitude than symmetrical faces. Unlike the observation from the right hemisphere, this finding was not driven by AT only, as shown by the fact that AT did not differ from AB ($p = .19$) and AB did differ from SB ($p < .05$).

### Vertex Positive Potential

A main effect of electrode [$F(1,17) = 5.47$, $p < .05$] reflected that VPP latencies peaked faster at the midline electrode (Cz). Moreover, as with the N170, there were main effects of vertical symmetry [$F(1,17) = 52.64$, $p < .001$], due to earlier peak latency for symmetrical faces, and of up–down featural arrangement [$F(1,17) = 6.52$, $p < .05$], due to delayed latencies for bottom-heavy faces. When only symmetrical faces were considered, a marginal, although nonsignificant, difference between top-heavy and bottom-heavy faces was found [ST vs. SB; $t(17) = 1.90$, $p = .07$]. Again, we performed a test of within-subjects contrasts that showed a linear latency increase of the VPP corresponding to an increase in perceptual distance from the ST canonical face, with SB scrambled faces preceding AT scrambled faces along the continuum [$F(1) = 52.21$, $p < .001$; Figure 5].

For VPP amplitude, there was a main effect of electrode [$F(1,17) = 21.75$, $p < .001$] due to the peaks elicited by the four stimuli being most prominent at the
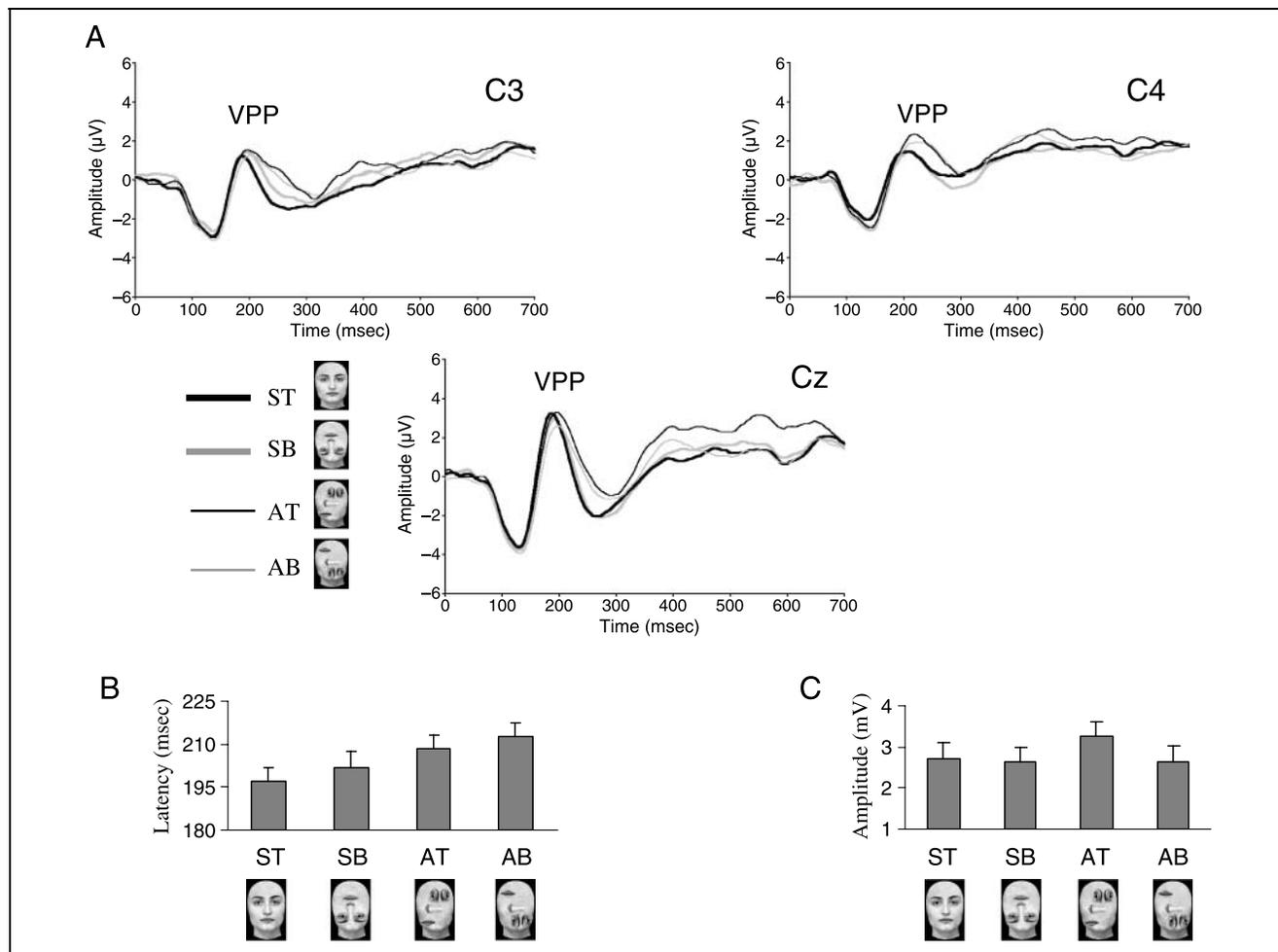
**Figure 5.** (A) Grand-average waveforms showing the VPP component at the left (C3), medial (Cz), and right (C4) central leads for the four stimulus categories. (B) The overall mean latencies of the VPP for the four stimulus categories at the three electrodes. Note the linear increase in the latency of the component for SB, AT, and AB scrambled faces as compared to ST canonical faces. (C) The overall mean amplitudes of the VPP for the four stimulus categories at the three electrodes. The VPP component is larger for AT scrambled faces compared to the other three stimuli.

midline electrode. There was also a marginal interaction between the factors vertical symmetry and up–down featural arrangement [$F(1,17) = 4.13, p = .058$], similar to that found for the amplitude of the N170. This was due to AT scrambled faces evoking the largest VPP response (AT vs. AB: $p < .02$; AT vs. ST, $p < .05$; AT vs. SB: $p < .005$) compared to the other three stimuli, which did not differ among each other ($p > .72$ for all comparisons) (Figure 5).

## DISCUSSION

The main purpose of this study was to investigate whether the general visual structural properties embedded in the face play specific roles in tuning the electrophysiological brain responses to this stimulus category. This was done by testing the effects produced by the selective disruption of two specific aspects of the face geometry, namely, vertical symmetry and up–down

featural arrangement, on the response properties of three early ERP components that are reported to be face-sensitive: the P1, the N170, and the VPP. Specifically, we predicted that an additive pattern may emerge, such that the combined violation of both face properties may modulate ERP responses more than the violation of each single property alone.

Support for this hypothesis of additive effects was found for each of the three studied components. Specifically, the amplitude of the P1 and the latency of both the N170 and the VPP all showed a significant linear increase among the four stimuli. Within the resulting continuum, canonical faces (ST) and scrambled faces with both properties disrupted (AB) lay at the two extremes. Additionally, the results showed that the violation of vertical symmetry had a more detrimental effect than the violation of up–down featural arrangement, rendering the SB stimulus before the AT stimulus at the two inner points on the continuum, as SB evoked a smaller

P1 (see Figure 3C) and a faster N170 (see Figure 4B) and VPP (see Figure 5B) than AT. The demonstration of a gradient of sensitivity at each component to the violation of the two considered properties speaks to the crucial role of these properties in modulating ERP responses to face stimuli. In particular, vertical symmetry seems to play a more prominent role than up–down featural arrangement in inducing a face-like response at the level of the P1, the N170, and the VPP.

The finding of a P1 difference during a face-processing task is consistent with previous reports (e.g., Itier & Taylor, 2004c; Halit, de Haan, & Johnson, 2000) and has been taken by some authors as evidence that the P1 reflects the earliest detection of a face as a face. However, differences found at the P1 have also been explained as possible reflections of more general perceptual differences between the stimuli used (see Itier & Taylor, 2002, 2004a; Halit et al., 2000 for discussion). Along these lines, the presence in our data of a linear gradient of sensitivity of the amplitude of the P1 to the selective violations of the two investigated structural properties of a face, analogous to that observed for the N170, could be explained in two ways. One hypothesis could be that the holistic processing leading to the rapid detection of the geometry of the human face begins as early as the P1. A more intriguing hypothesis is that the gradient of sensitivity observed at the P1 reflects the sensitivity of the visual system to the two structural properties of up–down featural arrangement and vertical symmetry. Support for this interpretation comes from developmental studies demonstrating that both of these are properties for which the perceptual system is particularly sensitive from the earliest stages of development. It has been shown that, within the first months of life, stimuli displaying a symmetrical distribution of elements along the vertical axis are more easily encoded, memorized, and recognized with respect to equally complex, nonsymmetric stimuli (Bornstein, Ferdinanndsen, & Gross, 1981; Fisher, Ferdinandsen, & Bornstein, 1981). Moreover, recent data show that the presence of more elements in the upper part of a configuration is one of the stimulus properties capable of triggering visual attention at birth, inducing a spontaneous preference in newborns (Simion, Valenza, Macchi Cassia, Turati, & Umiltà, 2002). In light of this evidence, it is not unlikely that these two properties may still play a relevant role in modulating the responses of the visual perceptual system in adulthood. This would explain why the P1 showed an enhanced response to each stimulus in which one of the two relevant perceptual properties was broken, and an even further enhanced response to the stimulus in which both properties were disrupted. In each of these three cases, additional processing was needed in comparison to the canonical face stimulus for which both properties were intact. Moreover, the fact that this same gradient of sensitivity is also observed for the latency of the N170 suggests

that the properties that modulate general visual perceptual responses are intrinsically tied to the later processing stage at which the structural properties of the face are encoded.

Although the hypothesis of an additive effect produced by the violation of the two investigated structural properties was supported in part by the ERP evidence, results from the amplitude of the N170 and the VPP did not follow the predicted additive pattern. Interestingly, for each of these components, the sole violation of the vertical symmetry property in the AT stimulus produced responses of the greatest amplitude (in the right hemisphere, in the case of the N170), whereas the violation of the up–down featural arrangement property did not seem to have any impairing effect. The absence of an amplitude increase to the SB face in comparison to the canonical ST face does not replicate previous observations of N170 amplitude sensitivity to face inversion (e.g., Sagiv & Bentin, 2001; Rossion, Gauthier, et al., 2000). However, although reported in the literature, this effect is less consistent than the latency shift produced by stimulus inversion, which in fact was observed also in the present study (e.g., Rossion, Joyce, et al., 2003; Bentin et al., 1996). Moreover, it should be noted that the inversion used in the current study was subtler than that used in previous face inversion studies, in that it relates exclusively to the inner features without including the outline of the face, and this may allow for the expectation of a smaller inversion effect in the present data.

A more striking finding is the lack of amplitude differentiation at the N170 and VPP between the AB scrambled face, in which both of the perceptual properties were disrupted, and both the ST canonical face and the SB face stimulus. Because the N170 is thought to reflect the encoding of the specific structure of the face, these results seem to indicate that no additional resources were required to encode either of the bottom-heavy stimuli used (SB and AB), as compared to the resources required to encode ST. In contrast, enhanced processing, reflected by larger N170 amplitude over the right hemisphere, is required to encode the AT stimulus, which differs from the ST canonical face by lack of vertical symmetry. This enhanced processing for the AT stimulus is also evident in comparison to the other two scrambled faces. This finding is strikingly analogous to the behavioral performance manifested by the subjects. Accuracy and efficiency measures demonstrated that the ST canonical face was the easiest stimulus to be detected and judged as upright, whereas the AT scrambled face was the most difficult, with no difference between the SB and AB stimuli. These findings, similar to the N170 and VPP amplitude findings, did not lend support to the hypothesis that disrupting both properties would have an additive impairing effect on orientation judgment responses. Rather, the drop in behavioral performance for the AT stimulus seems to reflect a difficulty in the

orientation judgment that mirrors the enhanced processing required to encode the stimulus at the structural encoding stage reflected by the N170/VPP complex.

Nevertheless, the relationship between the obtained behavioral and ERP findings allows for two possible interpretations. A first intriguing possibility is that the perceptual structural properties of the AT stimulus caused an increase in the resources required to encode this stimulus at the visual processing stage where the basic structure of a visual object is typically extracted, which carry over to the later occurring behavioral performance. Specifically, the presence in the AT stimulus of all of the properties typically embedded in faces (i.e., a face outline and an up–down disposition of the inner facial features with the eyes at the top and the mouth at the bottom), with the only exception of vertical symmetry in the disposition of the elements and the canonical local orientation of the features, may have rendered the AT stimulus a particularly ambiguous visual object. In particular, the top-heavy property displayed by the AT stimulus likely rendered this stimulus more ambiguous than the bottom-heavy AB stimulus, which also displayed a face outline, a vertically asymmetrical distribution of the elements and a local misorientation of the facial features. Although several hundred milliseconds and several processes separate the occurrence of the N170/VPP complex and the behavioral response given by the subject, the ambiguity at the structural encoding stage of visual processing of the AT stimulus may have had impairing effects on the later occurring behavioral performance.

An alternative interpretation of the concordance between the behavioral and ERP effects observed for the AT stimulus is that the demands of the behavioral task used in the present study may have induced enhanced processing of the AT stimulus at both the electrophysiological and behavioral levels. The task asked subjects to make an orientation judgment on the basis of the up–down arrangement of the inner facial features, with an upright judgment being correct for the ST as well as AT stimuli, and an inverted judgment being correct for the SB and AB stimuli. This task was intended to induce categorization of the stimuli on the basis of their general structural properties rather than their face-like resemblance. In this way, the task allowed for direct comparisons between the intact face and each of the three nonface stimuli used. Nevertheless, due to the nature of the stimuli used, subjects may have had a spontaneous bias to use a face versus nonface classification criterion. Although most subjects reported little difficulty in the orientation judgment task, stating that they used the placement of the eyes or mouth within the face outline to guide their decision, and subjects who reported using a different judgment criterion were removed from the study due to their low accuracy rates, it could be hypothesized that subjects may have shifted back and forth from the use of one criterion to another through-

out the task. If this were the case, the stimulus most penalized by the criterion shift would be AT, in that it would be the only stimulus that could correspond to either response key depending on the criterion used. For example, when the subject used a face versus nonface criterion, the AT stimulus would correspond to the same nonface key as the SB and AB stimuli. On the other hand, when using an upright versus inverted criterion, the AT stimulus would correspond to the same upright key used for the ST canonical face. Importantly, regardless of the judgment criterion being used, the response keys to which the other three stimuli corresponded would remain invariable. It may be hypothesized that the drop in behavioral performance in the orientation judgment task for the AT stimulus reflected the described inconsistency of the judgment criterion used by the subjects. Although still debated, there is evidence suggesting that the N170 is penetrable by high-order cognitive processes, such as natural familiarity (Caharel et al., 2002) and perceptual (e.g., Bentin & Golland, 2002) or familiarity effects induced by priming (Jemel et al., 2003). In light of this evidence, it could be proposed that the increased cognitive demands required to correctly classify the AT stimulus as upright, through top-down influences, may have induced extra processing at the encoding stage of visual processing, resulting in the exaggerated N170 and VPP amplitudes.

Although both of the above interpretations of the relationship between ERP and behavioral measures are broadly consistent with our findings, we favor the first, according to which the increased N170/VPP amplitude for the AT stimulus is a consequence of an enhanced difficulty in encoding the structural properties of this stimulus at the early perceptual stages of processing. In the present study, the enhanced amplitude effect for the AT stimulus was found only over the right hemisphere. This finding mirrors those obtained by a number of studies examining the effects of face inversion, which reported that differences in N170 amplitude between upright and inverted faces were more pronounced in the right as compared to left hemisphere (e.g., Eimer, 2000a; Rossion, Delvenne, et al., 1999). These data are typically taken as further evidence that stimulus inversion has a disruptive effect on the configural processes involved in the structural encoding stage of face processing, in which the right hemisphere, where the N170 is typically most prominent (e.g., Rossion, Joyce, et al., 2003; Bentin et al., 1996), has a greater involvement. Similarly, our demonstration of a right hemisphere localized amplitude effect for the AT stimulus reinforces the hypothesis that this effect is a result of a selective amplification of neural activity typically devoted to face processing, rather than a consequence of top-down influences induced by the demands of the behavioral task. Moreover, the majority of ERP investigations of the effects produced by face inversion also used a behavioral orientation judgment task, providing evidence for im-

paired performance for inverted as compared to upright faces. From these studies, the proposal has been made that the origin of this differential behavioral performance most likely arises from the structural encoding stage reflected by the N170 (e.g., Rossion, Delvenne, et al., 1999). This same interpretation could likely apply to the current observed concordance between behavioral and ERP measures.

A possible way to unravel which of the two abovementioned hypotheses could best explain the relationship between the obtained behavioral and ERP findings could be to conduct a further study testing subjects in a passive-viewing task using the same stimuli. By doing so, no task would be conducted which may interfere with the natural visual processing of the stimuli. If the N170/VPP amplitude data we have obtained are in fact influenced by the specific demands of the task we used, as described above, the prediction would be that, by eliminating the task, the amplitude data for the two components would mirror the additive pattern of results which was obtained for the latency of the same components. Alternatively, if the amplitude effects reflect the enhanced processing required to encode the AT stimulus on the basis of its structural properties, we could expect that results obtained from subjects tested in a free viewing condition would resemble those from the current study. As already mentioned, however, the vast majority of ERP studies examining the electrophysiological effects of face inversion have used an active-viewing orientation judgment task. In order for our results to be comparable to those studies, which provide the scarce available evidence concerning the effects of configural changes on early face-sensitive ERP components, the use of an orientation judgment task seemed more appropriate for the current study.

Regardless of the specific interpretation of the relationship between our behavioral and ERP findings, it should be highlighted that both of the abovementioned hypotheses hint to the ambiguous nature of the AT stimulus, which we believe can only be explained as deriving from its face-like top-heavy configuration. Indeed, the fact that more processing is required for the AT stimulus at the structural encoding stage, and/or that two different judgment criterions may have been used by the subjects to classify this stimulus, cannot depend on the misorientation of the features, which is also present in the two other nonface stimuli (SB and AB), nor on the vertically asymmetrical disposition of these features, a property which is also present in the AB stimulus.

It is interesting to note that the concordance between the amplitude effects at the N170/VPP and the behavioral performance is present only when accuracy is considered. Rather, reaction time data more closely resembled the latency results from the N170 and VPP, in that the AT stimulus did not produce the slowest overall reaction times.

Collectively, these data seem to indicate that the timing of the processes involved in the encoding of face stimuli has been affected strictly by the experimental manipulations, giving rise to an additive pattern in which the disruption of both the investigated structural properties had a more detrimental effect than the disruption of each single property alone. Instead, the amount of processing required appears to be more affected by one particular alteration of the face configuration, which is the one that disrupted the vertical symmetry in the feature distribution, leaving intact the top-heavy configuration of those features.

A secondary goal of the study was to verify if a concordance could be observed between the N170 and the VPP with each of the experimental manipulations. The presence of a significant linear increase in latency for both components, as well as the identical pattern of results observed for amplitude, confirms previous observations of a high degree of functional similarity between the response properties of the N170 and the central VPP (see Joyce & Rossion, 2005; Rossion, Joyce, et al., 2003). Moreover, the demonstration that the VPP can be modulated by specific alterations of the face configuration is particularly important, as only two studies have measured the effects of featural displacement on this component, providing conflicting results (Yamamoto & Kashikura, 1999; George et al., 1996).

The evidence gathered in the current study provides a number of contributions to different areas of research. Within the adult face processing literature, results from the current study complement and extend previous work, which has shown that disrupting the face configuration affects the face-specific brain responses. These effects are commonly explained as a consequence of the disruption of relational information processing (see Rossion & Gauthier, 2002). By evaluating how systematic changes in face structure affected face-related ERP components, the current study strived to determine the specific nature of the configural information that defines the face structure and that is required for normal face processing. For example, with respect to the face inversion effect literature, both our behavioral and ERP data replicated the typically reported performance impairment (e.g., Collishaw & Hole, 2000; Yin, 1969; also see Rossion, Joyce, et al., 2003; Rossion, Gauthier, et al., 2000 for results in a similar orientation judgment task) and latency delay observed for N170 and VPP components (e.g., Rossion, Joyce, et al., 2003; Itier & Taylor, 2002). Importantly, our data show that inversion is only one of the possible ways in which the face configuration can be disrupted and that the violation of the basic structural property of up–down featural arrangement is at least one of the factors explaining the face inversion effect. This last conclusion is strengthened by the fact that stimulus inversion in the current study involved exclusively the inner portion of the face and not the external contour, and therefore, the canonical face (ST)

and the inverted face (SB) differed mainly for the number of features appearing in the upper and lower parts of the image.

The only other difference between the ST and SB stimuli was related to the orientation of the local features, which were rotated by 180° in the SB stimulus. However, it is unlikely that differences in local feature orientation played a relevant role in the observed pattern of results. If this were the case, we would expect the differences between the ST and SB stimuli, which differed for both the local orientation (i.e., 0° vs. 180°) and the up–down arrangement of the features, to be more pronounced than the differences between the AT and AB stimuli, which differed only for the up–down featural arrangement, with both stimuli containing features oriented to the same degree (i.e., 90°). Instead, this was not the case. Overall, our ERP findings showed that differences between ST and SB were present for two of the four analyzed N170 and VPP measures, namely, the latency of the N170 and the latency of the VPP. In comparison, the AT and AB stimuli showed differentiation at three analyzed measures, namely, the amplitude of the N170, and the latency and amplitude of the VPP. Moreover, the lack of amplitude differences between the SB and AB stimuli, which contained features rotated to a different degree, although surprising in light of our additive hypothesis, further demonstrates that the local rotation of the features was not the driving factor in determining the effects observed in the current study. Although these two stimuli differed in latency of the N170 and the VPP, this finding was expected based on our hypothesis of an additive effect produced by the disruption of the two investigated structural properties, both of which were disrupted in the AB stimulus.

In addition to the abovementioned arguments favoring the idea that local rotation of the features was not fundamental in modulating the effects observed in the current study, it should be noted that there is no existing evidence in the literature concerning the specific effects produced by local misorientations of the facial features on face-sensitive ERP components. In fact, even the experiments investigating the role of specific facial features in modulating the N170 (Bentin et al., 1996) always used stimuli in which the features, importantly the eyes, retained their natural upright orientation. The same is true in studies which used real face images to investigate the effects provoked by dislocation of the features (Gliga & Dehaene-Lambertz, 2005; George et al., 1996).

Instead, we propose that the same logic used in the current study, which was to systematically disrupt each of the structural properties which combine to define a face with the aim of determining the specific nature of the configural information required for normal face processing, could be applied to the investigation of the effects produced by selective alterations of the orientation and/or location of different facial features. An investigation of this type would allow for a better understanding of the contribution of the different information present in a face to the specific electrophysiological markers of face processing. For example, in a recent study (Gliga & Dehaene-Lambertz, 2005), eye alignment (i.e., eyes appearing next to each other on the same horizontal plane) has been proposed to play a role in modulating the N170 response to eyes appearing in distorted faces. This suggestion was based on the observation that distorted faces in which the eyes were displaced independently did not evoke the typical enhanced amplitude responses observed for distorted faces containing aligned eyes (Bentin et al., 1996, Experiment 5; George et al., 1996). This amplitude enhancement was, on the other hand, observed in the current study for the AT stimulus, which did not display the canonical alignment of the eyes. Therefore, in general, the effects of orientation and/or specific dislocation of the features within the face merit further investigation. Lacking indications from the literature, the rotation of the eyes in each of the distorted face stimuli used in the current study was done with the intention of reducing the possibility that any evoked response could be due to a specific eye-sensitive detector such as that proposed by Bentin et al. (1996). In the same manner, the intentional removal of the hair was done to eliminate the possibility that the hair would provide too strong of a face context for each of the nonface scrambled stimuli. Thus, although N170 responses to faces without the external features have been shown to be smaller and attenuated in comparison to normal faces (Eimer, 2000b), in the current study this elimination was intended to allow for a more direct investigation of the differences produced by the manipulation of the two considered structural properties.

Finally, another area of research for which the results of the reported study appear particularly relevant is that of the development of face processing. Intriguingly, the results illustrate that both ERP and behavioral face-specific responses in adults are modulated by two nonspecific visual structural properties that have been shown to be particularly salient for the infant's perceptual system in the early stages of development. One of these properties (i.e., up–down featural arrangement) has been shown to play a crucial role in driving the early attentional bias toward schematic and real face images, which has been observed at birth (Macchi Cassia, Turati, et al., 2004; Turati et al., 2002). Specifically, the same AT stimulus, which in the current study elicited particularly enhanced processing and poor behavioral performance in adults, has also been shown to induce a spontaneous visual preference of the same extent of that induced by the canonical ST face in newborns (Macchi Cassia, Turati, et al., 2004).

Taken together, we interpret these findings as supporting the recent claim that the development of the

face processing system gets its start from a number of nonspecific attentional biases that are already at work at birth, which progressively tune part of the perceptual system into its expert and face-specific adult-like form. Support for this conclusion comes from a recent behavioral and ERP investigation with 3-month-old infants (Macchi Cassia, Kuefner, Westerlund, & Nelson, in press), which compared the canonical ST face and the AT stimulus, demonstrating that the two stimuli elicited differential behavioral attentional responses which were not present at birth. At the electrophysiological level, however, data from the infant ERP components thought to reflect the structural encoding stage of face processing (i.e., N290 and P400) indicate that the general visual structural property of up–down asymmetry still plays a crucial role in modulating brain responses to faces. The lack of electrophysiological differentiation between the ST and AT stimuli at 3 months points to the high degree of perceptual similarity between the two stimuli induced by their structural likeness, a factor that, in the current data, likely provoked the enhanced processing for the AT stimulus at the structural encoding stage of visual processing.

## Acknowledgments

## Note

1. The ANOVAs on the latency and amplitude of the P1 were performed on 14 of the 18 subjects. Four subjects were removed from these analyses because of bad signal at electrodes O1 and O2.

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