The role of horizontal facial structure on the N170 and N250

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ABSTRACT

Recent studies have shown that horizontal facial structure is important for face identification (Dakin and Watt, 2009; Goffaux and Dakin, 2010). Also, sensitivity to horizontal structure is associated with the size of the face inversion effect (Pachai et al., 2013). However, it is unclear how the N170 and N250, two components of visual event-related potentials ERPs that have been implicated in face perception, are modulated by oriented facial structure in an upright face identification task. Here, we recorded ERPs and behavioural accuracy from adult observers performing a 1-of-6 face identification task in conditions that parametrically manipulated the orientation structure of upright faces. Faces were filtered with ideal orientation filters centred on either 0 (horizontal) or 90 deg (vertical). Filter bandwidth was varied across conditions from ± 45 to ± 90 deg in steps of ± 9 deg. As has been reported previously, response accuracy was significantly higher for faces that contained horizontal structure than vertical structure, and the horizontal-vertical difference was correlated with accuracy for unfiltered faces. In addition, the N170 and N250 were affected by the manipulation of horizontal facial structure. Furthermore, for the N250, but not the N170, the relative sensitivity to horizontal compared to vertical facial structure was significantly correlated with identification accuracy for unfiltered faces. We suggest that in a face identification task, the N250 but not the N170 is modulated by the amount of diagnostic information conveyed by horizontal structure.

1. Introduction

Human adults can identify faces that differ in viewpoint, illumination, and expression, but have great difficulty identifying faces that are rotated 180 deg in the picture plane (Yin, 1969). This so-called face inversion effect (FIE) likely is the by-product of everyday experience with upright, but not inverted faces (Sekuler, Gaspar, Gold, & Bennett, 2004; Valentine, 1988), and the influence of experience on recognition has been demonstrated in several studies that have shown that practice can induce large inversion effects for non-face objects (Diamond & Carey, 1986; Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier & Bukach, 2007; Husk, Bennett, & Sekuler, 2007; Hussain, Sekuler, & Bennett, 2009).

Why does inversion impair face identification? One idea is that experience with upright faces leads to the development, or improvement, of holistic/configural processing which complements feature-based processing, but which is disrupted by stimulus inversion (Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Grand, & Mondloch, 2002; Tanaka & Farah, 1993). However, the configural/feature framework

has been hindered by a lack of consensus about what constitutes a feature or a configural cue (Piepers & Robbins, 2012). In addition, Konar, Bennett, and Sekuler (2010) showed that the inversion effect could not be accounted for by configural processing. Another idea is that qualitatively similar strategies are used to encode upright and inverted faces (Sekuler et al., 2004; Murphy & Cook, 2017; Willenbockel et al., 2010), but that experience and learning increases efficiency for upright faces relative to inverted faces (Gold, Bennett, & Sekuler, 1999; Gold, Sekuler, & Bennett, 2004). According to this hypothesis, if information at particular spatial scales was critical for face identification, then we might expect to see differences in the spatial frequency selectivity for upright and inverted face identification. If observers used different spatial scales to identify upright vs. inverted faces, one would expect to find differences in the spatial frequency tuning for upright and inverted faces. In fact, human observers do rely most heavily on facial information in the 8–13 cyc/face spatial frequency range when discriminating upright faces (Gold, Bennett, & Sekuler, 1999; Näsänen, 1999; Tanskanen, Näsänen, Montez, Päällysaho, & Hari, 2005; Gaspar, Sekuler, & Bennett, 2008; Keil, Lapedriza, Masip, & Vitria, 2008);

however, Gaspar et al. (2008) found no difference in spatial frequency selectivity for upright and inverted faces (also see Royer et al., 2017; Willenbockel et al., 2010). Another possibility is that observers use different spatial sampling strategies to collect information about upright and inverted faces; however, studies using classification images (Sekuler et al., 2004) and eye-tracking (Rodger, Kelly, Blais, & Caldara, 2009; Williams & Henderson, 2007) have found that observers identify both upright and inverted faces using information primarily conveyed by pixels around the eyes and brows. Hence, previous studies have failed to find dramatic effects of face orientation on spatial frequency selectivity or spatial sampling of facial information.

Researchers recently have begun studying how observers use information conveyed by oriented facial structure. Dakin and Watt (2009) noted that the most diagnostic information of a face's identity is carried by structure in a horizontal orientation band centered around 0 deg (Fig. 1a). Goffaux and Dakin (2010) demonstrated that selectively removing horizontal facial structure, but not vertical structure, significantly affected the face inversion effect, facial identity after-effect, face-matching across different viewpoints, and certain measures of holistic processing. Furthermore, Pachai, Sekuler, and Bennett (2013) found that greater sensitivity to horizontal relative to vertical structure was significantly correlated with overall face identification accuracy for upright but not inverted faces, and that the degree of horizontal tuning was correlated with the magnitude of the face inversion effect. These results suggest that differential sensitivity to horizontal facial structure may underlie the face inversion effect. More recently, sensitivity to horizontal facial structure has been shown to contribute to more accurate identification of familiar compared to unfamiliar faces (Pachai, Sekuler, Bennett, Schyns, & Ramon, 2017), whereas reduced sensitivity to horizontal structure has been linked to prosopagnosia (Pachai, Bennett, Sekuler, Corrow, & Barton, 2015). Sensitivity to horizontal facial structure also plays an important role in the perception of emotional expressions (Balas, Huynh, Saville, & Schmidt, 2015; Huynh & Balas, 2014), and changes in horizontal tuning have been linked to changes in face perception that occur during childhood (Balas, Schmidt, & Saville, 2015; Goffaux, Poncin, & Schiltz, 2015), normal ageing (de Heering et al., 2016; Obermeyer, Kolling, Schaich, & Knopf, 2012; Sekuler, Pachai, Hashemi, & Bennett, 2015), and central vision loss (Yu & Chung, 2011).

Horizontal tuning, or bias, also has been found in neural mechanisms underlying face processing. For example, preferential activation to horizontal compared to vertical facial structure has been found in neurons in the lateral anterior patch of monkey inferior temporal cortex (Taubert, Goffaux, Van Belle, Vanduffel, & Vogels, 2016), and in BOLD activation in the human fusiform face area (Goffaux, Duecker, Hausfeld, Schiltz, & Goebel, 2016). Jacques, Schiltz, and Goffaux (2014) examined the influence of horizontal structure on the N170, the earliest time-window in the event-related potential (ERP) that is differentially sensitive to faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion et al., 2000; Rousselet, Macé, & Fabre-Thorpe, 2004). The N170, like behavioural measures, exhibits a face inversion effect. That is to say, there is a reliable difference between N170 latency and/or amplitude evoked by upright and inverted faces (Bentin et al., 1996; de Haan, Pascalis, & Johnson, 2002; Eimer, 2000; Itier & Taylor, 2002; Rossion et al., 2000; Rousselet et al., 2004; Rousselet, Husk, Bennett, & Sekuler, 2008). Interestingly, the N170 and behavioural FIEs are correlated (Jacques & Rossion, 2007), which suggests that similar changes in perceptual processing may underlie the behavioural and ERP measures. Consistent with this idea, Jacques et al. (2014) found that the N170 inversion effect, like the behavioural effect, depends on horizontal facial structure remaining intact. Specifically, they found that phase-scrambling horizontal structure, but not vertical structure, in upright faces yielded N170s that differed from N170s evoked by normal, unscrambled faces.

Using the inversion effect as an index of intact face perception, Jacques et al. (2014) determined that horizontal structure is required for the N170 latency inversion effect, much as it is required for the behavioural face inversion effect (Dakin & Watt, 2009; Goffaux & Dakin, 2010; Pachai et al., 2013; Pachai, Bennett, & Sekuler, 2018). However, the exact contribution of horizontal structure in eliciting an N170 during upright face *identification* remains unclear. How does the N170 to an upright face change as a function of the orientation structure present? How are horizontal biases in electrophysiological and behavioural measures related? The current study examined these questions by measuring the effects of orientation filtering on face identification accuracy and the amplitude and latency of the N170.

The N170 is the earliest ERP for faces but, its relation to face identification is unclear: Although the N170 may habituate to repeated presentations of a single face identity (Heisz, Watter, & Shedden, 2006), it generally is not sensitive to face identity (Eimer, 2000; Amihai, Deouell, & Bentin, 2011). A slightly later ERP component, the N250, is more strongly associated with face identity (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002; Schweinberger, Huddy, & Burton, 2004). Tanaka and colleagues suggested that the N250 is the earliest memory-related component for object individuation (Scott, Tanaka, Sheinberg, & Curran, 2008), including face recognition (Tanaka, Curran, Porterfield, & Collins, 2006). After repeated exposures, the N250 is largest when stimuli are upright faces, compared to inverted faces or cars (Schweinberger et al., 2004). Additionally, the N250 is enhanced for repetitions of the same face identity but different viewpoints (Kaufmann, Schweinberger, Burton, & Kaufmann, 2009), implicating the N250 in the overall acquisition of facial identity. Tanaka et al. (2006) further showed that the N250 both was strongest for long-term familiar faces and for newly learned identities. Based on these results, we hypothesized that the N250 should be strongest when the facial identity is clearly observed (i.e., when horizontal structure is most preserved), and less pronounced when the identity is not clear (i.e., when horizontal structure is removed).

We compared ERPs elicited by unfiltered upright faces to ERPs evoked by orientation-filtered faces with varying degrees of horizontal and vertical structure. By parametrically increasing the amount of facial structure at each orientation, we hoped to understand what constitutes a typical N170 and N250.

2. Methods

2.1. Subjects

Twelve students from McMaster University participated in the experiment. One female participant's EEG data were excessively noisy, leaving eleven subjects for the analysis (6 males; range = 18–30 years old, M = 22.4, SD = 3.88). All were right-handed and had normal or corrected-to-normal Snellen acuity. Informed consent was obtained from each participant. Participants were reimbursed $10/hour or given partial course credit for participating. The experimental protocol was approved by the McMaster University Research Ethics Board.

2.2. Apparatus & stimuli

Stimuli were generated on an Apple Macintosh G5 computer using MATLAB (Mathworks, 2007) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Stimuli were presented on a 21-inch ViewSonic G225f display with a resolution of 1280 × 1024 pixels (32 pixels/cm) and a 85 Hz refresh rate. Viewing was binocular through natural pupils from a viewing distance of 100 cm. The stimuli were centered on a 256 × 256 pixel matrix and subtended 4.6° of visual angle. The stimuli were constructed from a set of 6 faces (3 male), all having the same amplitude spectrum, selected from the set of 10 faces used by Gold et al. (1999). Each face was filtered with an ideal band-pass orientation filter centered on either 0° (horizontal) or 90° (vertical). Orientation bandwidth varied from ± 45 deg to ± 90 deg in steps of ± 9 deg, which resulted in a total of 11 conditions: five conditions

(a)

(b)
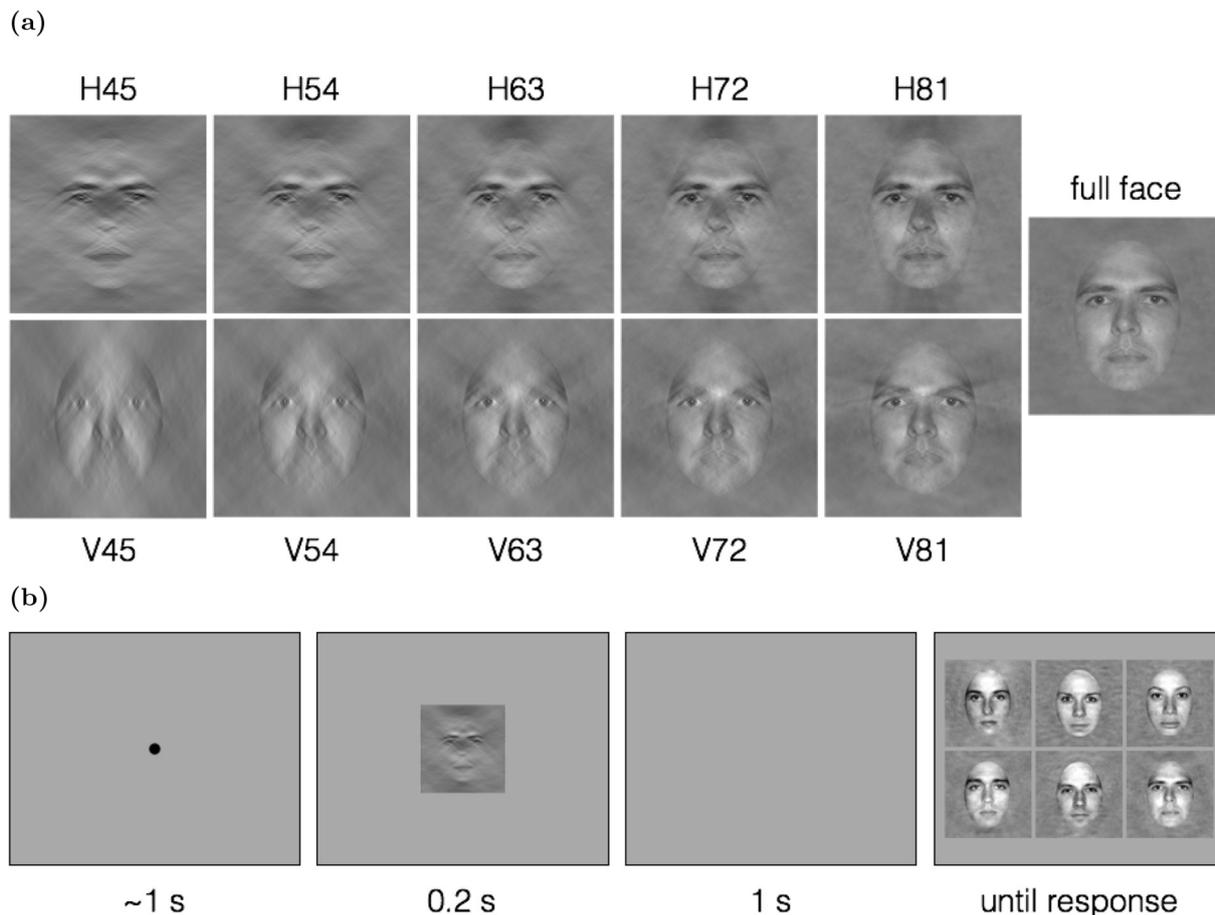
Fig. 1. (a) Examples of stimuli constructed from a single identity in all filter conditions. Horizontal (H) and vertical (V) filters had bandwidths ranging from ± 45° to ± 81°. The far right image is the full (i.e., unfiltered) face. (b) Sample trial structure. On each trial, a random temporal jitter between −100 and 100 ms was added to the fixation point duration.

using filters centered on 0 deg, five using filters centered on 90 deg, and one using an unfiltered face. Face RMS contrast was 0.05 prior to filtering. After filtering, RMS contrast varied with filter bandwidth (Table 1). Note that at all bandwidths, RMS contrast was ≈ 10% higher for stimuli constructed with vertical filters than horizontal filters.

2.3. Procedure

The task was a six alternative forced choice (6-AFC) identification task. The experiment began with 10 practice trials using only unfiltered faces to avoid prior exposure to filtered faces before the experimental trials. Each trial started with the presentation of a fixation point in the center of the display. After a random duration that varied from 0.9 to 1.1 s, the fixation point was extinguished and immediately followed by the presentation of a face stimulus for 0.2 s. The stimulus was replaced by a blank uniform screen for 1 s, and then by a response screen that

Table 1
RMS contrast for for stimuli constructed with orientation filters of various bandwidths centered on 90 (vertical) or 0 deg (horizontal). For each filter, all six face identities had the same RMS contrast. The ± 90 bandwidth passed all orientations, and therefore faces in that condition were identical to unfiltered faces.

Bandwidth (deg)	Vertical Filter	Horizontal Filter
± 45	0.0372	0.0334
± 54	0.0400	0.0359
± 63	0.0408	0.0376
± 72	0.0442	0.0407
± 81	0.0455	0.0418
± 90	0.0500	0.0500

contained all six faces (Fig. 1b). The response screen images were always unfiltered and had an RMS contrast of 0.3. The participant indicated his/her response by clicking on one of the faces with a computer mouse. Auditory feedback was provided after every response in the form of 600 and 200 Hz tones after correct and incorrect responses, respectively. The next trial started 0.25 s following the response. We did not record response times.

2.4. Design

In each 40 min session, participants were presented with each face seven times in 11 conditions, yielding a total of $6 \times 7 \times 11 = 462$ experimental trials per session. Each participant completed two sessions, or 924 total trials (i.e., 84 trials per condition). All conditions and faces were randomized across trials. Each session contained three brief rest periods. There was no *a priori* hypothesis about sessions, and to improve the signal-to-noise ratio of the ERPs, data were collapsed across the two days prior to conducting statistical analyses.

2.5. Electrophysiology

EEG data were acquired during the behavioural task using a 256-channel HydroCel Geodesic Sensor Net (Electric Geodesics Inc., Eugene, Oregon; Tucker, 1993). Data were referenced online to electrode Cz, and sampled at 500 Hz. Offline, data from each trial were segmented from −200 ms to 998 ms and transferred to MATLAB for further processing using the EEGLAB (Delorme & Makeig, 2004) and *LIMO EEG* (Pernet, Chauveau, Gaspar, & Rousselet, 2011) toolboxes. The responses to faces and objects occur primarily in the 5–15 Hz range (Rousselet, Husk, Bennett, & Sekuler, 2007), and therefore we applied a

30 Hz low-pass non-causal filter to the EEG data using *pop_eegfiltnew*. No high-pass filter was used. Baseline correction was applied using the average of the 200 ms of pre-stimulus activity. Trials with amplitudes above $+100 \mu V$ or below $-100 \mu V$ were rejected. No other artifact rejection was applied. Unless otherwise noted, statistical analysis was restricted to the average of two clusters of 15 electrodes, one cluster from each hemisphere, centred on electrodes PO7 and PO8. The average of clusters was used instead of a single electrodes to accommodate for the variable fit of the geodesic nets – that is, the same electrode was not necessarily at the same anatomical spot across participants, but was always within the cluster we chose to average across. Nonetheless, the pattern of results were unchanged if we only used electrodes PO7 and PO8.

2.6. EEG analysis

N170 mean amplitude was measured as the average voltage in a 42 ms time-window centred on the N170 peak of the grand-average ERP for each condition and hemisphere. By centering the time-window on each condition's grand-average latency, we reduced the influence of latency differences across conditions on our measure of amplitude (Luck, 2005). The P100 mean amplitude was measured using the same technique, but a smaller time-window of 22 ms centered on the P100 peak identified in the grand-average ERP for each condition and hemisphere.

Latency was measured as the time of the N170 peak, which was automatically selected as the lowest local peak found in the 140–220 ms time-window. The P100 peak latency was measured using the same technique, but between 80–140 ms, and was defined as the highest local peak. All peak selections were verified manually.

It was much more difficult to identify the peak of the N250, so a single time window of 250–300 ms was used to quantify the N250 mean amplitude for all conditions (Kaufmann et al., 2009; Schweinberger et al., 2004). Given the difficulty in identifying a discrete peak, no measure of N250 latency was computed.

3. Results

3.1. Behavioural results

To maintain an orthogonal design, the full face condition was omitted from all analyses of variance (ANOVAs), unless otherwise noted. Where appropriate, the Bonferroni correction for multiple comparisons was used to control familywise Type I error rate. For any main effects and interactions including *bandwidth* as a factor, we did not assume sphericity and report Huynh-Feldt corrected *p*-values instead. Effect size was measured using generalized eta squared (η_G^2), as described by Bakeman (2005) and Olejnik and Algina (2003) for repeated-measure designs. Lakens (2013) suggests that Cohen (1988)'s suggested benchmarks of effect size can be used when interpreting η_G^2 (small: 0.01, medium: 0.04, large: 0.16). For *t* tests, we report effect size using Cohen's *d*. Statistical analyses were performed with R (R. Core Team, 2017).

Response accuracy is plotted for each condition in Fig. 2, which shows that response accuracy generally increased as filter bandwidth increased from ± 45 to ± 81, and that the increase was greater for vertical filters (V) than horizontal filters (H). Proportion correct was submitted to a repeated-measures ANOVA with factors of *filter orientation* (horizontal and vertical) and *bandwidth* (±45, 54, 63, 72, and 81 degrees). The main effects of *filter orientation* ($F_{(1,10)} = 180$, $p < 0.0001$, $\eta_G^2 = 0.63$) and *bandwidth* ($F_{(4,40)} = 189$, $p_{HF} < 0.0001$, $\eta_G^2 = 0.50$) were significant, as was the *filter orientation × bandwidth* interaction ($F_{(4,40)} = 37.2$, $p_{HF} < 0.0001$, $\eta_G^2 = 0.25$). The interaction was significant because the effect of bandwidth was much larger with vertical filters ($F_{(4,40)} = 159$, $p < 0.0001$, $\eta_G^2 = 0.718$) than with horizontal filters ($F_{(4,40)} = 14.9$, $p < 0.0001$, $\eta_G^2 = 0.162$). For instance,
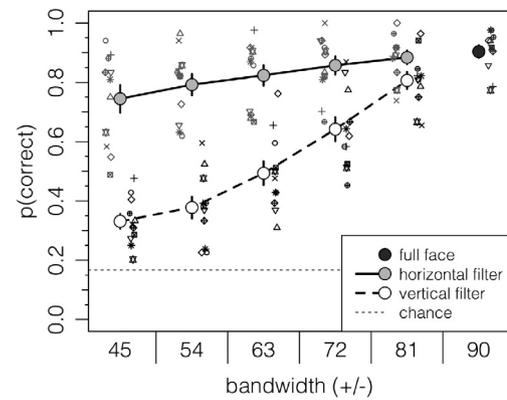

Fig. 2. Mean proportion correct plotted as a function of *bandwidth* (degrees), separately for the horizontal (grey) and vertical (white) *filter orientations*, and the full face condition (black). Individual subject results are also plotted, jittered for legibility. Error bars are ±1 SEM. Chance performance in the 6-AFC task is indicated with a horizontal dotted line. The effect of *bandwidth* is noticeably larger for the vertical filter orientation than the horizontal filter orientation, and accuracy in all conditions except the two that used horizontal filters with bandwidths of 72 and 81 deg was significantly different than from accuracy in the full face condition.

response accuracy improved by 48% from the smallest (V45) to the largest (V81) vertical filter bandwidth, but improved by only 14% from the smallest (H45) to the largest (H81) horizontal filter. Note that in the V81 condition, the bandwidth was so large that all orientations except those within ± 9 deg of horizontal were passed by the "vertical" filter. Thus, the conditions yielding the highest response accuracy always had considerable horizontal facial structure. Consistent with this idea, accuracy with the narrowest horizontal filter (H45, $M = 0.74$) was higher than accuracy in the V72 ($M = 0.64$) condition ($t_{10} = 3.17$, $p = 0.0101$, $d = 0.955$) and did not differ significantly from accuracy in the V81 ($M = 0.81$) condition ($t_{10} = -2.04$, $p = 0.0686$, $d = 0.615$).

Unfiltered faces contain information at all orientations, so we expected accuracy to be highest in that condition. Inspection of Fig. 2 is consistent with that expectation: accuracy in most conditions that used horizontally-filtered faces, and all conditions that used vertically-filtered faces, was lower than accuracy obtained with unfiltered faces. To evaluate this idea, we used one-tailed paired *t* tests to compare accuracy in each filtered-face condition to accuracy in the unfiltered face condition. We used the Bonferroni method to maintain a familywise Type I error rate of 0.05 by setting the per-comparison α to 0.005. Compared to full face identification accuracy ($M = 0.90$), accuracy with horizontally-filtered faces was significantly lower in the H45 ($M = 0.74$, $t_{10} = -4.85$, $p = 0.00034$, $d = 1.46$), H54 ($M = 0.79$, $t_{10} = -5.50$, $p = 0.00013$, $d = 1.66$), and H63 ($M = 0.82$, $t_{10} = -3.69$, $p = 0.0021$, $d = 1.11$) conditions, but not in the H72 ($M = 0.86$, $t_{10} = -3.14$, $p = 0.0053$, $d = 0.95$) or H81 ($M = 0.88$, $t_{10} = -1.66$, $p = 0.0637$, $d = 0.50$) conditions. In contrast, accuracy in all of the vertically-filtered conditions was significantly less than accuracy in the full face condition (V45: $M = 0.33$, $t_{10} = -31.1$, $p < 0.0001$, $d = 9.38$; V54: $M = 0.38$, $t_{10} = -25.4$, $p < 0.0001$, $d = 7.65$; V63: $M = 0.49$, $t_{10} = -15.$ 1, $p < 0.0001$, $d = 4.56$; V72: $M = 0.64$, $t_{10} = -9.32$, $p < 0.0001$, $d = 2.81$; and V81: $M = 0.81$, $t_{10} = -6.51$, $p < 0.0001$, $d = 1.96$). Differences between filtered and unfiltered faces were noticeably larger for the vertically-filtered than horizontally-filtered conditions.

3.2. Event-related potentials

3.2.1. Spatiotemporal analyses

We started our EEG analysis by inspecting the differences between the spatiotemporal responses obtained in three main conditions. First, we subtracted the mean ERP in the full face condition from the mean ERP obtained in the H45 condition. This comparison, illustrated in Fig. 3a, reveals differential activation when only horizontal structure is
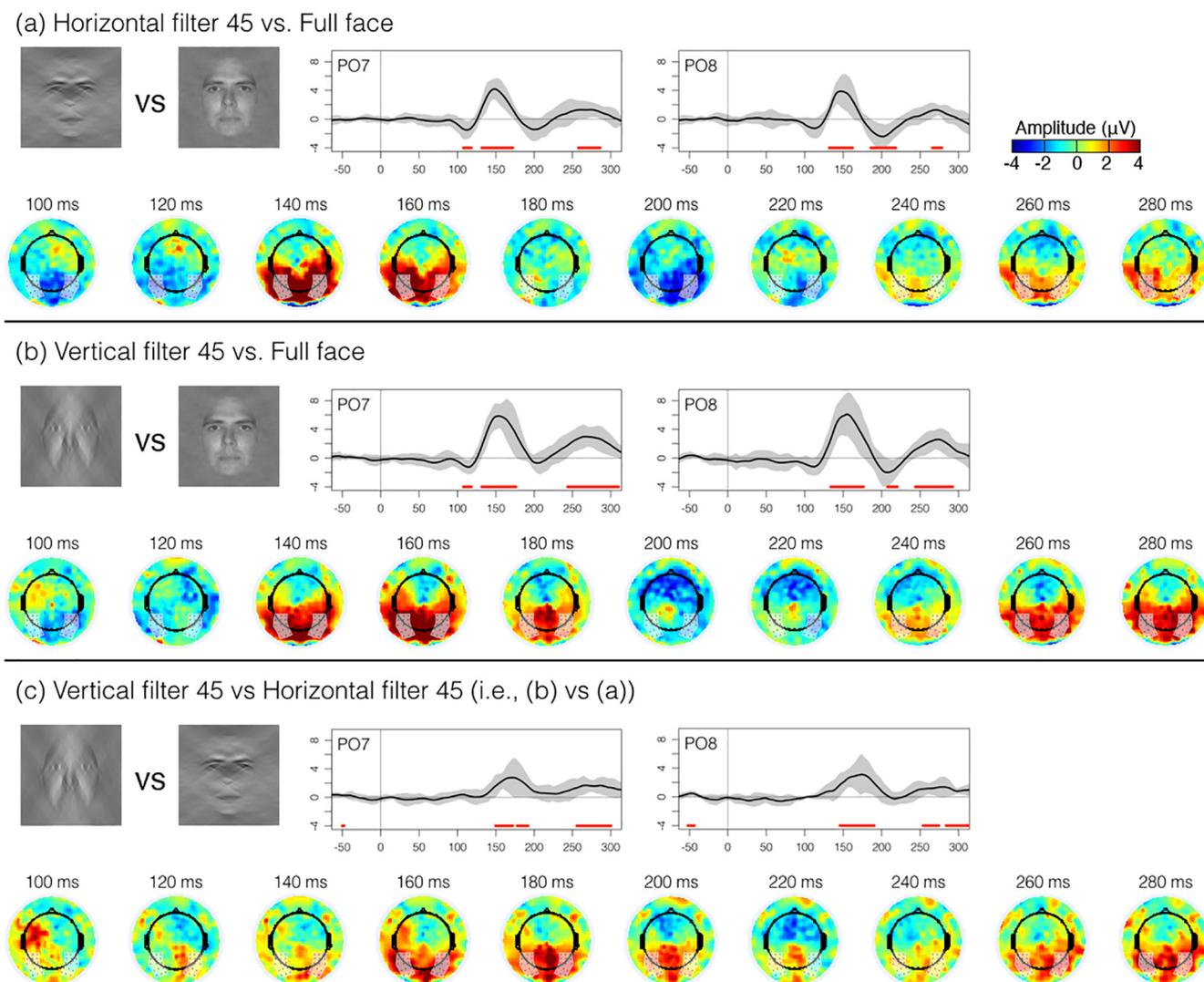
Fig. 3. Summary of ERP *differences* between the (a) H45 and full face conditions; (b) V45 and full face conditions; and (c) H45 and V45 conditions. Each panel shows the conditions being compared (left image minus right image), and the grand-average difference waves with 95% confidence intervals calculated for electrodes PO7 and PO8. Difference waves were evaluated at each point with *t* tests; significant ($p < .05$, uncorrected) deviations from zero are indicated by red dots on the bottom of each difference-wave plot. The bottom of each panel contains a series of topographic plots from 100 ms to 280 ms after stimulus-onset, in 20 ms intervals. The colour scale for the topographic plots is shown on the right in (a). White shaded regions in the topographic plots represent the two 15-electrode clusters averaged for analysis. The LIMO EEG toolbox (Pernet et al., 2011) was used to construct topographic plots, estimate confidence intervals, and perform the *t* tests.

present compared to when all orientation structure is present. We did the same comparison between ERPs obtained in the V45 and full face conditions (Fig. 3b) to reveal differential activation when only vertical structure is present compared to when all orientation structure is present. Finally, we computed the difference between ERPs in the V45 and H45 conditions (Fig. 3c). This third comparison is between two conditions that used stimuli that contained structure that fell within a 90 deg band, and therefore highlights differences between ERPs evoked by vertical and horizontal facial structure without possible confounds due to differences in stimulus bandwidth.

The topographic difference plots in Fig. 3a and b reveal that compared to H45 and V45, the full faces produced a significantly more negative ERP in the N170 ($\approx$150–200 ms) and N250 ($\approx$250–300 ms) time windows. These differences were broadly distributed in the posterior/occipital region. To visualize the effect in a more typical ERP, we plotted the ERP differences at the PO7 and PO8 electrodes for each comparison. The comparison between H45 and V45 (Fig. 3c) revealed that the two filtered conditions also differed significantly in the N170 and N250 time windows. These differences were, again, broadly distributed in the posterior/occipital region.

The analyses illustrated in Fig. 3 were done to visualize the spatiotemporal distribution of the differential activity seen across critical conditions. As such, no corrections were done, nor were any additional analyses of the entire time-series across the entire topography. We focused the remainder of our analysis on the N170 and N250 time windows, and on two clusters of electrodes centred on PO7 and PO8. As a control, we also analyzed the P100 time window at the same regions.

*3.2.2. N170 amplitude & latency*

Average ERPs recorded at PO7- and PO8-centered clusters in the left and right hemispheres are plotted in Fig. 4. Inspection of Fig. 4 suggests that N170 amplitude decreased when horizontal structure was removed from faces, and that amplitude was affected more by the manipulation of horizontal structure than vertical structure. These trends are more evident in Fig. 5a&b, which plot mean N170 amplitudes measured in the left and right hemispheres as a function of filter orientation and bandwidth. N170 amplitudes were analyzed with a 2 (*filter orientation*) × 5 (*bandwidth*) × 2 (*hemisphere*) ANOVA. The main effects of *filter orientation* ($F_{(1,10)} = 18.9$, $p = 0.0015$, $\eta_G^2 = 0.007$) and *bandwidth* ($F_{(4,40)} = 7.30$, $p_{HF} = 0.0015$, $\eta_G^2 = 0.022$) were significant. These main
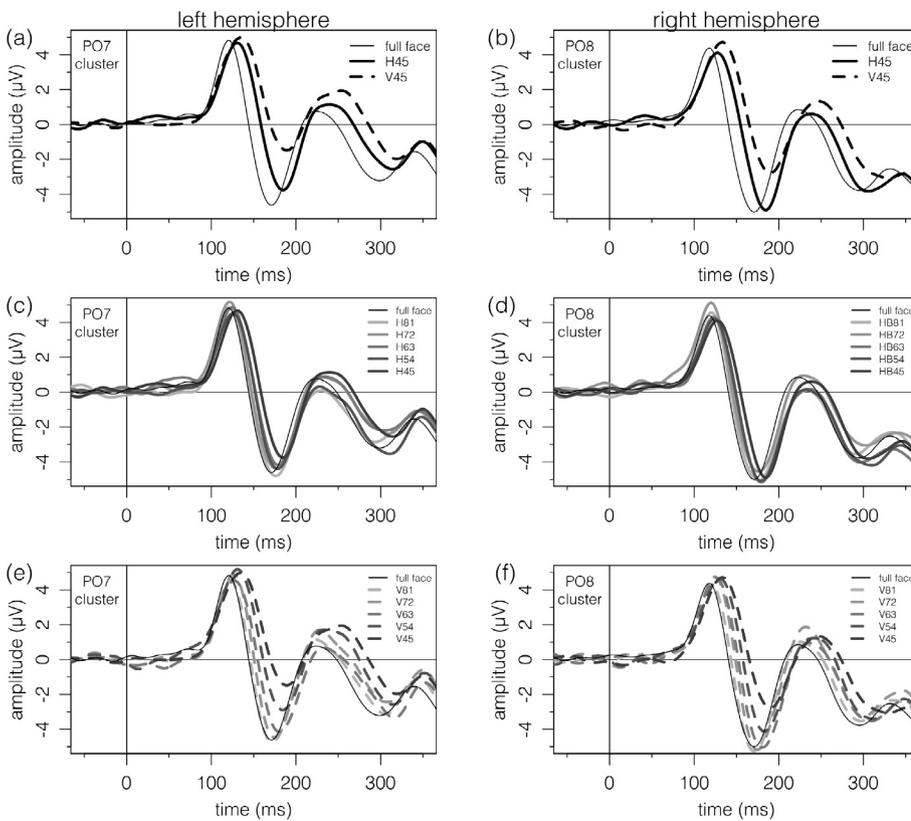
Fig. 4. Grand average ERP traces plotted separately for the left and right hemispheres. (a, b) Full face (grey), Horizontal Base 45 (black solid), and Vertical Base 45 (dashed) are shown in a single plot to reveal how affected the N170 is when horizontal structure is omitted (VB45) compared to when vertical structure is omitted (HB45). There is a noticeable difference between parametrically adding vertical structure to a horizontal base (c, d) and adding horizontal structure to a vertical base (e, f), demonstrating how it is the presence of horizontal structure that primarily modulates the N170. The presence or absence of vertical structure affects the N170 minimally.

effects were qualified by a significant *orientation × bandwidth* interaction ($F_{(4,40)} = 7.39$, $p_{HF} = 0.0007$, $\eta^2_G = 0.010$). The interaction was significant because the effect of bandwidth was much larger with vertical filters ($F_{(4,40)} = 12.3$, $p_{HF} < 0.0001$, $\eta^2_G = 0.064$) than with horizontal filters ($F_{(4,40)} = 1.15$, $p_{HF} = 0.34$, $\eta^2_G = 0.0005$). There was no main effect of

hemisphere ($F_{(1,10)} = 0.99$, $p = 0.344$, $\eta^2_G = 0.009$), nor did it interact with *filter orientation* ($F_{(1,10)} = 0.576$, $p = 0.466$, $\eta^2_G = 0.0002$). There was a significant *hemisphere × bandwidth* interaction ($F_{(4,40)} = 5.23$, $p_{HF} = 0.0050$, $\eta^2_G = 0.0013$), driven by a stronger bandwidth effect in the left ($F_{(4,40)} = 8.52$, $p_{HF} = 0.00016$, $\eta^2_G = 0.033$) than
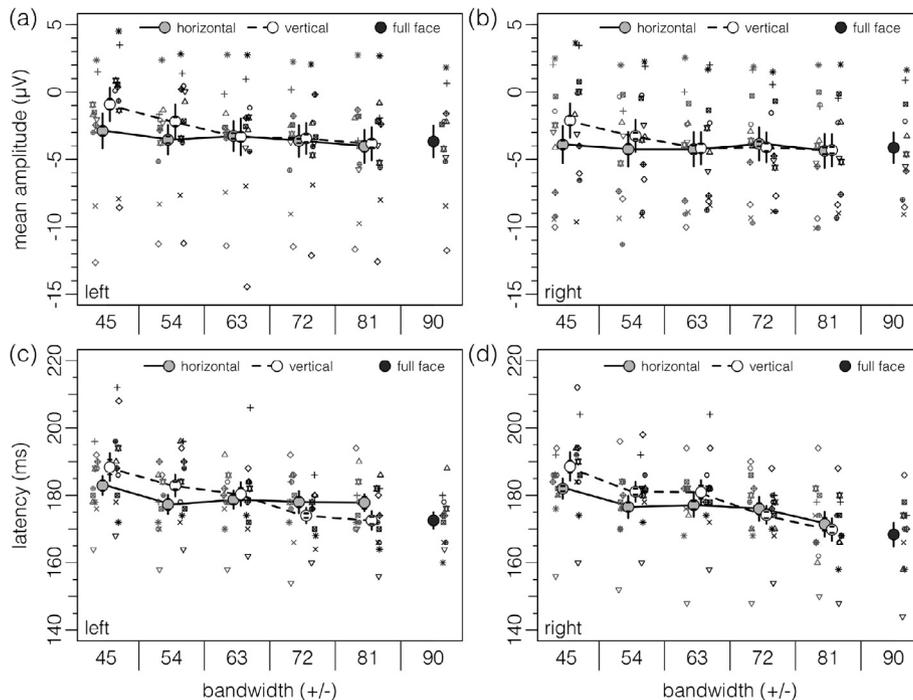
Fig. 5. N170 mean amplitude (top) and latency (bottom) averaged across all subjects, separately for left and right hemispheres. Error bars represent ±1 SEM. Due to the inherently large between-subject variance in ERP data, and the repeated-measure design of the experiment, within-subjects corrected SEMs are also plotted as horizontal ticks on the SEM bars, as described by Loftus and Masson (1994), Cousineau (2005), and Morey (2008). Individual subject data also is plotted, and is jittered for legibility. Symbols are unique to each observer and preserved across conditions and figures.

right hemisphere ($F_{(4,40)} = 5.29$, $p_{HF} = 0.0016$, $\eta_G^2 = 0.015$). The three way interaction was not significant ($F_{(4,40)} = 0.561$, $p_{HF} = 0.688$, $\eta_G^2 = 0.0002$). Finally, we used paired *t* tests to test if the two conditions with the narrowest filters produced N170 amplitudes that differed from the amplitude produced by the unfiltered face, or each other ($\alpha_{corrected} = 0.05/6 = 0.0083$). In the left hemisphere, the N170 to unfiltered faces ($M = -3.67\,\mu V$) did not differ from the N170 to H45 stimuli ($M = -2.89$, $t_{10} = 1.81$, $p = 0.100$, $d = 0.546$), but was significantly larger than the N170 to V45 stimuli ($M = -0.914$, $t_{10} = 6.70$, $p < 0.0001$, $d = 2.02$), and the N170 amplitude was larger for H45 than V45 stimuli ($t_{10} = 5.77$, $p = 0.00018$, $d = 1.44$). The results were similar in the right hemisphere: N170 amplitude to unfiltered faces ($M = -4.13$) was not significantly different than H45 ($M = -3.91$, $t_{10} = 0.532$, $p = 0.606$, $d = 0.16$), but it was significantly more negative than V45 ($M = -2.11$, $t_{10} = 5.51$, $p = 0.00026$, $d = 1.66$), and the N170 amplitude was larger for H45 than V45 stimuli ($t_{10} = 4.39$, $p = 0.0013$, $d = 1.32$).

N170 peak latencies are presented in Fig. 5c&d. In some respects the latency results were similar to those obtained with N170 amplitude. In particular, N170 latency was affected by filter bandwidth and the effect appeared stronger for vertical compared to horizontal filters. The latency data were analyzed with an ANOVA that was identical to the one used to analyze N170 amplitudes. The main effect of *filter orientation* on peak latency was not significant ($F_{(1,10)} = 1.32$, $p = 0.28$, $\eta_G^2 = 0.005$); however, the ANOVA did reveal a significant main effect of *bandwidth* ($F_{(4,40)} = 24.4$, $p_{HF} < 0.0001$, $\eta_G^2 = 0.15$) and a significant *filter orientation* × *bandwidth* interaction ($F_{(4,40)} = 8.66$, $p_{HF} = 0.0003$, $\eta_G^2 = 0.036$). The interaction was significant because the effect of *bandwidth* was greater for vertical filters ($F_{(4,40)} = 33.9$, $p_{HF} < 0.0001$, $\eta_G^2 = 0.266$) than horizontal filters ($F_{(4,40)} = 5.16$, $p_{HF} = 0.0036$, $\eta_G^2 = 0.072$). There was no significant main effect of *hemisphere* ($F_{(1,10)} = 0.931$, $p = 0.357$, $\eta_G^2 = 0.0056$), nor did it interact with *filter orientation* ($F_{(1,10)} = 3.89$, $p = 0.077$, $\eta_G^2 = 0.0015$) or *bandwidth* ($F_{(4,40)} = 2.42$, $p_{HF} = 0.110$, $\eta_G^2 = 0.0057$). The three-way interaction also was not significant ($F_{(4,40)} = 1.66$, $p_{HF} = 0.179$, $\eta_G^2 = 0.0015$). Finally, we used paired *t* tests ($\alpha_{corrected} = 0.0083$) to test if the two conditions with the narrowest filters produced N170 latencies that differed from each other and from the latency for unfiltered faces. In the left hemisphere, N170 latency was shorter for unfiltered faces ($M = 172.5\,ms$) than for H45 ($M = 182.9$, $t_{10} = 3.99$, $p = 0.00256$, $d = 1.20$) and V45 stimuli ($M = 188.4$, $t_{10} = 4.63$, $p = 0.00094$, $d = 1.40$). N170 latencies for H45 and V45 stimuli did not differ significantly ($t_{10} = 2.29$, $p = 0.0451$, $d = 0.69$). The results were similar in the right hemisphere: N170 latency was significantly shorter for unfiltered faces ($M = 168.4$) than H45 ($M = 182.0$, $t_{10} = 9.11$, $p < 0.0001$, $d = 2.75$) and V45 stimuli ($M = 188.5$, $t_{10} = 7.96$, $p < 0.0001$, $d = 2.40$), and N170 latency was significantly shorter for H45 than V45 stimuli ($t_{10} = 3.43$, $p = 0.0064$, $d = 1.03$).

3.2.3. N250 amplitude

N250 mean amplitudes are presented in Fig. 6. N250 mean amplitude was more negative for the horizontal filter than vertical filter conditions. The amplitude became more negative as the vertical filter's bandwidth was increased, but was approximately constant as the horizontal filter's bandwidth increased. This pattern of results resembles the effects of stimulus filtering on N170 amplitude. N250 amplitudes were analyzed with a 2 (*filter orientation*) × 5 (*bandwidth*) × 2 (*hemisphere*) ANOVA. As with N170 amplitude, there were significant main effects of *filter orientation* ($F_{(1,10)} = 11.3$, $p = 0.007$, $\eta_G^2 = 0.015$) and *bandwidth* ($F_{(4,40)} = 5.06$, $p_{HF} = 0.0026$, $\eta_G^2 = 0.023$). The *filter orientation* × *bandwidth* interaction also was significant ($F_{(4,40)} = 4.14$, $p_{HF} = 0.0075$, $\eta_G^2 = 0.007$), reflecting the fact that the effect of *bandwidth* was larger for vertical filters ($F_{(4,40)} = 6.59$, $p_{HF} = 0.0008$, $\eta_G^2 = 0.053$) than horizontal filters ($F_{(4,40)} = 2.93$, $p_{HF} = 0.037$, $\eta_G^2 = 0.018$). There was no significant main

effect of *hemisphere* ($F_{(1,10)} = 1.60$, $p = 0.235$, $\eta_G^2 = 0.0165$), nor did *hemisphere* interact significantly with *filter orientation* ($F_{(1,10)} = 0.222$, $p = 0.65$, $\eta_G^2 = 0.0001$) or *bandwidth* ($F_{(4,40)} = 1.92$, $p_{HF} = 0.130$, $\eta_G^2 = 0.0009$). The three way interaction also was not significant ($F_{(4,40)} = 1.94$, $p_{HF} = 0.151$, $\eta_G^2 = 0.0016$). Finally, we used paired *t* tests ($\alpha_{corrected} = 0.0083$) to test if the conditions using the two narrowest filters produced N250 amplitudes different than the unfiltered face, or from each other. In the left hemisphere, the N250 amplitude evoked by unfiltered faces ($M = -2.04\,\mu V$) was significantly larger (more negative) than the N250 evoked by V45 stimuli ($M = 0.727$, $t_{10} = 5.26$, $p = 0.00037$, $d = 1.56$), but not H45 stimuli ($M = -0.57$, $t_{10} = 2.99$, $p = 0.0135$, $d = 0.902$). Also, the N250 was significantly more negative for H45 than V45 stimuli ($t_{10} = 3.33$, $p = 0.0076$, $d = 1.01$). The results were similar in the right hemisphere: N250 amplitude to unfiltered faces ($M = -2.62$) was significantly more negative than the N250 amplitude to V45 stimuli ($M = -0.319$, $t_{10} = 6.06$, $p = 0.00012$, $d = 1.83$), but did not differ significantly from the N250 amplitude to H45 stimuli ($M = -1.76$, $t_{10} = 2.78$, $p = 0.0193$, $d = 0.840$).

A reviewer suggested that our measure of the N250 (1) was potentially too early and therefore may have included the P200 component; and (2) should be compared across sessions/blocks to capture effects of learning/familiarity, since the N250 is known to be sensitive to face familiarity (Kaufmann et al., 2009). To address both of these issues, we re-analyzed the N250 amplitude using the mean amplitude in a $\pm 30\,ms$ time-window centered on the grand average N250 peak, calculated separately per hemisphere, per session ($\approx 306\,ms$). Additionally, we analyzed the P200 using the similar approach: a $\pm 20\,ms$ time-window centered on the grand average P200 peak ($\approx 234\,ms$), separately per hemisphere, per session.

The new measure of N250 mean amplitude was submitted to a 2 (*hemisphere*) × 2 (*filter orientation*) × 5 (*bandwidth*) × 2 (*session*) ANOVA. Unlike what was found with our original measure of N250 amplitude, the main effects of *filter orientation* ($F_{(1,10)} = 3.67$, $p = 0.0845$, $\eta_G^2 = 0.003$) and *bandwidth* ($F_{(4,40)} = 1.90$, $p_{HF} = 0.129$, $\eta_G^2 = 0.004$) were not significant. Critically, the *filter orientation* × *bandwidth* interaction ($F_{(4,40)} = 3.50$, $p_{HF} = 0.0206$, $\eta_G^2 = 0.005$) remained significant because the main effect of *bandwidth* was larger for vertically oriented filters ($F_{(4,40)} = 3.10$, $p_{HF} = 0.0259$, $\eta_G^2 = 0.0116$) than for horizontally oriented filters ($F_{(4,40)} = 2.17$, $p_{HF} = 0.114$, $\eta_G^2 = 0.010$). This interaction is similar to the one obtained with our original N250 measure. Furthermore, as the reviewer predicted, there was a significant main effect of *session* ($F_{(1,10)} = 11.3$, $p = 0.0072$, $\eta_G^2 = 0.0139$), reflecting the fact that the N250 amplitude was greater during the first session ($-2.78\,\mu V$) than the second session (-1.94). The *filter orientation* × *bandwidth* × *hemisphere* interaction ($F_{(4,40)} = 2.64$, $p_{HF} = 0.0741$, $\eta_G^2 = 0.0014$) was not significant. All other interactions did not approach significance ($F \leqslant 1.48$, $p \geqslant 0.25$, $\eta_G^2 \leqslant 0.0017$).

P200 mean amplitude was submitted to a 2 (*hemisphere*) × 2 (*filter orientation*) × 5 (*bandwidth*) × 2 (*session*) ANOVA. There was a significant main effect of *filter orientation* ($F_{(1,10)} = 5.40$, $p = 0.0425$, $\eta_G^2 = 0.0105$). The main effects of *bandwidth* ($F_{(4,40)} = 1.24$, $p_{HF} = 0.309$, $\eta_G^2 = 0.003$), *hemisphere* ($F_{(1,10)} = 0.057$, $p = 0.816$, $\eta_G^2 = 0.0005$), and *session* ($F_{(1,10)} = 2.93$, $p = 0.118$, $\eta_G^2 = 0.0117$) were not significant. The *filter orientation* × *bandwidth* × *hemisphere* interaction was not significant ($F_{(4,40)} = 2.84$, $p_{HF} = 0.0559$, $\eta_G^2 = 0.0015$). All other interactions also were not significant ($F \leqslant 1.49$, $p \geqslant 0.22$, $\eta_G^2 \leqslant 0.0033$). We analyzed the main effect of *filter orientation* by comparing the average of the horizontally filtered ($M = 0.557\,\mu V$) and vertically filtered ($M = 1.23$) conditions to the full face condition ($M = 0.736$). Average P200 amplitude was larger (i.e., more positive) in the vertical filter condition than the horizontal filter condition ($t_{10} = 2.32$, $p = 0.0425$, $d = 0.701$), but the P200 to full faces did not differ from the P200 amplitude in the horizontal ($t_{10} = 0.609$, $p = 0.556$, $d = 0.184$) or vertical conditions
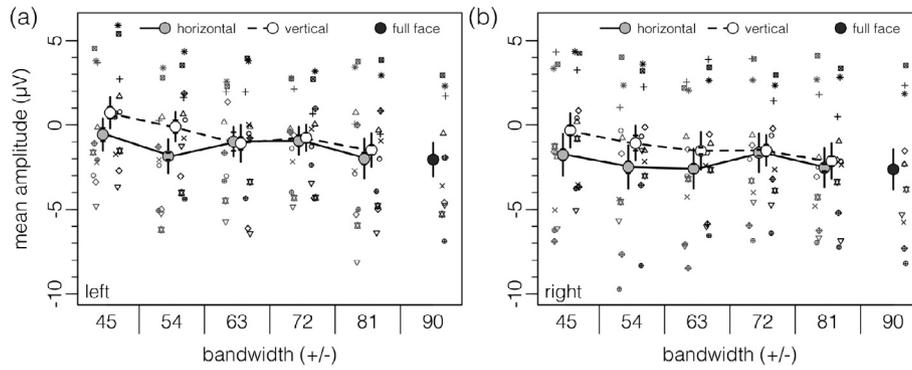
Fig. 6. N250 mean amplitude averaged across all subjects, separately for left and right hemispheres. Error bars represent ±1 SEM, and within-subject corrected error bars are shown as horizontal ticks. Refer to Fig. 5 for details.

($t_{10} = 1.21$, $p = 0.255$, $d = 0.364$). Like the N250, the P200 was different for vertically filtered faces than either horizontally filtered or unfiltered faces. The P200 amplitude was not significantly modulated by bandwidth, suggesting that the P200 was less sensitive than the N250 to facial structure.

3.2.4. P100 amplitude & latency

The N170 is thought to be the earliest ERP component to be sensitive to faces *per se*. Differential activity before the N170 usually is thought to reflect differences in low-level stimulus characteristics (Johnson & Olshausen, 2003; Rousselet, Macé, Thorpe, & Fabre-Thorpe, 2007; VanRullen & Thorpe, 2001). The orientation filtering that we used to construct our faces clearly produced low-level stimulus differences among our conditions (e.g., Table 1 & Fig. 1a). These stimulus differences may have produced differences in very early ERP components (Fig. 4), which in turn may have affected subsequent components (i.e., the N170). To investigate this possibility, we submitted P100 amplitudes to a 2 (*filter orientation*) × 5 (*bandwidth*) × 2 (*hemisphere*) ANOVA. The ANOVA failed to find any significant effects, and all of the effect sizes were very small (in all cases, $0.343 \leqslant F \leqslant 1.76$, $0.158 \leqslant p \leqslant 0.571$, $0.0001 \leqslant \eta_G^2 \leqslant 0.0006$). This analysis indicates that the variability in P100 amplitude was not associated with changes in filter orientation or bandwidth, and that P100 amplitude was similar in the two hemispheres.

Despite not being significantly modulated by our independent variables, variability in the P100 amplitude could still be associated with the systematic variability we saw in the N170 amplitude. To test this idea, we re-analyzed the N170 amplitude results, but this time included P100 amplitude as a covariate. The ANCOVA revealed significant main effects of *filter orientation* ($F_{(1,9)} = 18.3$, $p = 0.0021$, $\eta_G^2 = 0.0069$) and *bandwidth* ($F_{(4,39)} = 8.07$, $p < 0.0001$, $\eta_G^2 = 0.0213$). The main effect of *hemisphere* ($F_{(1,9)} = 0.649$, $p = 0.441$, $\eta_G^2 = 0.0069$) was not significant. The *hemisphere* × *filter orientation* interaction ($F_{(1,9)} = 2.28$, $p = 0.166$, $\eta_G^2 = 0.0004$) was not significant, but the *hemisphere* × *bandwidth* interaction ($F_{(4,39)} = 5.03$, $p = 0.0023$, $\eta_G^2 = 0.0009$) was significant. The three-way *hemisphere* × *filter orientation* × *bandwidth* interaction ($F_{(4,39)} = 0.128$, $p = 0.971$, $\eta_G^2 < 0.0001$) was not significant. Critically, the *filter orientation* × *bandwidth* interaction ($F_{(4,39)} = 5.87$, $p = 0.0008$, $\eta_G^2 = 0.0055$) was significant. This interaction was analyzed by conducting separate ANCOVAs on the horizontal and vertical filter conditions. We found that the main effect of *bandwidth* was significant for the vertical filter orientation ($F_{(4,39)} = 11.2$, $p < 0.0001$, $\eta_G^2 = 0.0453$), but not the horizontal filter orientation ($F_{(4,39)} = 2.17$, $p = 0.0902$, $\eta_G^2 = 0.0065$). These analyses suggest that the N170 amplitude effects reported earlier are largely unaffected by incorporating P100 amplitude into the analyses.

We also re-analyzed the results obtained with our original and revised measure of N250 amplitude using the P100 amplitude as a covariate. For brevity, we report the ANCOVA results using the original

measure of the N250, but the pattern of results was unchanged for the revised measure of the N250 amplitude. The main effects of *filter orientation* ($F_{(1,9)} = 12.5$, $p = 0.0064$, $\eta_G^2 = 0.0118$) and *bandwidth* ($F_{(4,39)} = 4.69$, $p = 0.0035$, $\eta_G^2 = 0.0208$) were significant, but the main effect of *hemisphere* ($F_{(1,9)} = 0.958$, $p = 0.353$, $\eta_G^2 = 0.0102$) was not. The two-way interactions between *hemisphere* and *filter orientation* ($F_{(1,9)} = 0.169$, $p = 0.691$, $\eta_G^2 < 0.0001$), and between *hemisphere* and *bandwidth* ($F_{(4,39)} = 1.94$, $p = 0.123$, $\eta_G^2 = 0.0007$) were not significant, nor was the three-way interaction between *hemisphere*, *filter orientation*, and *bandwidth* ($F_{(4,39)} = 0.923$, $p = 0.460$, $\eta_G^2 = 0.0007$). The *filter orientation* × *bandwidth* interaction ($F_{(4,39)} = 2.33$, $p = 0.0727$, $\eta_G^2 = 0.0034$) was not significant. Nevertheless, as was done in our other analyses, we conducted separate ANCOVAs to evaluate the effect of *bandwidth* in the horizontal and vertical filter conditions. As was found in the analysis without a covariate, the main effect of *bandwidth* was significant for both the vertical filter orientation ($F_{(4,39)} = 5.27$, $p < 0.0017$, $\eta_G^2 = 0.0366$) and the horizontal filter orientation ($F_{(4,39)} = 3.13$, $p = 0.0250$, $\eta_G^2 = 0.0145$). These analyses suggest that incorporating P100 amplitude into our analyses of N250 amplitude slightly reduced the magnitude of the *filter orientation* × *bandwidth* interaction, but otherwise left the N250 amplitude effects reported earlier largely unaffected.

The P100 latency was also submitted to a 2 × 5 × 2 ANOVA. The ANOVA found significant main effects of *filter orientation* ($F_{(1,10)} = 7.63$, $p = 0.0201$, $\eta_G^2 = 0.0480$) and *bandwidth* ($F_{(4,40)} = 35.9$, $p_{HF} < 0.0001$, $\eta_G^2 = 0.175$), but not *hemisphere* ($F_{(1,10)} = 1.30$, $p = 0.281$, $\eta_G^2 = 0.0012$). The two-way interactions between *filter orientation* × *bandwidth* ($F_{(4,40)} = 1.67$, $p = 0.176$, $\eta_G^2 = 0.009$), *filter orientation* × *hemisphere* ($F_{(1,10)} = 2.72$, $p = 0.130$, $\eta_G^2 = 0.0007$), and *bandwidth* × *hemisphere* ($F_{(4,40)} = 1.18$, $p = 0.333$, $\eta_G^2 = 0.005$) were not significant, nor was the three-way interaction ($F_{(4,40)} = 0.0362$, $p = 0.997$, $\eta_G^2 = 0.00006$).

Finally, P100 latency was used as a covariate in a re-analysis of the N170 latency in a 2 × 5 × 2 ANCOVA, which found that the main effect of *bandwidth* ($F_{(4,39)} = 4.91$, $p = 0.0027$, $\eta_G^2 = 0.0453$) remained significant, and the main effects of *filter orientation* ($F_{(1,9)} = 0.012$, $p = 0.916$, $\eta_G^2 < 0.0001$) and *hemisphere* ($F_{(1,9)} = 0.064$, $p = 0.807$, $\eta_G^2 = 0.0003$) remained non-significant. The two-way interaction between *filter orientation* × *bandwidth* ($F_{(4,39)} = 8.12$, $p < 0.0001$, $\eta_G^2 = 0.0470$) was significant, and was due to larger effect of *bandwidth* in the vertical filter condition ($F_{(4,39)} = 11.7$, $p < 0.0001$, $\eta_G^2 = 0.1256$) than the horizontal filter condition ($F_{(4,39)} = 1.79$, $p = 0.150$, $\eta_G^2 = 0.0334$). The *filter orientation* × *hemisphere* interaction ($F_{(1,9)} = 12.4$, $p = 0.0065$, $\eta_G^2 = 0.0040$) also was significant, and was driven by a larger main effect of *bandwidth* for the right hemisphere ($F_{(4,39)} = 11.1$, $p < 0.0001$, $\eta_G^2 = 0.1215$) than the left hemisphere ($F_{(4,39)} = 2.57$, $p = 0.0528$, $\eta_G^2 = 0.0318$). The *bandwidth* × *hemisphere* interaction ($F_{(4,39)} = 2.41$, $p = 0.0653$, $\eta_G^2 = 0.0079$) and the three-way interaction ($F_{(4,39)} = 1.62$, $p = 0.190$, $\eta_G^2 = 0.0020$) were not

significant. The analysis suggests that incorporating P100 latency into our analyses of N170 latency revealed a *bandwidth × hemisphere* interaction but otherwise left the other effects, including the *filter orientation × bandwidth* interaction, unaffected.

3.2.5. Correlations between behaviour & ERPs

Previous studies have shown that relative sensitivity for horizontal compared to vertical facial structure is correlated with better performance in a face identification task and with the magnitude of the face inversion effect (Pachai et al., 2013). Here we examine whether a horizontal bias in our behavioural and ERP measures were correlated with face identification accuracy. We computed behavioural horizontal bias as the difference between accuracy in the H45 and V45 conditions, which are the two conditions that used the largest non-overlapping horizontal and vertical filters. Using the same formula, ERP horizontal bias was also calculated for the P100 amplitude, P100 latency, N170 amplitude, N170 latency, and N250 amplitude, separately for each hemisphere. We correlated each of our measures of horizontal bias with identification accuracy to full, unfiltered faces.

The correlation between behavioural horizontal bias and full face identification (Fig. 7a) was not significant ($r = 0.46$, $t_9 = 1.57$, $p = 0.076$, 1-tailed). Although the correlation was not statistically significant, its magnitude was similar to the value of 0.52 reported by Pachai et al. (2013) who had a significantly larger sample size ($n = 32$) than the one used in the current experiment, and who measured face identification *thresholds*, which had greater variability than our measure of proportion correct. Hence, although the correlation was not statistically significant, our results are consistent with previous reports that relative sensitivity to horizontal structure is correlated positively with, and accounts for 20–25% of the variance in, face identification performance.

The relations between response accuracy in the full face condition and horizontal bias of the P100, N170, and N250 are shown in Fig. 7b-f. As expected, full-face identification accuracy was not significantly correlated with either horizontal bias in P100 amplitude (Fig. 7b) or P100 latency (Fig. 7c). Full-face identification accuracy also was not correlated

with the horizontal bias of N170 amplitude (Fig. 7d) or N170 latency (Fig. 7e). However, full-face identification accuracy *was* significantly correlated with the horizontal bias of N250 amplitude (Fig. 7f) in both hemispheres (left: $r = 0.787$, $t_9 = -3.82$, $p = 0.0041$; right: $r = 0.666$, $t_9 = -2.68$, $p = 0.0253$). Averaging the results across hemispheres did not change the results: full face identification accuracy was not correlated with the horizontal bias of the P100 amplitude ($r = -0.308$, $t_9 = -0.97$, $p = 0.358$), P100 latency ($r = -0.407$, $t_9 = -1.34$, $p = 0.214$), N170 amplitude ($r = -0.169$, $t_9 = -0.513$, $p = 0.620$), or N170 latency ($r = 0.270$, $t_9 = 0.840$, $p = 0.423$), but was significantly correlated with the horizontal bias of the N250 amplitude ($r = -0.799$, $t_9 = -3.99$, $p = 0.003$).

Given that we re-analyzed the N250 using a reviewer-suggested time-window, and added a P200 analysis, we asked if either of these measures were correlated with full face identification. P200 and N250 were averaged across hemispheres, horizontal bias of the mean amplitudes was calculated, and the horizontal biases were correlated with full face identification accuracy separately in each session. Full face identification was not correlated with P200 horizontal bias in the first ($r = -0.349$, $t_9 = -1.12$, $p = 0.293$) or second ($r = 0.020$, $t_9 = 0.061$, $p = 0.953$) session, nor was it correlated with the revised N250 horizontal in the first ($r = -0.449$, $t_9 = -1.51$, $p = 0.166$) or second ($r = -0.312$, $t_9 = -0.981$, $p = 0.352$) session. However, the revised N250 horizontal bias averaged across sessions was significantly correlated with full face identification accuracy ($r = -0.685$, $t_9 = -2.82$, $p = 0.020$). Given this effect of session, we re-calculated the correlation between our original N250 measure (averaged across hemispheres) and behaviour for each session: as was found with the revised N250 measure, the correlation was smaller and non-significant in both the first ($r = -0.449$, $t_9 = -1.51$, $p = 0.166$) and second ($r = -0.311$, $t_9 = -0.981$, $p = 0.352$) session.

The fact that the brain-behaviour correlation depended significantly on the precise definition of the N250 raises the possibility that the significant correlation shown in Fig. 7 was spurious and/or driven by a few, sparse time points in the ERP. To evaluate this idea, we correlated face identification accuracy and ERP-horizontal bias at every time-point
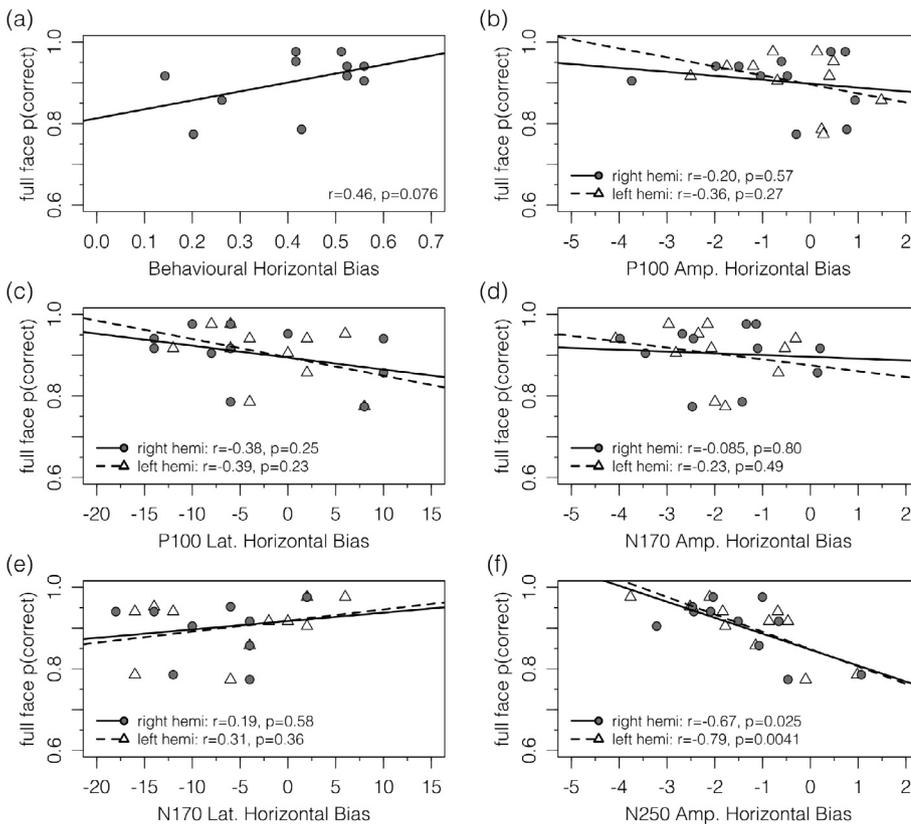

Fig. 7. Correlations between full face identification accuracy (y-axes) and different measures of horizontal bias (x-axes). Horizontal bias was measured for the (a) behaviour, (b) P100 amplitude, (c) P100 latency, (d) N170 amplitude, (e) N170 latency, and (f) N250 amplitude. Data are presented separately for the left (grey triangle, dashed line) and right (white circle, solid line) hemispheres. Pearson's correlations were computed using least squares method, with correlation values reported in the text. The only significant correlations were for the N250 mean amplitude (e) in both hemispheres.
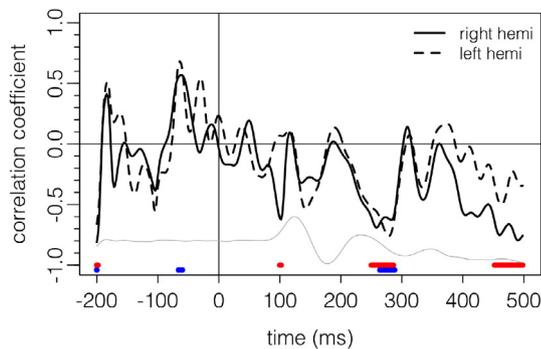
Fig. 8. Time-series of the Pearson's least-squares correlation coefficient (*r*) between neural horizontal bias (H45 – V45) and full face identification accuracy, separately for the right (solid) and left (dashed) hemispheres. Along the bottom, red and blue dots indicate statistically significant correlations (*p* < .05, uncorrected) for the right and left hemispheres, respectively. In both hemispheres, there was a sustained correlation between approximately 250–300 ms, which falls between the nearest peak and trough in the ERP. In the right hemisphere, there was a second sustained correlation between 450–500 ms. As a temporal reference, the grand-average ERP is shown in the thin grey line – note that the y-axis does not apply to this ERP. See Fig. 4 for ERP traces.

from −200 to 500 ms, separately for the left and right hemispheres. We found that the correlation was significant for sustained periods of 250–285 ms and 264–288 ms in the right and left hemispheres, respectively (Fig. 8). We also found, unexpectedly, a sustained correlation from 452–500 ms, but only in the right hemisphere.

4. Discussion

We measured response accuracy and ERPs in subjects performing a 1-of-6 identification task with faces that varied systematically in diagnostic vertical and horizontal structure. We found that identification was most accurate when faces contained horizontal structure, and was least accurate when faces lacked horizontal structure (Fig. 2). Although the correlation between full face identification accuracy and our behavioural measure of horizontal tuning was not statistically significant (Fig. 7a), the direction and magnitude of the correlation was similar to the one reported by Pachai et al. (2013). In addition, we found that N170 and N250 amplitudes were greatest (Figs. 5a&b and 6, respectively), and N170 latency was shortest (Fig. 5c&d), in response to faces that contained horizontal structure. Finally, we found that the horizontal bias of the N250 (Fig. 7f), but not the N170 (Fig. 7d&e), was significantly correlated with response accuracy with unfiltered faces. Overall, our results are consistent with previous studies showing that horizontal facial structure is important for upright face identification (Dakin & Watt, 2009; Pachai et al., 2013; Pachai et al., 2017), and suggest that the behavioural effects of manipulating oriented facial structure are more closely associated with the N250 than the N170.

We found that faces containing horizontal structure evoked the largest and earliest N170. Interestingly, the presence of horizontal structure had different effects on N170 amplitude and latency. Specifically, horizontal structure was necessary and sufficient to produce an N170 with an amplitude equal to that evoked by an unfiltered faces; however, horizontal structure was necessary but *not* sufficient to evoke an N170 with the same latency as the one evoked by an unfiltered face. Indeed, we found that, relative to the unfiltered condition, N170 latencies were longer in both the H45 and V45 conditions. N170 latency also was longer in the H81 condition, which contained structure at all orientations except those within ± 9 deg of vertical. These results are similar to those reported by Jacques et al. (2014), who found that phase randomization of vertical facial structure produced a slightly delayed N170, despite the presence of undistorted horizontal structure. In their study, all of the faces contained structure at all orientations, though the phase randomization reduced the information conveyed by selected bands of orientations. One interpretation of our results, and

those of Jacques et al. (2014), is that N170 latency is more sensitive than N170 amplitude to image manipulations that render a face less *face-like*. According to this hypothesis, manipulations of orientated structure that do not introduce obvious image distortions should have minimal affects on N170 latency. Hashemi, Pachai, Bennett, and Sekuler (2012) provide data that supports this idea: they used a 1-of-10 identification task with faces whose diagnostic orientation structure was manipulated using filters that were similar to those used here. However, instead of removing the filtered orientations, the filtered components were replaced with non-informative, oriented structure that was derived from the average of the 10 faces comprising the stimulus set. Hence, all faces in all conditions contained structure at all orientations and therefore appeared equally face-like in all conditions (for stimulus examples, see Pachai et al., 2018). When faces contained diagnostic horizontal structure but non-diagnostic vertical structure, Hashemi et al. (2012) found the N170 was not delayed relative to the N170 evoked by an unfiltered face. These results are consistent with the idea that N170 latency is more sensitive than N170 amplitude to manipulations, such as inversion (Bentin et al., 1996; Rossion et al., 2000; Itier, Alain, Sedore, & McIntosh, 2007; Rousselet, Pernet, Bennett, & Sekuler, 2008), that visibly distort a face: that is, the shortest latency N170 will be to an unmanipulated, intact, familiar face, and manipulations that produce visible differences from this baseline face will result in longer N170 latencies.

Unlike what was found with N170 latency, N170 amplitude in the H45 condition, which contained horizontal but not vertical structure, did not differ from N170 amplitude in the full-face condition. On the other hand, N170 amplitude in the V45 condition, which contained vertical but not horizontal structure, was significantly lower than N170 amplitude in the H45 and full-face conditions. Taken together, these results suggest that horizontal facial structure was necessary and sufficient to obtain normal N170 amplitudes. These results are consistent with Jemel et al.'s (2003) finding that N170 amplitude is approximately linearly related to the signal-to-noise ratio of full-face stimuli embedded in white noise if we assume that the effects of the noise were caused primarily by masking of horizontal facial structure (also see Rousselet et al., 2008). Previous studies have shown that sensitivity to horizontal structure also is important for face discrimination and identification (Goffaux & Greenwood, 2016; Pachai et al., 2013), and therefore one might expect that N170 amplitude would be associated with behavioural measures of discrimination and identification accuracy. However, contrary to this hypothesis, we found a very small and non-significant correlation between the N170 amplitude and behaviour (Fig. 7d). One potential explanation for this failure to find a correlation is that N170 amplitude depends on the presence of horizontal facial structure regardless of whether that information is or is not informative about face identity. This hypothesis is consistent with results reported by Hashemi et al. (2012), who found that N170 amplitude in a face identification task was similar in conditions that contained informative and non-informative horizontal facial structure. Also, Jacques et al. (2014) found that scrambling the relative phase spectrum of horizontal facial structure had negligible effects on N170 amplitude evoked by upright faces. Both findings are consistent with the idea that N170 amplitude is not particularly sensitive to the information about face identity that may be conveyed by horizontal facial structure. Instead, the N170 may reflect neural processes that use horizontal structure to detect the presence of eyes (Bentin et al., 1996; de Lissa et al., 2014; Itier et al., 2007; Nemrodov, Anderson, Preston, & Itier, 2014; Sekuler et al., 2015; Rousselet, Ince, Rijsbergen, & Schyns, 2014).

Like the N170, the N250 amplitude was most negative for conditions containing horizontal structure (Fig. 6). However, we also found a significant correlation between the horizontal bias of N250 amplitude and full-face identification accuracy (Fig. 7f). This result suggests that N250 amplitude, unlike N170 amplitude, may be associated with *diagnostic* horizontal facial structure. This hypothesis is consistent with previous studies showing that the N250 is sensitive to the information

that distinguishes a particular face from the average of an ensemble of faces (Zheng, Mondloch, & Segalowitz, 2012), and that the N250 responds differentially to familiar and unfamiliar faces (Kaufmann et al., 2009; Schweinberger et al., 2002; Schweinberger et al., 2004; Tanaka et al., 2006). When the N250 was measured using a later time-window, the correlation was smaller but still significant. This result, together with the correlations at each time point in the ERP (Fig. 8), suggests that the horizontal bias found between 250 and 300 ms after stimulus onset may not necessarily be constrained to correspond to the N250 *per se*, or to any other ERP component defined by a peak. Therefore, the so-called N250 may have varied significantly across subjects and therefore produced a grand average N250 that was unlike N250s in individual subjects. Even within subjects, the N250 varied between conditions and between sessions, such that the correlation with behaviour was smaller and not significant when the N250 was calculated separately in each session. Furthermore, initial studies of the N250 reported difficulty in finding a well-defined N250 for all subjects and conditions (Tanaka et al., 2006), and therefore subsequent studies have used several time-windows to calculate an average N250 amplitude. For instance, Tanaka et al. (2006) used 230–320 ms, Kaufmann et al. (2009) used 240–280 ms, and a recent review reports the N250 occurring between 200 ms to 400 ms (Schweinberger & Neumann, 2016). In fact, as part of a cognitive model of face perception, activity starting at 450 ms onwards is thought to reflect high level semantic representations and name retrieval (Schweinberger & Neumann, 2016), both of which would intrinsically rely on the identity processing which occurs earlier during the N250 time. In light of the variability in and correlations with the later parts of the ERP, analyses that are less reliant on pre-defined times-of-interest, such as the one illustrated in Fig. 8, or robust approaches such as that seen in Rousselet et al. (2014), will be useful to investigate the association between neural horizontal bias in the entire ERP and face identification.

In summary, the current study shows that manipulating the horizontal and vertical structure of upright faces in a 1-of-6 face identification task similarly affects response accuracy, N170 amplitude and latency, and N250 amplitude. We found that the presence of horizontal facial structure was associated with higher response accuracy, higher amplitude and shorter latency N170s, and higher amplitude N250s. Finally, we found that the identification accuracy for unfiltered faces was correlated with the horizontal bias of N250 amplitude but not N170 amplitude. We suggest that both the N170 and N250 are sensitive to the presence of horizontal facial structure, but only the N250 is affected by the information value of such structure for face identification.

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