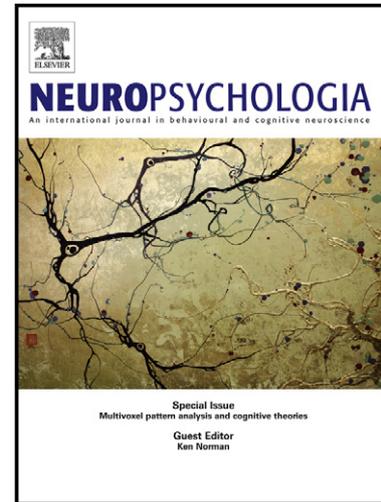# Author's Accepted Manuscript

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Fixation location on upright and inverted faces modulates the N170

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Abstract

The current study used event-related potentials (ERP) in combination with a variable viewing

position paradigm (VVPP) to direct fixations to specific face parts (eyes or mouths) in

upright or inverted whole faces. The N170 elicited by the VVPP was greater to faces than to

non-face objects (wristwatches), and was delayed and enhanced in response to face inversion.

A larger N170 response was elicited when the participants' fixation was directed to the eyes

than when directed to the mouths of both upright and inverted faces, an effect that was also

modulated by the spatial location of the face in the visual field. The N170 face inversion

effect (upright minus inverted) was greater when fixations were directed to the mouth than

when directed to the eyes, suggesting that the point of fixation within a face modulates brain

potentials due to contributions from the features themselves, as well as their relative location

in the visual field.

1. Introduction

Data from a large body of behavioural studies suggests that face perception involves the interplay between two levels of processing. These are featural processing of the individual parts of a face, principally the eyes, the mouth, and the nose and holistic processing, which refers to the integration of information across the whole face (see McKone & Yovel, 2009, for a review; Sergent, 1984). While upright faces are processed holistically, inverting faces disrupts holistic processing and affects the ability to recognise aspects of faces, such as their identity, emotion and gender (e.g., Calder et al., 2000; Chatterjee & Nakayama, 2012; Rossion, 2012). Electrophysiological studies examining the relationship between these modes of processing have focused on the earliest face-sensitive event-related potential (ERP) that can be reliably measured: the N170. This bilateral peak, occurring over occipito-temporal regions between 130 and 200 ms, is typically larger to faces than non-face stimuli (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer 1998; Rossion et al., 2000) and is typically delayed and enhanced for inverted, as compared to upright, faces (Itier, Latinus & Taylor, 2006; Itier & Taylor, 2004; Linkenkaer-Hansen et al. 1998; Rossion et al., 2000). This inversion effect has been interpreted as reflecting a disruption to holistic processing (e.g., Itier & Batty, 2009; Robbins & McKone, 2007; Rossion & Caharel, 2011; Van Belle de Graef, Verfaillie, Rossion & Lefèvre, 2010).

While holistic processing has been found to be an important dimension of face processing, the individual face features themselves also appear to contribute when participants are asked to judge face identity and familiarity (Roberts & Bruce, 1988) or gender (Best, Minsaw & Strauss, 2010; Roberts & Bruce, 1988; Shepherd, 1981). These studies suggest that the eyes, relative to other features, carry the most relevant information

for these task. However it should be noted that the procedures in these experiments have involved either the masking of certain features or the presentation of features in isolation, which intrinsically disrupts holistic processing. Similar patterns have been observed in ERP studies, where eyes presented in isolation have been found to elicit larger N170 responses than other face features, such as the mouth (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Similarly, when participants are presented with whole faces in which only small regions can be seen in "Bubbles", the N170 is largest when the eyes can be seen as compared to other parts of the face (Schyns et al., 2003). Interestingly, eyes presented in isolation trigger a larger N170 than faces without eyes (Itier, Alain, Sedore & McIntosh, 2007), and paradoxically, the response to isolated eyes is even larger than to whole faces that include the eyes (Bentin, et al., 1996). This, and other findings, led Itier and colleagues (2007; also see Itier & Batty, 2009) to propose a model of N170 face and eye-sensitivity, whereby the N170 reflects the operation of both eye-sensitive and face-sensitive neurons, but that the latter exert a degree of inhibition on eye-sensitive neurons when presented within whole upright faces. A refinement to the model was proposed by Nemrodov and Itier (2011), whereby eye-sensitive neurons are also able to modulate face-sensitive neurons when viewing inverted faces. Thus, in upright faces, which are processed holistically, the N170 reflects responses of primarily face-sensitive neurons In contrast, the larger N170 in response to inverted faces where holistic processing is disrupted is theorised to be due to the summed response from both face- and eye-sensitive neurons. Similarly, whole faces with the eye region removed or masked only activate face-sensitive neurons, where N170 amplitudes are equivalent for upright whole faces with and without eyes (Itier et al., 2007). A strongly reduced inversion effect for faces without eyes found in that study, coupled with a similar magnitude N170 elicited in response to isolated eyes and whole inverted faces (which would be expected if inverted faces and

isolated eyes activate both eye-sensitive and face-sensitive neurons) further points to the eyes as exerting a significant influence over the N170 peak.

While it is clear that the eye region strongly contributes to the N170, the exact role of the eyes in the early processing of faces is still unresolved. For instance, Sadeh and Yovel (2010) agree with Itier and colleagues that the N170 is larger for inverted than upright faces because additional neural mechanisms are recruited for inverted face processing, but they question whether they are eye-selective neurons or more general object processing mechanisms. More recent studies by Itier and colleagues (Nemrodov & Itier, 2011) also suggest that eyes may serve as an anchor point, forming a reference for the processing of others features and/or structures. This suggestion implicates not only the importance of the eyes themselves to the N170, but the role the eyes might play as a reference point for the processing of other features or face structures.

However, disrupting holistic processing has been found to modulate performance on behavioural tasks (e.g., the composite effects, Rossion, 2012) as well as the N170 peak (e.g., Rossion, 2000). Thus, the majority of previous studies which suggest that the eyes disproportionately contribute to N170 responses have used paradigms that also disrupt the normal face configuration (i.e., presenting eyes in isolation or faces with eyes removed) and as such, have also disrupted holistic processing (Bentin, Allison, Puce, Perez & McCarthy, 1996; Itier, Alain, Sedore & McIntosh, 2007; O'Conner, Hamm & Kirk, 2007). Thus, a question remains as to how the eyes are processed when presented within an intact whole face, which facilitates holistic processing and is the more naturalistic context in which eyes are perceived. McPartland, Cheung, Perszyk and Mayes (2010) investigated whether the N170 to intact whole face was modulated by varying the point of gaze, finding an enhanced N170 amplitude when participants' gaze was cued to the upper (approximately between the eyes) and lower (approximately the mouth) parts of a face compared to when gaze was cued

to the centre (approximately the nose) or when there was no gaze cue at all. In contrast to the

previous studies using more artificial stimuli, this study suggests that in whole faces both the

eye and mouth regions enhance N170 responses. However, McPartland and colleagues

presented fixation crosshairs for a long time (between 500 to 1,000 ms) so that multiple eye-

movements could have been made away from the cues before the presentation of the faces.

That study also did not monitor gaze, and it is therefore uncertain whether the participants

were looking where directed. As such, it is premature to conclude that the mouth is as

important as the eyes when whole intact faces are processed.

Here, we revisit the question of whether the eyes disproportionately modulate N170

responses when presented in whole faces by integrating ERPs with the variable viewing

position paradigm (VVPP), which allows for the initial fixation to a particular stimulus to be

directed over particular regions of a visual stimulus (O'Regan, Lévy-Schoen, Pynte, &

Brugaillere, 1984; O'Regan & Jacobs, 1992). In this study, participants were asked to fixate

on a central fixation cross, triggering the presentation of a whole face. The face was

positioned so that the participants' gaze fell directly on either the left eye, the right eye, or on

the mouth. We also used a non-face control condition – wrist-watches – where the VVPP

paradigm directed fixations to the exact same locations on these as to the faces. We chose

wrist-watches because they were familiar objects, similar in shape to the faces (i.e., round),

and have been used as non-face stimuli in previous ERP studies (e.g., Bentin, DeGutis,

D'Esposito & Roberston, 2007). The first aim of this study was to confirm that stimulus

presentation through the VVPP elicits activity that is comparable to that found in traditional

ERP paradigms – that is greater N170 amplitude to faces than non-faces (watches vs. faces),

and a delayed and enhanced N170 peak in response to face inversion (upright vs. inverted

faces). The second aim was to determine whether the N170 amplitude would be enhanced

when fixations were directed towards the eyes rather than another face part (the mouth), *when*

presented in the context of a whole face. As well as measuring N170 responses elicited by

fixations to the eyes and the mouth in whole upright faces, we also measured the response to

fixations on these features in inverted faces, to determine whether any difference in the

contributions of the eyes and the mouth to the N170 peak is modulated by the disruption of

holistic processing. Finally, the third aim was to determine whether fixations to the eyes of a

whole face enhance performance on a face-processing task (gender discrimination) compared

to fixations on the mouth, similar to the facilitation observed in response to these features in

isolation when asked to judge gender (Best, Minsaw & Strauss, 2010; Roberts & Bruce,

1988), and whether any such facilitation is modulated when holistic processing is disrupted

by face inversion.

2. Methods

The Human Ethics Committee at Macquarie University approved the methods and

procedure used in this study.

2.1. Participants

Eighteen participants (13 females, 16 right-handed), aged between 19 and 30 years

(mean age = 24.2 years), took part in the study. All participants had normal or corrected-to-

normal vision, and gave their informed consent before participating in the study. Sixteen

participants were Caucasian. Two participants were Asian but had resided in Australia for at

least three years, and thus had extensive exposure to the race of the face stimuli (i.e.,

Caucasian faces). Participants volunteered or were reimbursed $30 for their time.

2.2. Stimuli

Face stimuli consisted of 200 grey-scale images of Caucasian individuals (100 female, 100 male). The faces were presented twice each: Once upright and once inverted. Faces were emotionally neutral, and cropped within a standard sized oval frame where only the internal face parts were visible (see Figure 1). The face images were obtained from seven databases: NimStim (Tottenham, et al., 2002), the Karolinska Directed Emotional Faces (KDEF; Lundqvist, et al., 1998), Gur et al. (2002), Computational Vision Archive (courtesy of Caltech), the MIT-CBCL (Weyrauch, et al., 2004), the Ekman and Friesen face set (Ekman & Friesen, 1976), and a set from Kieran Lee and David Perrett of St Andrews University.

As well as measuring the N170 to upright and inverted faces, we measured the N170 to upright and inverted non-face stimuli to ensure that our N170 was analogous to the face-sensitive N170 indexed by previous face processing studies. The non-face stimuli were grey-scale images of 50 different wristwatches (see Figure 1), sourced from the University of Kansas Information and Telecommunication Technology Center database. The images were presented once in an upright condition and once in an inverted condition. Like the face stimuli, each wristwatch was cropped to fit within a standard size oval frame.

The face and watch stimuli were presented on a 19" CRT computer monitor with a refresh rate of 100 Hz at a distance of 50cm from the participant. As such, each image was 12.7^0 x 17.4^0 degrees of visual angle.

2.3. On-line electroencephalogram (EEG) and eye-tracking

The EEG was recorded using 30 Ag-AgCl sintered electrodes embedded in an elastic cap (EasyCap) positioned according to the 10-20 system. The left and right earlobes were used as online and offline references, respectively. The ground electrode was located between the Fz and FPz electrodes. Electrode impedances were kept below 5 kΩ. Ocular movement was recorded with bipolar electrodes placed at the outer canthi, and above and below the left eye. The online EEG was sampled with a Synamps II amplifier at a sampling rate of 1000 Hz, with an online band-pass filter of 0.05 to 100 Hz, and a notch filter at 50 Hz Participants' eye-movements were tracked and recorded with a monocular (right eye) Eyelink 1000 eye-tracker sampling at 1000 Hz.

2.4. Procedure

Participants were fitted with the EEG cap and positioned in the eye-tracking headrest. Stimulus presentation was controlled by Experiment Builder software (version 1.6.1) utilising a gaze-contingent central fixation cross to initiate the presentation of the images. Participants were instructed to judge whether the presented stimulus was a female face, male face, or watch using buttons on a keypad. Each trial started with a centrally-presented white fixation cross on a black background. Once the participant had fixated on the cross for 150 ms, an upright or inverted face or watch was presented for 200 ms. Each stimulus was positioned so that the participant's gaze fell on the right eye, the left eye, or the mouth of a human face, or the corresponding regions of a watch face. The "right" and "left" eye refers to the right and left side from the perspective of the viewer. The face presentation was followed by a black screen that lasted until a button response was recorded. Finally, a "blink now" screen was displayed for 1500 ms before the next trial started. Accuracy and response latencies of button

responses were recorded. The onset of each stimulus sent a serial port code to the online EEG

recording. The order of stimuli presentation was randomised.

There were 500 trials in total: 200 for upright faces (100 with gaze directed equally to

either right and left eye, 100 with gaze directed toward the mouth), 200 for inverted faces

(with fixations directed to the eyes and mouth in the same manner), 50 trials with upright

watches (25 with gaze directed to locations corresponding the eye on faces, and 25

corresponding to the mouth on faces) and 50 trials with inverted watches (with fixations

directed in the same manner as in upright watches). There were fewer trials in the watch than

face conditions because the non-face condition was not of primary interest and we wanted to

minimise the length of the testing session. It is important, however, to note that the

proportion of trials in which participants' gaze was directed toward the three key regions was

kept in proportion across face and watch conditions.

2.5. Offline ERP processing

The EEG data was analysed offline with Neuroscan 4.3 software. Re-referencing of

scalp EEGs was achieved through a common average of all electrodes (excluding ocular

sites), following the removal of VEOG artefacts from EEG sites using a standard ocular

reduction algorithm. EEG epochs and condition averages were time-locked to the onset of the

fixation-driven stimulus presentation. These -100 to 600 ms EEG epochs were baseline

corrected using the period 100ms prior to stimulus onset, and were filtered through a band-

pass of 0.1 – 30 Hz with 12 dB/octave roll-off. Trials containing EEG artefacts exceeding +/-

80 µV were excluded from analysis. Participants' recorded eye-movements were analysed

with Eyelink Data viewer 1.10.1 software in order to remove trials that involved eye-

movements away from the relevant face parts (beyond a circular region 2 degrees of visual

angle in diameter centred on the face-part) within the 200ms of stimulus presentation. This

process excluded approximately 20% of the trials, resulting in the analysis of, on average, 42 left eye, 42 right eye, and 72 mouth trials for upright faces, 42 left eye, 42 right eye, and 83 mouth trials for inverted faces and 38 trials for upright and 41 inverted watches, respectively. The latter were split into 19 trials for fixations to regions corresponding to the eyes, and 18 corresponding to the mouth in upright watches, and 20 and 21 trials respectively for inverted watches, providing a limited number of trials, yet yielding a generally balanced upper versus lower region comparison for the watch stimuli to determine whether any differences between the eyes and the mouths in the face stimuli might be driven by a simple upper versus lower visual field effect due to low-level visual properties.

Visual analysis of the condition average waveforms revealed the N170 peak latencies and amplitudes to be maximal at the occipito-temporal left P7 and right P8 electrodes, which is similar to the findings of previous studies (see Rossion & Jacques, 2007 for review). A grand average formed from all upright stimuli showed a distinct N170 peak occurring at around 160 ms, and accordingly a peak detection algorithm was applied over a time window of 130-190 ms (30 ms either side of this N170 peak in the grand average waveform) in order to extract the latency and amplitude measures for the N170 peaks. P1 and a P1 to N170 peak-to-peak analyses were performed to account for possible differences in the baselines leading into the N170 peaks. Accordingly, P1 peak values were extracted from a time window of 70-130 ms (30 ms either side of 100 ms), and subtracted from the N170 peak amplitudes to form the peak-to-peak amplitude difference values. The resulting P1 and peak-to-peak values were analysed separately with ANOVAs.

3. Results and Discussion

Levene's test of normality confirmed that the distributions of the N170 peak amplitude and latency data were normally distributed. Thus, repeated measures ANOVAs were used to address the three main aims of the study: (1) To determine whether faces presented through the VVPP exhibit a face-sensitive N170 response pattern comparable to that found in traditional ERP presentation, (2) to determine whether the N170 response is modulated by which part of a face is fixated upon in upright and inverted whole faces, and 3) to determine whether accuracy and correct response times on a gender discrimination task are modulated by the point of fixation on upright and inverted faces.

3.1. Is the N170 measured with the variable-viewing position paradigm (VVPP) face-sensitive?

The N170 measured using the VVPP paradigm showed face-sensitivity (larger amplitude for faces than watches), particularly over the right hemisphere (see Figure 2), irrespective of fixation location. This is in line with previous studies, which have typically presented faces with fixation in the centre of the face (e.g., Bentin et al., 1996; Eimer 1998; Rossion et al, 2000). Furthermore, the ERP-VVPP paradigm replicated the typical face inversion effect, with a larger and delayed N170 in response to face inversion (e.g., Itier, Latinus & Taylor, 2006; Itier & Taylor, 2004; Linkenkaer-Hansen et al. 1998; Rossion et al., 2000) (Figure 2). In contrast, the N170 response for watches was not modulated by inversion, which is in line with previous results suggesting that the N170 to objects is less sensitive to inversion compared to faces (Rossion et al., 2000).

Supporting statistics (described below) were obtained via ANOVAs with three repeated-measures factors: Hemisphere (P7 on the left; P8 on the right), Stimulus Type

(Face; Watch) and Stimulus Orientation (Upright; Inverted). Interactions were investigated with follow-up ANOVAs and paired comparisons.

N170 peak amplitude.

There was a main effect of Stimulus Type, where N170 peaks elicited by faces (M = -9.16 µV; SE = .99 µV) were significantly larger than those elicited by watches (M = -2.85 µV; SD = .68 µV) [$F(1, 17) = 61.45, p < .001$]. There was also a main effect of Stimulus Orientation, where inverted stimuli elicited a larger N170 (M = -6.56 µV; SE = .75 µV) than upright stimuli (M = -5.45 µV; SE = .78 µV) [$F(1, 17) = 13.53, p < .002$]. There was also a main effect of Hemisphere [$F(1, 17) = 10.49, p = .005$], with N170 peaks significantly larger at the right P8 electrode (M = -7.19 µV; SE = .92 µV) than at the left P7 electrode (M = -4.82 µV; SE = .75 µV).

These main effects were moderated by two significant interactions. First, an interaction between Hemisphere and Stimulus Type was observed [$F(1, 17) = 5.78, p = .028$]. Although larger peaks were elicited by faces than watches at both P7 (-7.38 µV; SE =.96 µV versus -2.26 µV; SE = 71 µV) [$p < .001$] and P8 (-10.95 µV; SE = 1.26 µV versus -3.44 µV; SE = .83 µV) [$p < .001$] electrodes, there was a greater difference between the stimuli at the right P8 electrode (-7.5 µV; SE = 1.09) than at the left P7 (-5.12 µV; SE =.77 µV) (see Figure 2). Second, a Stimulus Type by Stimulus Orientation interaction [$F(1, 17) = 10.59, p = .005$] was observed, due to a significant increase in N170 amplitude when faces were inverted (Mean difference = -1.65 µV; SE = 3.99) [$p = .001$], whereas inversion of the watch stimuli did not lead to a significant amplitude increase (Mean difference = -0.57 µV; SE = 2.8 µV) [$p = .057$]

N170 peak latency.

      This ANOVA revealed a main effect of Stimulus Orientation [$F(1, 17) = 5.69$, $p =$ .029], with inverted stimuli (M = 164 ms; SE = 2) eliciting a later N170 compared to upright (M = 162 ms; SE = 3) stimuli. There was also an interaction between Stimulus type and Stimulus orientation [$F(1, 17) = 5.77$, $p = .028$], with a delay in N170 peak observed when faces were inverted (M = 164 ms, SE = 3) as compared to upright (M = 160, SE = 4) [$p =$ .008] but no difference in latency between inverted (M = 164, SE = 3) and upright (M = 164, SE = 3) watches [$p = .886$] (See Figure 2).

3.2. Does the point of fixation on a face modulate the strength of the N170?

      A critical finding in the present study was that the point of fixation clearly modulated the strength of the face-sensitive N170 response. For both upright and inverted faces, N170 amplitudes were larger when either the left or right eyes were fixated, as compared to the mouth (see Figure 3 and 4b). This was seen clearly over P8, in which the N170 amplitude was in general larger. A similar pattern was seen over P7, but here the amplitude was only larger for the right eye as compared to mouth (although note that amplitudes to right and left eye did not significantly differ, see Figure 4b). Fixations to the right eye evoked a quicker N170 than fixations to the left eye or mouth, although this was only evident over P8 (see Figure 4c). Inversion of the faces delayed the N170 regardless of which feature was centrally fixated (see Figure 4a & 4d). An increase in amplitude in response to face inversion was observed when the mouth, and left and right eyes were fixated, however this face inversion effect was strongest when the mouth was fixated compared to the eyes in general, suggesting this effect was modulated by the point of fixation (Figure 4a & 4c).

Supporting statistics (described below) were provided via ANOVAs with three repeated-measures factors: Hemisphere (P7 on the left; P8 on the right), Fixation Type (Left Eye; Right Eye; Mouth) and Stimulus Orientation (Upright; Inverted). Significant interactions were investigated with Bonferonni corrected paired comparisons.

Face N170 peak amplitude.

There was a main effect of Hemisphere [$F(1, 17) = 10.07$, $p = .006$], with N170 peaks significantly larger at P8 than P7 and a main effect for Orientation [$F(1, 17) = 62.91$, $p < .001$], with the N170 significantly larger to inverted than upright faces. A significant effect of Fixation Type [$F(2, 34) = 18.73$, $p < .001$] was moderated by two interactions. First, there was an interaction between Fixation Type and Orientation [$F(2, 34) = 10.07$, $p = .006$]. Examining this interaction showed that for upright faces, N170 amplitudes were larger when either the left or right eyes were fixated as compared to the mouth ($p < .001$ for both comparisons), whereas fixations to the left and the right eye did not differ from each other ($p = .43$). The same pattern was seen for inverted faces: larger N170 amplitudes for left and right eyes as compared to mouth ($p = .02$ and $.03$, respectively) and no significant difference between the left and right eyes ($p = 1$) (see Figure 3 & 4b). We also compared the effect of face inversion at each fixation type (i.e., the difference in N170 amplitude between upright and inverted faces). A larger N170 inversion effect was observed when fixations were on the mouth rather than the left eye or the right eye (see Figure 4a & 4c), but only the former comparison was statistically significant when corrected for multiple comparisons (left eye vs. mouth: $p < .001$; right eye vs. mouth: $p = .15$, or $.049$ before correction).

There was also an interaction between Hemisphere and Fixation Type [$F(2, 34) = 5.05$, $p = .012$]. At P7 N170 peaks were larger for fixations to the right eye than to the mouth

(p = .017), with no significant difference between the right eye and the left eye (p = .623) or

the left eye and mouth (p = .475). At P8, fixations to both left and right eyes elicited larger

N170 peaks than fixations to mouths ($p's$ < .002), with no significant difference between the

left and right eye (p = .237).

Face N170 peak latency.

There was a main effect of Orientation, where inverted faces elicited significantly

later N170 peaks (M = 163) compared to upright faces (M = 157) [$F(1, 17)$ = 60.43, p <

.001] (Figure 4c). There was also an interaction between Hemisphere and Fixation Type [$F(2,$

34) = 4.58, p = .017]. An ANOVA on the right P8 electrode revealed a significant effect of

Fixation Type [$F(2, 34)$ = 9.94, p < .001], due to fixations to the right eye leading to earlier

N170 peaks than fixations made to the left eye (p = .002) or the mouth (p = .02) but no

significant difference between the left eye and the mouth (p = .851). There was no significant

effect of Fixation Type at the left P7 site (p = .259) (Figure 4d).

P1 peak amplitude

The ANOVA performed on P1 peak values revealed significant main effects of

Fixation Type [$F(1.5, 24.9)$ = 11.75, p < .001] and Hemisphere [$F(1, 17)$ = 8.87, p = .008],

while there was no significant effect for Stimulus Orientation (p = .065). The significant

effects were however modulated by an interaction between Hemisphere and Fixation Type

[$F(1.5, 25.9)$ = 48.4, p < .001]. ANOVAs performed at each electrode site separately revealed

a significant effect of Fixation Type at P7 [$F(1.4, 23.2)$ = 25.56, p < .001] and P8 [$F(2, 34)$ =

45.04, p < .001] electrode sites. However, at the left P7 electrode pairwise comparisons

showed that fixations to the left eye lead to larger P1 peaks than fixations to either the right

eye (p < .001) or the mouth (p < .001), which were not different from each other (p = .817),

whereas at the right P8 electrode fixations to the right eye lead to larger P1 peaks than

fixations to either the left eye ($p < .001$), or the mouth ($p < .005$), and fixations to the left eye

lead to larger peaks than to the mouth ($p < .001$). This pattern is more clearly depicted in

figure 3, where it can be seen that a larger P1 peak was elicited in the hemisphere ipsilateral

to the eye fixated. As the P1 has been found to be most sensitive to low-level physical

properties such as brightness and contrast (Ganis, Smith & Schendan, 2012), it is likely that

this effect was driven by the differing amounts of visual information that was projected into

the participants' visual systems. In the case of a fixation centred on the right eye, more visual

information would have been present in the left visual field than in the right, which would

then project more information to the right cerebral hemisphere, and vice-versa for a fixation

centred on the left eye. It is notable that this pattern is present for both upright and inverted

faces, suggesting that the orientation of the faces did not alter this low-level visual factor.

P1-N170 peak-to-peak amplitude

Given that the P1 peaks were modulated by fixation point, the potential for different

baselines from which the N170 peaks arose was addressed through P1-N170 peak-to-peak

analysis, where an omnibus ANOVA revealed significant main effects of: Fixation Type

[$F(2, 16) = 32.31$, $p < .001$], Stimulus Orientation [$F(1, 17) = 73.26$, $p < .001$], and

Hemisphere [$F(1, 17) = 17.61$, $p = .001$]. These main effects were modulated by interactions

between Hemisphere and Fixation Type [$F(2, 34) = 16.74$, $p < .001$] and Stimulus

Orientation and Fixation Type [$F(2, 34) = 5.36$, $p = .009$]. Separate ANOVAs conducted at

each electrode site were performed to clarify the interaction between Hemisphere and

Fixation Type, revealing a significant effect of Fixation Type at both P7 [$F(2, 34) = 14.25$, $p

< .001$] and P8 [$F(2, 34) = 30.52$, $p < .001$]. Pairwise comparisons investigating Fixation

Type at each electrode site revealed similar patterns as the analyses of P1 peak amplitudes,

where fixations to the left eye lead to larger peak-to-peak amplitudes at the left P7 electrode than fixations to the right eye ($p < .001$) or the mouth ($p < .001$), which were not significantly different from each other ($p = .29$). Similarly, fixations to the right eye lead to larger peak-to-peak amplitudes than fixations to the left eye ($p < .001$) or the mouth ($p < .001$) at the right P8 electrode, which were also not significantly different from each other ($p = .069$).

A main effect of Fixation Type was found for both upright [$F(2, 34) = 31.86$, $p < .001$] and inverted faces [$F(2, 34) = 12.06$, $p < .001$]. Pairwise comparisons revealed that fixations to the mouth lead to significantly lower peak-to-peak amplitudes than fixations to the left eye ($p < .001$) or the right eye ($p < .001$) in upright faces, as well as inverted faces ($p = .001$ & $.033$, respectively), while similar amplitudes were elicited by the left and right eyes in both upright and inverted faces. As these analyses did not fully clarify the interaction between Fixation Type and Stimulus Orientation observed in the omnibus ANOVA, an analysis of the effects of stimulus inversion for each Fixation Type was performed, revealing a larger amplitude increase in response to face inversion when the mouth was fixated compared to the left eye ($p = .001$), with no significant difference between the mouth and the right eye ($p = .193$) or the left eye and the right eye ($p = .12$).

The peak-to-peak analysis revealed patterns that displayed similarities to both the P1 and N170 analyses where fixation-location modulated peak amplitude differences, indicating a strong influence of the eyes to the N170 response, as well as where the eyes were positioned in the visual field. In addition to the effects observed in the N170 analysis, the peak-to-peak analysis suggests that the relative N170 response is modulated not only by whether an eye is centrally fixated, but also by the relative position of the face in the visual field which manifested in larger responses in the hemisphere ipsilateral to the visual field containing the larger amount of the face.

VVPP for Faces vs. Watches

Using the VVPP we found that, for both upright and inverted faces, N170 amplitudes were larger when either the left or right eyes were fixated, as compared to the mouth. In order to clarify whether this pattern of results was particular to faces, we also examined whether the N170 was modified by fixation location to the watches. Given that there were fewer trials to watches than faces, and the previous analysis revealed that responses to the left and right eye were typically equivalent, we opted to only compare upper and lower fixations on the watches (i.e., the fixations to the regions of the left and right eye were combined). ANOVA's with the factors Hemisphere (P7; P8), Fixation Type (Upper; Lower region) and Orientation (Upright; Inverted) revealed no significant main effects or interactions, for either peak amplitude or latencies (see Figure 5).

3.3. Is the ability to judge gender modulated by the point of fixation on upright and inverted faces?

For upright faces, participants were more accurate and quicker at judging the gender of a face when the fixations were to the eyes than the mouth. However, fixation location did not affect the ability to judge gender in inverted faces. Accuracy and response times to judge the gender of the faces were analysed with repeated measures ANOVAs and Bonferroni-corrected paired comparison with the factors: Fixation Type (Left eye; Right eye; Mouth) and Orientation (Upright; Inverted).

Accuracy

A significant main effect for Orientation was observed [$F(1, 17) = 203.12$, $p = .017$], where upright faces elicited more correct responses (M = 92%, SE = .8) than inverted faces (M = 81.2%; SE = 1.1). There was an interaction between Fixation Type and Orientation [$F(1.4, 24.5) = 8.12$, $p = .004$], which further ANOVAs at each orientation revealed was due to an

effect of Fixation Type for upright faces [$F(2, 34) = 13.81$, $p < .001$], but not for inverted

faces. Pairwise comparisons of the different Fixation Types in the upright face condition

revealed that accuracy was significantly greater when participants fixated the left ($p = .001$)

and right ($p = .003$) eye compared to when they fixated the mouth (see Figure 6a), while the

eyes did not differ from each other ($p = 1$).

Response times

Significant main effects were observed for Fixation Type [$F(2, 34) = 3.97$, $p = .028$],

and Orientation [$F(1, 17) = 66.79$, $p < .001$], as well as an interaction between these two

factors [$F(2, 34) = 4.58$, $p = .017$]. A significant effect of Fixation in upright faces [$F(2, 34)$

$= 7.2$, $p = .002$] was due to slower responses when fixations were on the mouth rather than to

the left eye ($p = .006$) or the right eye ($p = .02$), which were not different from each other ($p =$

1). The effect for inverted faces only approached significance, $F(2, 34) = 3.25$, $p = .051$] (see

Figure 6b),

4. General Discussion

The primary novel aim of the current study was to use the VVPP-ERP paradigm to

determine whether the eyes contribute disproportionately to the N170 response compared to

the mouth when viewed within configurally intact whole upright faces, and also in inverted

faces where holistic processing is disrupted. There were three critical findings in the present

study that illustrate the influence of fixation location to the N170 response. The first was that

the N170 (and also P1-N170 peak-to-peak) amplitudes were larger when fixations were

directed to eyes than mouths in whole upright faces. The second was that fixations to the eyes

of inverted faces also lead to larger N170 peaks than fixations to the mouth, suggesting that

the eyes contribute significantly to the N170 whether holistic processing is impaired or intact.

The third finding of significance was that the enhancement of the N170 peak was greater in

response to inverted faces when the mouth was centrally fixated than when the eyes were

fixated. The first two findings point to a generally larger influence of the eyes to the N170

response in faces, supporting previous suggestions about their relative importance as features

compared to other face parts (Itier et al., 2007). However, the third finding of an enhanced

inversion effect for mouth fixations, coupled with the findings of other recent studies

highlighting the importance of where in the visual field face parts are presented (Issa &

DiCarlo, 2012; Zerouali et al., 2013), suggests that there is an interplay between the salience

of the features themselves and their spatial location. This is further highlighted by the peak-

to-peak analysis, which found that the laterality of the eye-sensitive N170 effect was

modulated by the positioning of the face in the participants' visual field. We interpret the

findings of the current study as relating to these two distinct yet interacting factors: the

salience of the eyes as features and the spatial location of faces in the visual field.

4.1. The salience of the eyes as features

The larger N170 response when fixations were to the eyes of a whole upright face

compared to the mouth reinforces the findings of previous studies that have found similarly

large N170 peaks to eyes when features were presented in isolation (Bentin et al, 1996) or

selectively occluded (Schyns et al., 2003), and further indicates that the eyes contribute

strongly to the size of the N170 peak when holistic processing is intact. This pattern contrasts

with the results of a recent study by McPartland et al. (2010) that cued participants' gaze to

different parts of whole upright faces, which found the N170 elicited by the eye and mouth

regions to be of comparable amplitude. However, that paradigm involved visual attention

directed to a general eye-region rather than specifically to either eye, and did not control

participants' eye-position with an eye-tracker. It is therefore possible that the differing pattern

of results between the two studies may be due in part to a more specified fixation to the eyes

in the current study. In addition to finding larger responses to the eyes within upright faces, we also observed larger N170 responses to the eyes within inverted faces, indicating that the eyes retain their importance to the N170 peak when holistic processing is disrupted by face inversion. Importantly, while gaze modulated responses to faces, this was not the case for our non-face control condition, wrist-watches. This is in line with Kloth, Itier and Schweinberger (2013) who used fronts of cars with and without headlights and found that car fronts elicited an N170, but this was not modulated by inversion, and moreover, that the N170 to upright and inverted car fronts, with and without lights, was larger than to isolated lights. The present study and that of Kloth et al. indicate that specialized effects for eyes do not transfer to similarly organized non-face objects.

The larger N170 response to eyes in whole upright faces, however, is not in accord with Itier et al.'s (2007) model (and Nemrodov and Itier's later refinement in 2011) of face and eye-sensitive neurons, which predicts the activation of eye-sensitive neurons in response to a disruption of holistic processing, but not when holistic processing is intact. It seems therefore likely that the eyes themselves contributed significantly to the N170 response in the current study without the necessity of a disruption to holistic processing. This effect may be due to the response of additional neurons that are particularly sensitive to the eyes, as theorised by Nemrodov and Itier (2011), activated by a direct fixation on an eye within whole upright faces. Alternatively, the eyes may simply possess a more general face-like quality and therefore recruit more face-sensitive neurons than the mouth. Such a suggestion is plausible given findings of a recent primate single-cell/multiunit study where recording locations were pre-defined via fMRI, which found that most face-selective cells in a macaque posterior face-patch to be driven by the presence of one eye within a face outline (Issa & DiCarlo, 2012). Interestingly, Issa and DiCarlo found that the presence of an eye in a visual field led to a strong response in the contralateral hemisphere. Here we also saw a lateralisation of the eye-

sensitivity in P1-N170 peak-to-peak amplitudes, where differences between the eyes and the

mouth manifested in the hemisphere ipsilateral to the eye that was centrally fixated. This

pattern is similar to that observed by Issa and DiCarlo, where larger cortical responses were

found to eyes presented in the contralateral visual field, as a fixation to the left eye in the

current study would have lead to the right eye being present in the right visual field, and thus

projected to the contralateral visual cortex, and vice-versa for right-eye fixations. These

findings suggest that the relative positioning of the eyes in participants' visual field may

significantly modulate the manifestation of eye-sensitivity.

The finding that fixations to the eyes elicited larger N170 responses than fixations to

the mouth in both upright and inverted whole faces suggests that the eyes possess a large

degree of salience as features. However, the influence of fixation location on which

hemisphere this eye-sensitivity manifested, coupled with the disproportionate increase of

N170 amplitudes in response to face inversion when the mouth was centrally fixated

compared to the eyes suggests that the spatial positioning of faces in the visual field may also

strongly influence face-sensitive neural responses.

4.2. The spatial location of faces in the visual field

Modulating the location of a fixation to a whole face not only determines which

features are centrally foveated, but it also controls where other face information is presented

in the visual field. This influence was observed in the current study, where fixations made to

the left or right eye in both upright and inverted faces were seen to modulate the P1-N170

peak-to-peak amplitudes. Given the enhanced amplitude to eyes in general, the larger N170

amplitude increase observed in response to face inversion when the mouth was centrally

fixated compared to fixations to eyes also suggests the influence of a factor beyond the

salience of the features themselves. The difference in the effect of inversion when the mouth

was fixated points to more to a general upper versus lower visual field advantage in face

processing. When fixations were made to the eyes of upright faces in the current study, face-

information projected to participants' central (the eyes) and lower (the mouth) visual fields.

When fixations were made to the mouth, face-information was projected to the central

(mouth) and upper (the eyes) visual fields (see Figure 1). This lead to a difference of where in

the visual field face-information was presented. Thus, inverting the faces in the current study

not only disrupted holistic processing, but also led to a difference in which visual fields face-

information was projected. This factor may, in part, explain the increased face inversion

when the mouth was centrally fixated compared to the eyes, since this also entailed a change

in which visual field relevant face-information was projected. It is possible that repeated

experience with upright faces may lead to the central and lower visual fields becoming most

sensitively tuned to respond to face-information. If this were the case, then the greater N170

response to the eyes in whole upright faces observed in our study could be explained as being

due to a simple effect of face information projecting into visual fields that are typical for such

stimuli and a general advantage of fixating the upper part of a face, regardless of orientation,

rather than an enhanced response to the eyes.

This argument was recently suggested by Zerouali et al. (2013), who directed

fixations to various regions of upright and inverted faces, modulating where in the visual

field these and other features were presented (Zerouali et al., 2013), and found larger N170

responses to the eyes in upright faces, but that face inversion disproportionately enhanced the

N170 when the mouth was centrally fixated compared to the eyes. However, in that study the

eyes no longer elicited a larger N170 than the mouth in inverted faces, suggesting a general

upper-field advantage for fixations to faces, regardless of orientation. This is in contrast to

the results of the current study, where even though a larger N170 inversion effect was

observed in the current study when fixations were made to the upper part of an inverted face

(the mouth), the eyes still elicited larger N170 amplitudes in general regardless of face

orientation. In lieu of conceptual differences between the present study and that presented by

Zerouali et al. (2013), it is possible that a combination of differences between the chosen

stimuli and the method of directing fixations to relevant face parts might provide insight into

the different patterns of activation in response to face inversion observed in the two studies.

While the face stimuli presented by Zerouali et al. were larger than that presented in the

current study (17^0 x 23^0 versus 12.7^0 x 17.4^0 degrees of visual angle, respectively), the

regions of the faces that participants were directed to fixate were also larger in the former

study (7.5% of the whole face area for each eye region, and 12.3% for the mouth region).

This, combined with transient saccadic movement before actual face presentation, lead to a

greater variety of landing positions on the faces compared to the landing positions in the

current study, which fell within a circular zone over each of the eyes and the mouth,

encompassing 1% of the whole face area for each. This focused the fixations to the precise

face parts rather than additional surrounding regions. It is possible that the more specifically

targeted fixations to the eyes and the mouths themselves in the current study may have lead

to a different level of activation from each feature in response to face inversion, which has

been suggested to lead to enhanced featural processing due to impairment of holistic

processing (Rossion, 2012 for review). Given that Zerouali et al. sampled N170 responses to

fixations over broader regions of a face, it is possible that the influence of the individual

features were minimised, contributing less to the N170 response than a more targeted

fixation.

Issa and Dicarlo's (2012) study implicating the importance of where in the visual field

the eyes are positioned further illustrates the potential influence face-size has over neural

responses. If such an effect were in part driving the larger N170 response to eyes in the

current study, then the reduced N170 response when the mouth was viewed in upright and

inverted faces might be due to the eyes being further away from the central visual field than when they were centrally fixated. Thus, the larger the faces appeared in the visual field the less the eyes would contribute to the N170 when the mouth was centrally fixated, and the greater the difference in N170 elicited.

4.3. The influence of fixation location in a gender-discrimination task

An additional important finding of the current study is that fixations directed to the eyes in upright faces lead to significantly faster and more accurate responses on a gender discrimination task compared to fixations on the mouth. This echoes the findings of behavioural studies that have found isolated upright eyes to provide greater facilitation on this task than isolated upright mouths (Best, Minsaw & Strauss, 2010; Roberts & Bruce, 1988), but further suggests that the eyes facilitate this judgment when they can be processed holistically. Interestingly, fixating the eyes was not beneficial when the faces were inverted, suggesting that a disruption to holistic processing impairs the use of the eye region. This is similar to the findings of Scheller et al. (2012), who observed that performance on a gender task was enhanced when participants fixated on the eye region of fearfully expressive faces compared to the mouth, but unlike in the current study, this effect was not found for neutral faces. Hills et al. (2011) used a similar behavioural paradigm as used in the current study but asked participants to judge identity rather than gender. They found that fixating on the eye region facilitated performance compared to fixating on the mouth, in both upright and inverted faces. In fact, in that study the deleterious effect of face inversion was reduced by directing fixations to the eyes. Although gender and identity both involve judgements about invariant aspects of faces, a comparison of these two studies suggests that differences in the processing of gender and identity (e.g., see Chatterjee and Nakayama, 2012 for a study showing intact gender processing but impaired identity processing in developmental

prosospagnosia) can be modulated by directing eye fixations. Although it was not the goal of

the current study to compare the patterns of the N170 neural response and performance on the

gender-discrimination task, it is interesting to note that although the eyes elicited larger N170

peaks in inverted faces compared to the mouth, this imbalance of activation did not translate

to a benefit of fixating the eyes in the task. In consideration of the different patterns of

influence that fixation-location had in the different behavioural tasks implemented by

Scheller et al. (2012) and Hills et al. (2011), a direction of future research into the importance

of fixation-location on face-sensitive N170 responses should seek to clarify whether task-

demands may modulate this factor.

5. Conclusions

The outcomes of the present study support the use of the VVPP-ERP paradigm to investigate

face processing. Using this paradigm, a number of well-established effects of face processing

on the N170 were replicated, with two theoretically relevant exceptions. First, for the

processing of upright faces, the VVPP-ERP paradigm revealed that the N170 when fixations

were directed to eyes was larger than when fixations were directed to mouths, suggesting that

the eyes provide a strong contribution to the N170 response in configurally-intact faces.

Second, fixations to the eyes of an inverted face also led to a larger N170 response than

fixations to the mouth, suggesting that eyes lead to increased N170 responses in the presence

and absence of holistic processing in whole faces. While an inversion effect was found when

viewing either eyes or mouths, the inversion effect was greater when fixating mouths rather

than eyes. This suggests that the location of the feature in the participants' visual fields, as

well as the contribution of the features themselves, affects the N170. A broader conclusion is

that since the point of fixation was found to mediate the timing and strength of the face-

sensitive N170 peak, further studies investigating the neural processing of faces will benefit

from controlling the initial point of fixation.

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Fig. 1. *Examples of presented stimuli (stimuli were presented relative to a central fixation cross where a participant's gaze was directed to be over the left eye, right eye, mouth or corresponding regions of a wristwatch to upright and inverted faces and watches). The white grid-lines denoting the central positioning of the images are for illustration purposes only.*

Fig. 2. *N170 waveforms at left P7 and right P8 electrodes in response to upright and inverted face and watch stimuli, averaged across fixation location.*

Fig. 3. *(a) N170 waveforms in response to fixations directed to the left eye, the right eye, and the mouth of upright and inverted faces.*

Fig. 4. (a) *N170 waveforms illustrating the effect of inversion at each fixation point, and plotted values of (b) N170 peak amplitude elicited by each fixation point in upright and inverted faces at left P7 and right P8 electrodes, (c) N170 amplitude increase in response to face inversion for each fixation-type (upright face values subtracted from inverted face values) at each electrode site, and (d) N170 peak latencies for each fixation location in upright and inverted faces at each electrode. Error bars represent standard error.*

Fig. 5. *N170 responses to the upright and inverted watch stimuli when fixations were directed to the regions corresponding to the eyes and the mouths of the face stimuli.*

Fig. 6. *Accuracy and reaction time results of participants' performance on the gender discrimination task when fixations were directed to the left eye, the right eye and the mouth of upright and inverted faces. Error bars represent standard error.*
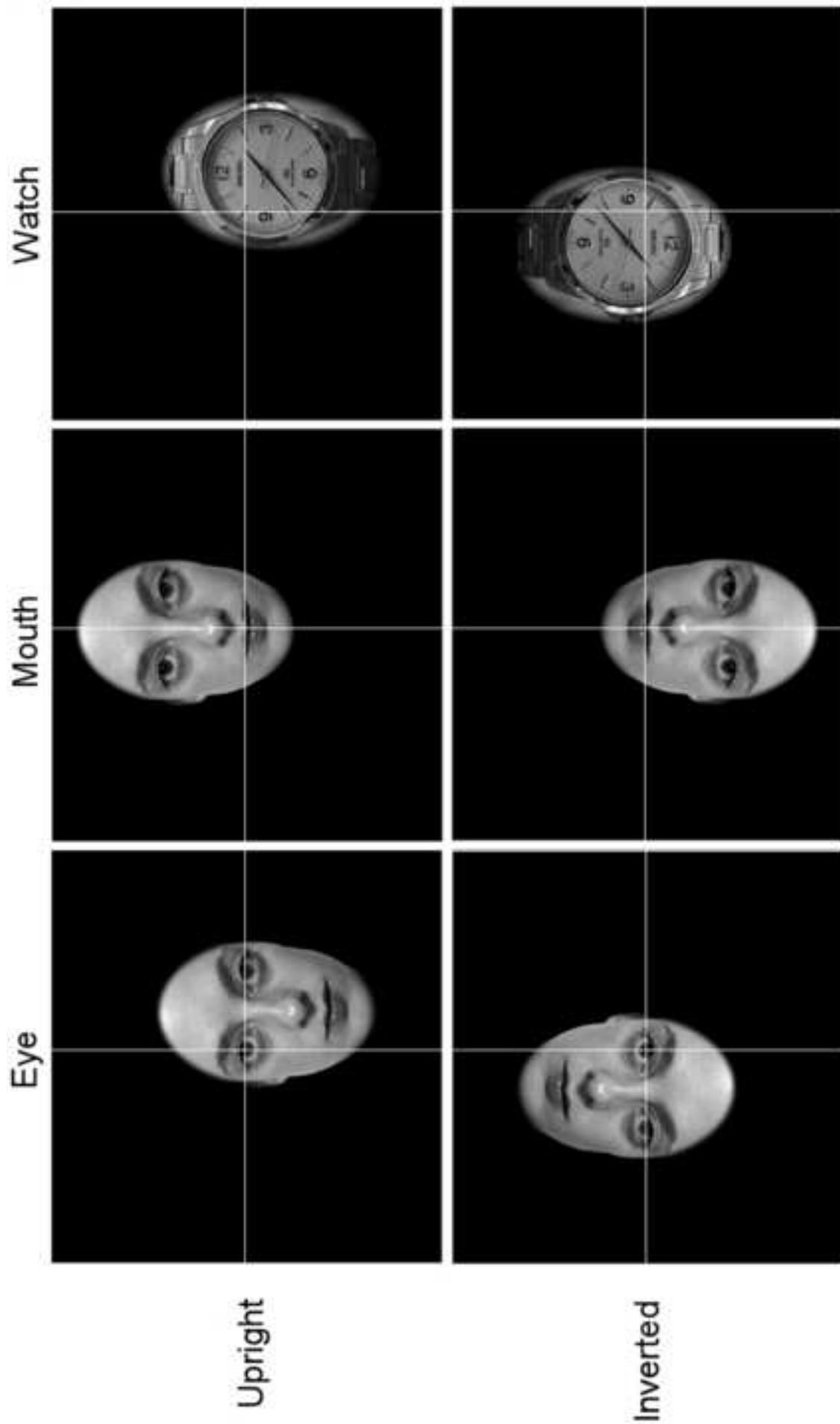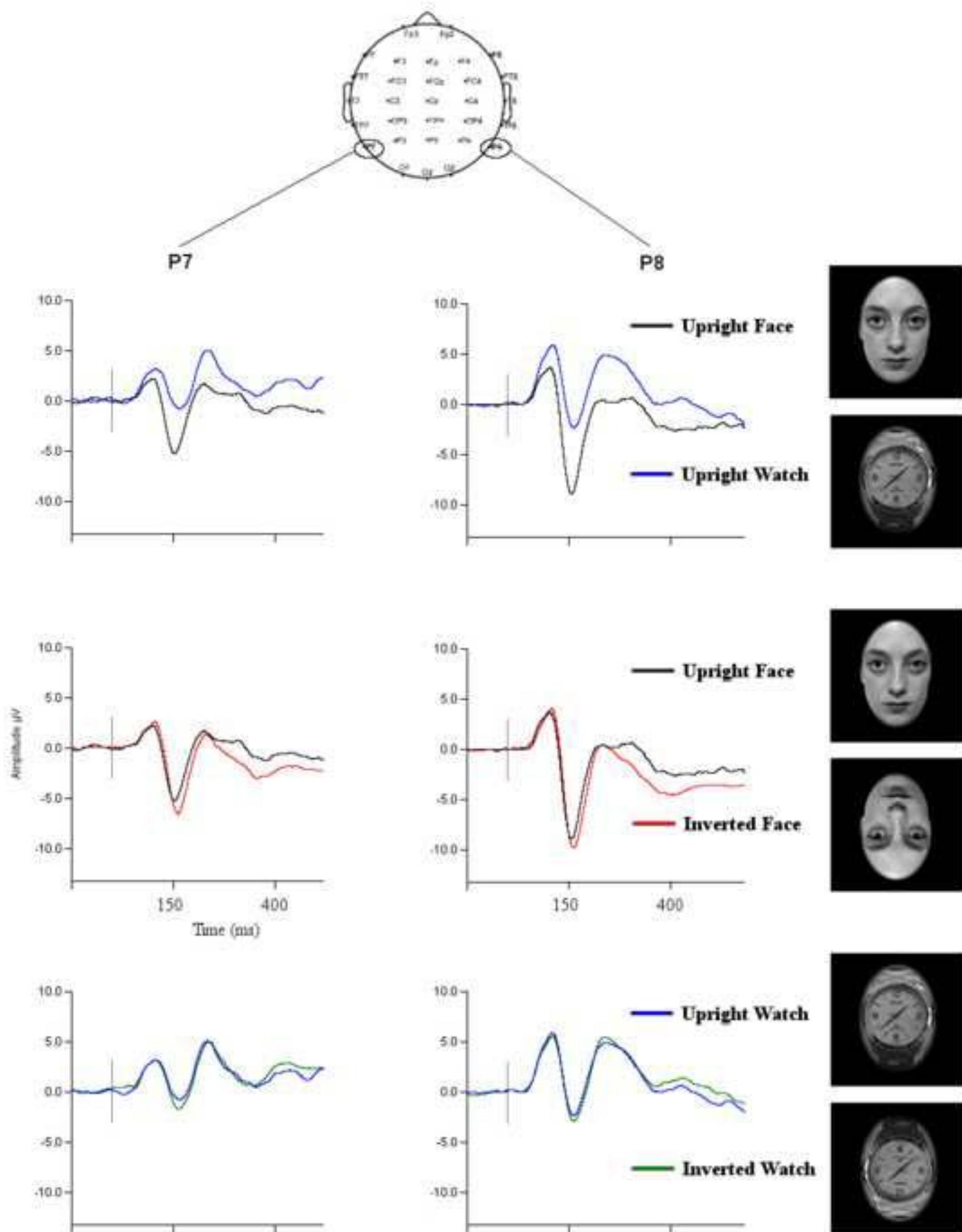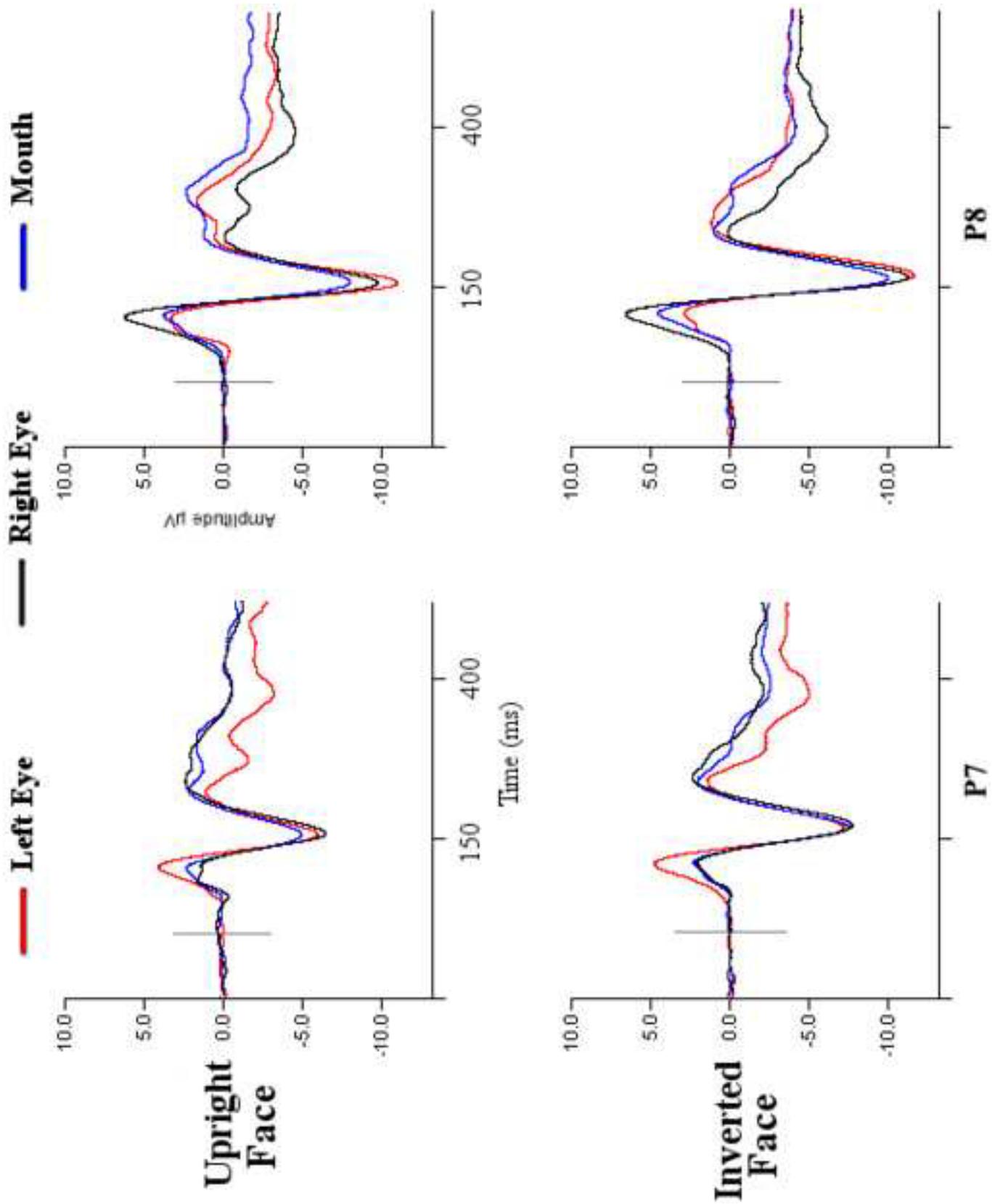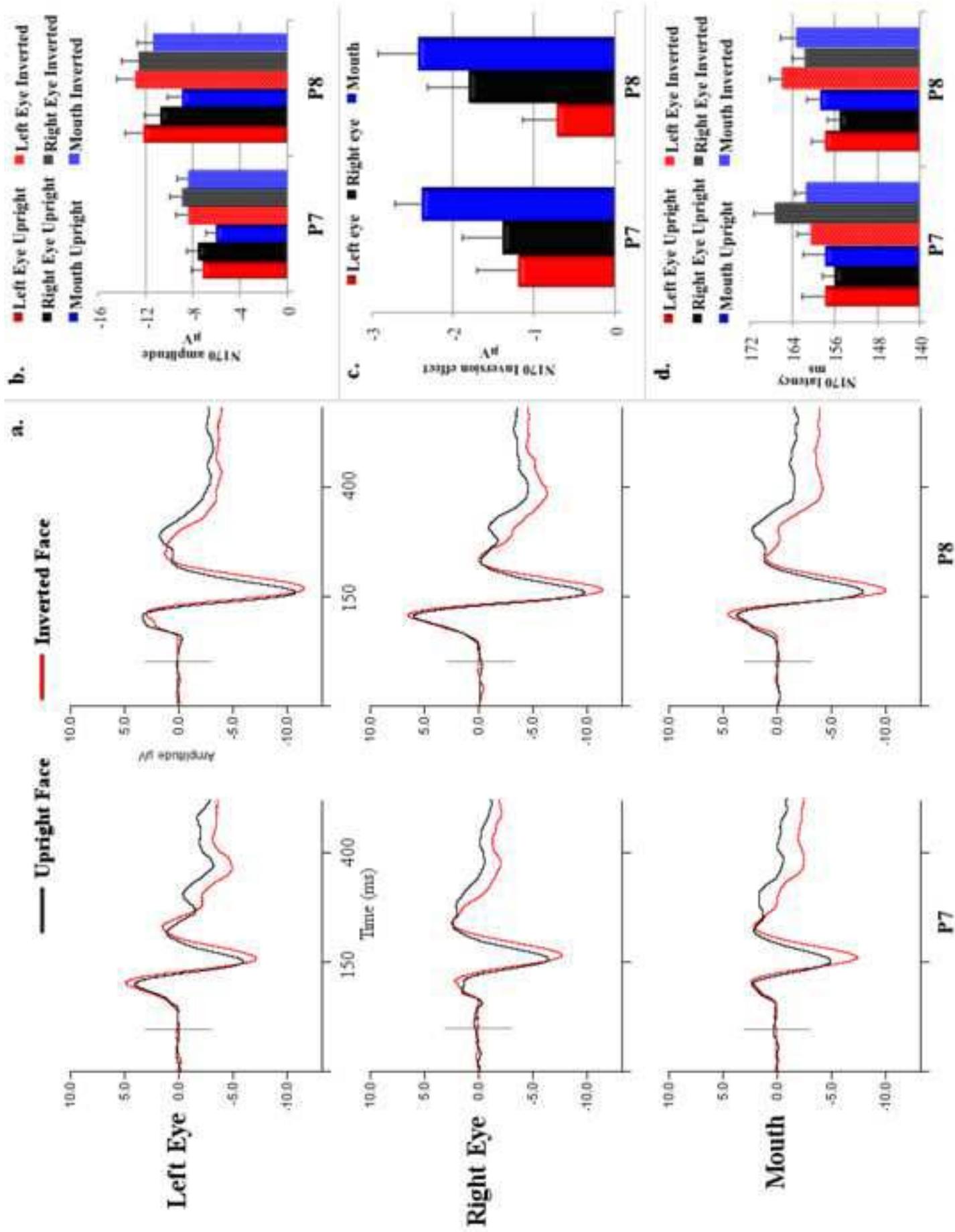
Figure 1

Figure 2

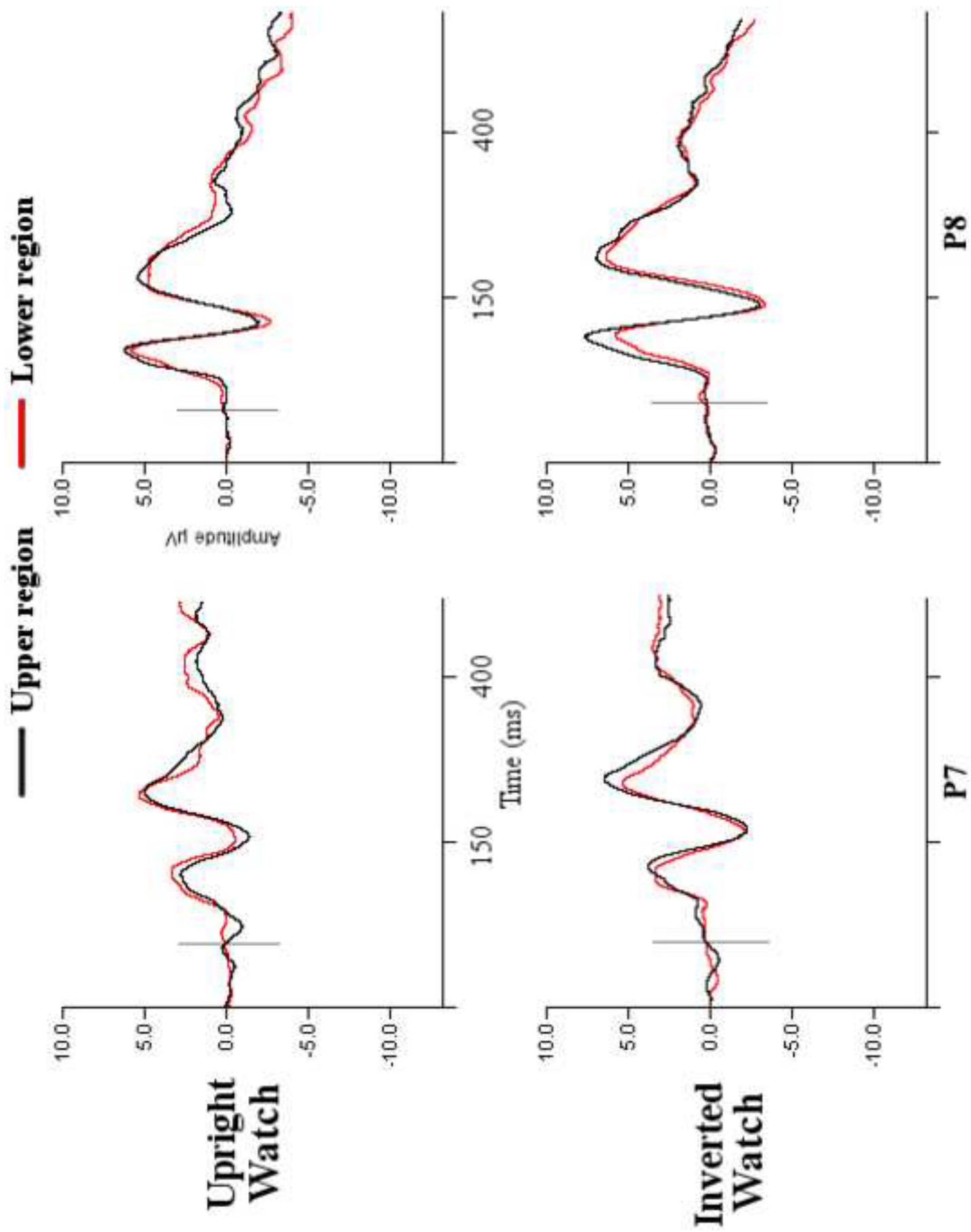ACCEPTED MANUSCRIPT
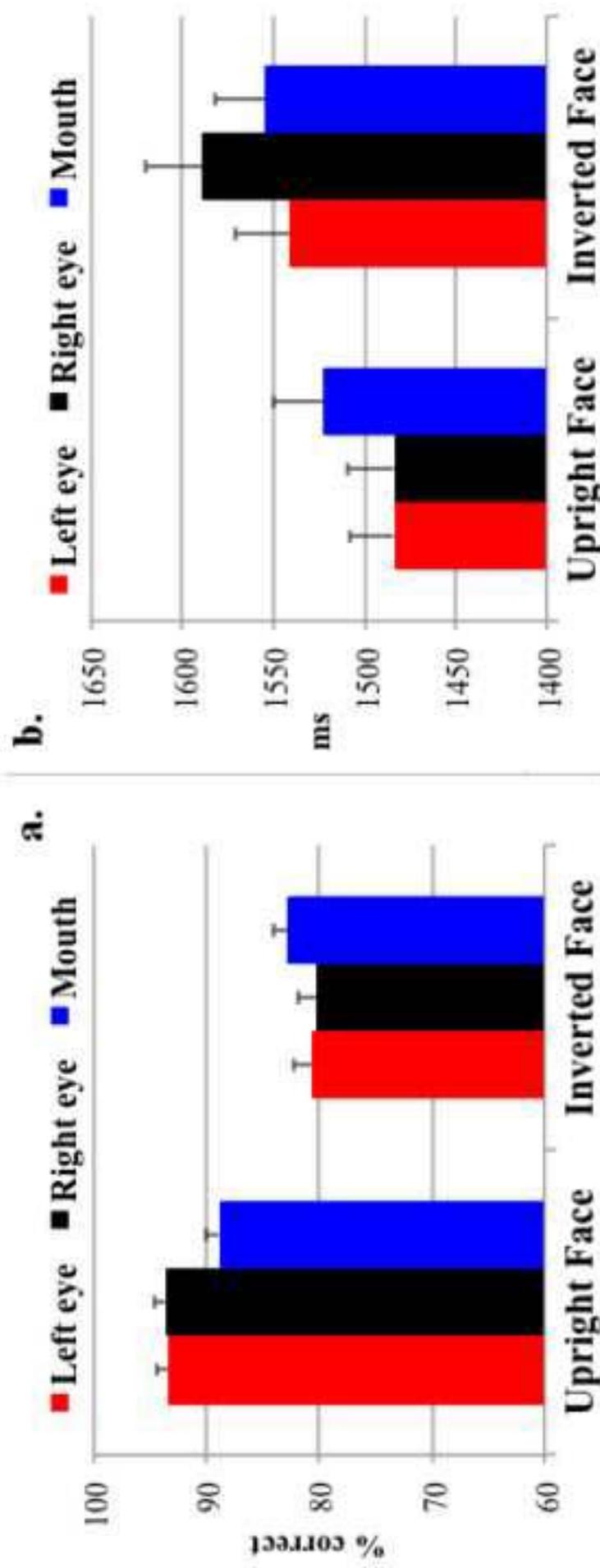
Figure 3

Figure 4

Figure 5

Figure 6

Highlights

- We directed fixations to the eyes and mouths in upright and inverted whole faces

- Eyes elicit stronger N170 responses when fixated in both upright and inverted faces

  compared to mouths

- The effect of face inversion is greater when viewing mouths than eyes

- Fixations to eyes enhanced performance on a gender discrimination task for upright

  faces only