RUNNING HEADING: Hemispheric emotion processing

Neurophysiological evidence (ERPs) for hemispheric processing of facial expressions of emotions:

Evidence from whole face and chimeric face stimuli

Nikoleta Damaskinou and Dawn Watling

Royal Holloway, University of London

Corresponding author: Dawn Watling, Department of Psychology, Royal Holloway, University of

London, Egham Hill, Egham, Surrey, TW2 0EX. Telephone: +44 (0) 1784 443706. Email:

Dawn.Watling@rhul.ac.uk.

Abstract

This study was designed to investigate the patterns of electrophysiological responses of early emotional processing at frontocentral sites in adults and to explore whether adults' activation patterns show hemispheric lateralisation for facial emotion processing. Thirty-five adults viewed full face and chimeric face stimuli. After viewing two faces, sequentially, participants were asked to decide which of the two faces was more emotive. The findings from the standard faces and the chimeric faces suggest that emotion processing is present during the early phases of face processing in the frontocentral sites. In particular, sad emotional faces are processed differently than neutral and happy (including happy chimeras) faces in these early phases of processing. Further, there were differences in the electrode amplitudes over the left and right hemisphere, particularly in the early temporal window. This research provides supporting evidence that the chimeric face test is a test of emotion processing that elicits right hemispheric processing.

Keywords: emotion recognition, lateralisation, chimeric faces, ERP

INTRODUCTION

The ability to quickly and accurately identify emotions in others is an important skill needed in successful social interactions; yet, still little is known about how (or where) emotions are processed in the brain. Research to date suggests that a broadly distributed network of brain areas is recruited when processing emotions (e.g., the occipito-temporal cortices, the orbitofrontal cortex, the amygdala, the basal ganglia and the right parietal cortices; Adolphs, 2002). However, how these regions are configured in order to process emotional input remains largely unknown. Beyond the exploration of specific brain regions, some researchers have explored possible hemispheric differences in processing emotional information (see Bourne, 2010 for a review).

Theories of hemispheric asymmetry of emotion processing

There are three key models of laterality for emotion processing, the Valence Hypothesis, the Approach-withdrawal model and the Right Hemisphere Hypothesis. The Valence Hypothesis proposes that the pattern of hemispheric asymmetry depends on the valence of the emotion so that the right hemisphere (RH) is specialized for processing negative/unpleasant emotions (sadness, fear, anger and disgust) whilst positive/pleasant emotions (happiness and surprise) are processed by the left hemisphere (LH; Davidson, 1992). There are a number of behavioural studies (e.g., Jansari, Tranel, & Adolphs, 2000; Reuter-Lorentz & Davidson, 1981; Reuter-Lorenz, Givis, & Moscovitch, 1983) and EEG studies (e.g., Adolphs, Damasio, Tranel, & Damasio, 1996; Krolak-Salmon, Fischer, Vighetto, & Mauguière, 2001) that lend support to the Valence Hypothesis. In particular, the evidence suggests that the negative emotions are more likely to be processed in the right hemisphere, but it is less clear how positive emotions are processed.

The approach-withdrawal model of emotion processing is similar to the Valence hypothesis, as most negative emotions (fear, disgust) elicit withdrawal behaviour and most positive (happiness, surprise) elicit approach behaviour. The approach-withdrawal model focuses on emotional experience and

behaviour, wherein happiness, surprise, and anger are classified as approach emotions as they drive the individual towards the environmental stimuli. In contrast, sadness, fear, and disgust are classified as withdrawal emotions as they drive the individual away from aversive stimulation in the environment. Of note, empirical evidence for the approach-withdrawal model shows that emotional experience is lateralized within frontal brain regions; namely, approach behaviour and positive affect show activation in the left prefrontal cortex and withdrawal behaviour and negative affect show activation in the right prefrontal cortex (Demaree et al., 2005; Sutton and Davidson, 1997).

In contrast to the Valence Hypothesis and the approach-withdrawal model, the Right Hemisphere Hypothesis posits that the right hemisphere plays a dominant role in processing all emotions and emotional behaviour, including the perception, expression and experience of emotions, regardless of valence (both positive and negative; e.g., Borod et al., 1998; Demaree, Everhart, Youngstrom & Harrison, 2005; Killgore & Yurgelun-Todd, 2007; Murphy, Nimmo-Smith, & Lawrence, 2003). The evidence supporting the Right Hemisphere Hypothesis for adults is consistent across studies using varied methodologies with unilaterally brain damaged patients and neurologically intact participants. There is evidence supporting the right hemisphere processing of both positive and negative emotions (e.g., Bourne, 2005, 2010; Kucharska-Pietura & David, 2003; Nakamura et al., 1999).

In the light of these contrasting theories, and their respective supporting evidence, Killgore and Yurgelun-Todd (2007) examined the underlying neural processes. In an fMRI study, chimeras masked by a full neutral face were presented unilaterally. Chimeras that displayed a single face centrally with the emotional side of the face was present on the left side of the image being viewed (i.e., to the left visual field; LVF) had greater activation within the posterior RH compared to when the emotional side of the face was present on the right side of the image being viewed (i.e., to the right visual field; RVF). These, findings are consistent with the contralateral organisation of the visual system. However, the magnitude and extent of activation produced by the stimuli presented in the LVF was

modulated by the valence of the stimuli. Specifically, there was greater responsiveness to the LVF presentations of sad relative to happy faces, which suggests that the RH is specialized particularly for processing negative valence. Workman, Peters, and Taylor (2000) and Bourne (2010) contrasted the Valence and Right Hemisphere hypotheses using chimeric face stimuli for the six basic emotions (happy, sad, anger, fear, disgust, and surprise); both studies found that all six emotions showed a RH bias. However, the strength of lateralisation within the RH varied across emotions. Bourne, proposed that it was simply the degree of right hemisphere laterality that varied, while Workman and colleagues looked more closely at existing models and called for revision of these. They suggested that the RH may be important in processing emotions quickly, and that where the emotion may be pro-social (lead to a social communicative interaction) there may be superimposed activation in the left hemisphere (participant is preparing for communication so language processing areas are activated in the LH), resulting in weaker laterality effects in pro-social emotions (e.g., happiness, pleasant surprise, sadness) in comparison to the anti-social emotions (disgust, fear, and anger).

There appears to be consistency with regard to sad, anger, and fear facial emotion processing occurring in the RH. Indeed, following a systematic review, Najt, Bayer, and Hausmann (2013) proposed a new framework, where the aforementioned subset of negative valence stimuli receive preferential processing in the RH hemisphere, whereas there would not be any hemispheric hypotheses or predictions for happy, surprise, and disgust facial emotion processing. Consistent with the idea that emotion processing does not all happen in one hemisphere, were also the findings of Tamietto, Geminiani, and de Gelder (2005) and Compton et al. (2005).

In our study, we have chosen to investigate happy and sad emotion processing. We have chosen these as according to the Valence hypothesis and the Approach/Withdrawal model, both of which are emotion classification systems that are widely represented in the literature, and which have happy and sad emotions placed in differing categories (happy is positive valence and is an approach emotion, while sad is negative valence and is a withdrawal emotion).

The Chimeric Faces Test (CFT)

Researchers have used various methods to assess hemispheric lateralisation for facial emotion processing. Methods traditionally involved presenting stimuli unilaterally, to one hemisphere, for a short period of time and assessing accuracy and reaction time (The Divided Visual Field Paradigm; e.g., Killgore & Yurgelun-Todd, 2007; Najt et al., 2013). Another method for assessing laterality for emotion processing has been the CFT, which is a free viewing paradigm.

Chimeric faces are designed so that one half of the face displays an emotion expression and the second half of the face displays a neutral expression. A mirror image of the face is then created so that the face can be displayed with the emotion presented in the opposite side. Chimeric faces are traditionally shown centrally one above the other and participants are asked to decide which of the two faces is more emotive. The CFT relies on the crossed nature of the visual system which projects information from one half of the viewer's visual field to the opposite hemisphere. A stimulus with the emotion presented on the left side of the chimeric image (LVF) is initially processed by the Right Hemisphere (RH) and a stimulus with the emotion presented on the right side of the chimeric image (RVF) is initially processed by the Left Hemisphere (LH; Beaumont, 1983).

The CFT has been validated as a test of laterality with patients who had unilateral brain lesions. Kucharska-Pietura and David (2003) compared chimera judgments of a group of individuals with unilateral LH lesions, unilateral RH lesions, and a healthy control group. They found a LVF bias (RH advantage) in both the controls and the patients with LH lesions when judging chimeric faces, but patients with RH lesions showed a significantly reduced LVF bias. Similarly, Bava, Ballantyne, May, and Trauner (2005) reported the same bias in children with unilateral congenital brain damage. However, there is still some question concerning how this works in healthy controls as a test of laterality when the image is viewed (i.e., is there greater activation in the contralateral brain hemisphere to the field of view in which the emotion is presented). This study will use EEG methods

to assess activation to chimeric faces and address a key question for researchers in the field, namely is the CFT a test of laterality?

Many EEG studies to date (e.g., Batty & Taylor, 2003; Kayser, Tenke, Nordby, Hammerborg, Hugdahl, & Erdmann, 1997; Kestenbaum, 1992; Laurian, Bader, Lanares, & Oros, 1991; Munte, Brack, Grootheer, Wieringa, Matzke, & Johannes 1998; Vandeerploeg, Brown, & Marsh, 1987) that have explored emotion recognition have placed an emphasis on the timing of when emotions are being processed in the brain and have not examined the extent to which lateralisation of emotional processing may exist. To our knowledge there have yet to be any systematic studies that explore electrophysiological activity following the presentation of chimeric faces. This study investigated ERPs at left and right electrode sites to assess hemispheric lateralisation of facial emotion processing in adults using the CFT and an emotion recognition task. This study was designed to investigate the patterns of electrophysiological responses of early emotional processing at frontocentral sites in adults and to explore whether adults' activation patterns show hemispheric lateralisation for facial emotion processing. In addition to exploring lateralisation using the CFT methodology, an emotion recognition task was used to assess free viewing activation of facial emotion to assess activation patterns.

Several studies have supported a model of automatic, rapid, processing of emotional expressions that are indicated by an early (from 90-120ms) positive wave (P1) recorded at parietal sites which reverses its polarity at frontocentral sites becoming a negative wave (N1). The P1/N1 is when the global processing of faces takes place, including the detection of configural changes in faces (Itier & Taylor, 2002); this is when the emotional/non emotional distinction is observed. Following the P1/N1 there is a negative wave at about 170ms (N170) which is a face specific ERP (Blau, Maurer, Tottenham, & McCandliss, 2007) and has its positive counterpart over central sites (VPP). The N170/VPP has been suggested to index the initiation of some structural encoding system and reflects the processing of the components of faces as well as a holistic face processor prior to face

recognition (Sagiv & Bentin, 2001). We look at this face specific ERP because several studies have reported modulation from emotional information of faces. At the later latency (200-400ms) there tends to be a positive wave over the frontocentral sites (P300). This late positive wave has been identified as reflecting the process for discrimination and recognition of emotive visual stimuli (Carretie, Iglesias, & Ballesteros, 1996). The N1/P1 and P300/N300 potentials identified are thought to reflect two stages of emotional processing. First, there is an early stage of emotion processing (N1) during which time the emotional/non-emotional distinction of neutral from emotional stimuli, as a categorical decision, is performed. Second, there is a later stage of emotion processing (P300) during which time the positive/negative distinction is continually processed, the processing of emotional stimuli is completed, and memory-updating occurs. The face specific N170/VPP modulations by emotional faces are of interest because they reflect the independence of face versus facial emotion processing (Bruce &Young, 1986).

The aim of this study is to examine whether activation patterns when free viewing emotional faces support the valence hypothesis and the approach-withdrawal model, or the right hemisphere hypothesis of emotional processing within the first 400ms of processing the emotion. We used both standard full faces and chimeric faces to assess laterality for emotion processing to explore activation patterns for both types of stimuli. When viewing standard faces we expected to see different activation patterns in the left and right hemispheres. When viewing chimeric faces we expected to see that the ERP activation to happy and sad chimeras would reflect the crossed nature of the visual system whereby chimeras with the emotion displayed on the left side of the face would elicit greater amplitude over the RH and chimeras with the emotion displayed on the right side of the face would elicit greater amplitude over the LH; evidence for the crossed nature of the visual system through activation patterns would provide additional evidence of the CFT as a test of laterality. Additionally, it was expected that presenting participants with an emotional face would result in different activation patterns (amplitudes) than presentation of neutral faces, and this would be more pronounced in the RH.

In summary, this study aims, first, to investigate the patterns of early electrophysiological responses to full (standard) emotive and neutral faces at frontocentral sites in adults and to assess whether there is evidence that these are lateralized; while having their EEG responses recorded, participants completed an explicit emotion recognition task with happy, sad and neutral facial stimuli. Second, this study aims to explore whether the behavioural test of laterality, the CFT, is a valid test of laterality using electrophysiological measures; while having their EEG responses recorded, participants completed a chimeric faces task with happy and sad chimera as exemplars of positive and negative valence chimera.

METHOD

Participants

Thirty-five undergraduates (M_{age} = 26.9 years, SD = 7.7, Range = 17 to 49; 9 males) participated in this study and were given course credit for their participation. All participants reported having normal or corrected to normal eyesight, were not on any medication that would influence performance, and did not have any brain damage. Three participants (2 females and 1 male) were removed from the data analyses as they reported being left-handed, the remaining right handed participants had a mean score of 30.9 (SD = 5.7; range from 21 to 51) on Dorthe, Blumenthal, Jason, and Lantz's (1995) handedness questionnaire; scores on this measure typically range between -51 (strongly left handed) to +51 (strongly right handed). Additionally, 1 participant (female) was removed from the data analyses due to having fewer than 30 individual waveforms (due to artefacts and eyeblinks, both assessed as a form of post hoc fixation control).

This study was approved by the Departmental Ethics Committee at Royal Holloway, University of London and participants provided written informed consent.

Materials

The stimuli were a selection of happy and sad facial images from the National Institute of Mental Health (NIMH) NimStim image set. This image set includes 43 professional actors, who are from different races or ethnicities, posing for neutral face and for both closed and open mouth happy and sad images (as well as for the emotions of disgust, fear, anger, surprise). These images were developed for use in studies of face and emotion recognition. Images are available in full colour from http://www.macbrain.org/.

Standard faces for the emotion recognition task. In total 15 individuals were selected from the NimStim image set, each individual chosen had three images (happy, sad and neutral); thus, there were 15 happy images,15 sad images as well as 15 neutral images. All face stimuli were converted to grayscale, a black oval mask was placed over the image to remove hair, neck, and background information and display just the facial information, and all images were presented on a black background. The size of each image, as presented on the monitor, was 17.5 x 26 cm.

Chimeric faces for the chimeric faces task. From the standard face greyscale images, a set of chimeric face stimuli were created. All faces were vertically split (using the nose as a reference for central division) with Adobe Photoshop CS4. The right side of the emotive image / left side of the poser's face (the left side of the face has been found to be more emotive; Mandal & Ambady, 2004) was used in the creation of the chimeras. The emotion hemifaces then were attached to neutral hemifaces so that half of the face showed an emotional expression (happy or sad), and the other half showed a neutral expression from the same poser. A black oval mask was placed over the chimeric face to cover all outer face information and hair, and only allow the facial information to be seen. The size of the image, as presented on the monitor, was 17.5 x 26 cm and it was presented on a black background. In total 15 happy chimeras, and 15 sad chimeras were created. A mirror image of each original chimeric was then created by 'flipping' horizontally the image, to create a set of images where one chimeric image had the emotion displayed on the left side of the face and one chimeric

image (an identical image) had the emotion displayed on the right side (mirror image) as seen by the viewer.

Procedure

Each participant was seated in a dark room with a keyboard in front of him/her, with their head supported by a chin rest, in front of a 17" CRT computer monitor at a viewing distance of 70 cm. Participants were asked to put their right index finger on the number 1 key and their right middle finger on the number 2 key on the keyboard numeric keypad.

The participants performed an emotion recognition and a chimeric faces task whilst having their electroencephalogram (EEG) recorded. Tasks were randomised as to which was first and second. Additionally, within each task there were two experimental blocks (happy or sad image blocks), for which the order was balanced. Each block contained 80 trials. Each trial had a fixation point presented for 1000 ms, followed by a face presented for 500 ms, then by a second fixation point for 1000 ms, and lastly a second face presented for 500 ms. For instance, in the emotion recognition task each trial had one face image displayed that was emotive (happy or sad depending on the block) and one face image displayed that was neutral, and in the chimeric faces task each trial had one face image displayed with the emotion on the left side of the image and one face image displayed with the emotion on the right side of the image. Stimuli within each trial were presented in a block randomised order (to balance the number of times each type of face stimuli was presented first and the number of times each type of face stimuli was presented second). The trials were randomised within each emotion block. Following the presentation of the second face participants made a judgement on "which of the two faces looked happier" in the happy trial block, and "which of the two faces looked sadder" in the sad trial block.

Emotion recognition task. In this task half of the 80 trials within a block presented an emotional face first (happy in the happy block, and sad in the sad block) and a neutral face second and half the trials

had the opposite order of presentation. Participants were asked to judge which of the two successive faces displayed the emotion (see Figure 1). Participants pressed 1 with their right-hand index finger if they thought the first image displayed an emotion and pressed 2 with the right-hand middle finger if they thought the second image displayed an emotion.

Chimeric faces task. In this task half of the 80 trials within a block presented the image with the emotional part of the face on the left side of the image (happy in the happy block, and sad in the sad block) and neutral on the right side of the image followed by the image with the emotional part of the face on the right side of the image and neutral on the left side of the image, and half the trials had the opposite order of presentation (see Figure 2). Participants were instructed to press 1 with their right index finger if they thought that the first chimera was more emotive (happier or sadder) than the second and press 2 with the right middle finger if they thought the second chimera was more emotive (happier or sadder) than the first.

[Insert Figure 1 and Figure 2 about here]

ERP Recording and Analysis

ERPs were recorded with Ag-AgCl electrodes and linked-mastoid reference using a 10-20 system. Recordings were used at frontal regions, Fz (midline), F3 (left), and F4 (right), and central regions, Cz (centre), C3 (left), and C4 (right). The sampling rate was 1000 Hz and a band-pass filter of 0.01 Hz was used. Horizontal electrooculography (EOG) was recorded bipolarly from the outer canthi of both eyes, allowing us to record eye movements. The impedance for all electrodes was kept below 10 KΩ.

All recordings were analysed and processed off-line after data acquisition. After visual inspection of

the raw data, trials containing artefacts, mainly eye movements, were removed from the analysis as

a form of post-hoc fixation control. The remaining EEG and EOG were epoched off-line into 500 ms

periods, starting 100 ms pre-stimulus and ending 400 ms post-stimulus onset. Each participant had

to have at least 30 waveforms after removal of artefacts to be included in the analyses; these

waveforms were averaged and thereby contributed to the average waveform for any condition (see

Figure 3, 4a and 4b for grand average waveforms for each task, condition, and electrode site). For

each task, and within each emotion block (happy or sad), analyses were conducted on the ERP

responses to the first face of the pairs only. Looking only at ERP responses to the first face allowed

control of knowledge about emotional content and would mean that the analyses were not

confounded by uncontrolled expectancy or response preparation effects in relation to either of the

experimental tasks. The first facial image was always predictive of the emotional content or

otherwise of the second face. Further, for the emotion recognition task, only where participants

correctly stated which face was happy or sad (depending on the presentation block) was the

recording used in the analyses; for the chimeric faces there was no correct response. Separate

averages were computed for each participant, at each of the six electrodes sites (F3, Fz, F4, C3, Cz,

C4), for each task, and within each block. In the Emotion recognition task, as neutral was used both

in the happy block and in the sad block, with strong correlations for amplitude at the three key

components and electrode sites (N1, all correlations (rs) $\geq$ .472, all probabilities (ps) $\leq$ .007; VPP, rs

all $\geq$ .732, ps all $\leq$ .001; P300, rs all $\geq$ .715, ps all $\leq$ .001), the amplitude in the two neutral conditions

was averaged to allow a combined analysis (happy, sad, and neutral). Grand averages were

calculated for all participants in each condition.

[Insert Figure 3 and Figures 4a, 4b about here]

Given the age range of the participants, we controlled for age within the analyses. The averages from the standard face trials were analysed using 3 way repeated measures ANCOVAs, with expression (happy, sad, and neutral) X hemisphere electrode site (left, midline, and right) X electrode region (frontal and central) as within-participant measures. The averages from the chimeric face trials were analysed using 4 way repeated measures ANCOVAs, with emotion (happy and sad), hemisphere (left and right), visual field presentation of the emotion (LVF and RVF), and electrode site (frontal and central) as the within-participants measures. Significant interactions were followed-up with simple effects analyses and post-hoc comparisons with Bonferroni correction. Type 1 errors associated with inhomogeneity of variance were controlled by using the Greenhouse-Geisser epsilon where appropriate (Jennings & Wood, 1976).

For all of our ANCOVAs, we performed separate analysis on the average amplitude for each of the time windows (80-120 ms, 120-180 ms, and 180-400 ms). The general cortical response included a prominent, early negative peak between 80- 120 ms, a subsequent positive peak from 130-180ms and later positivity from 180-400 ms. Whilst it might not be helpful to assign labels to these windows, these are analogous to the N1, VPP and P3 (Joyce & Rossion, 2005; Luck, 2005; Picton, Lins, & Scherg, 1995).

As we are interested in hemispheric differences of activation, rather than region of activation main effects of electrode region (frontal or central) are not reported here.

RESULTS

Standard faces

Table 1 shows the mean and standard error of the amplitudes within these temporal windows, for each of the standard face conditions. We submitted the mean voltages for each of these windows to a set of repeated measures ANCOVA (as described above).

[Insert Table 1 about here]

Early temporal window (80-120ms), N1

In the time window most closely resembling the N1 effect, there was a significant main effect of emotion, F (2, 58) = 4.06, p = .022, η_p^2 = .12. Post hoc comparisons with Bonferroni corrections for multiple comparisons showed that there were significantly greater amplitudes for happy faces than sad faces, p = .045, M (SE) = -0.20 (.03) and -0.15 (.03), respectively. There was no significant difference in the amplitudes between happy and neutral faces (M = -0.17, SE = .02), p = .290, nor between sad and neutral faces, p = .748. Importantly, there was a main effect of hemisphere electrode site, F (2, 58) = 30.16, p < .001, η_p^2 = .51. Post hoc comparisons with Bonferroni corrections for multiple comparisons showed that the mean amplitude for the midline electrodes (M = -.24, SE = .03) was significantly greater than the amplitude for LH electrodes (M = -.12, SE = .02), p < .001, and the RH electrodes (M = -.16, SE = .03), p < .001; additionally, there is significantly greater negativity for amplitudes recorded over the RH electrode sites than for those recorded over the LH electrode sites, p = .046.

Middle temporal window (130-180ms), VPP

In the time window most closely resembling the VPP effect, there was a significant main effect of emotion, F (1.38, 40.08) = 25.95, p < .001, η_p^2 = .472. Post hoc comparisons with Bonferroni corrections for multiple comparisons showed that there was a significant difference between happy (M = 0.37, SE = .04) and sad faces (M = 0.18, SE = .03), p < .001, and between sad and neutral faces, (M = 0.34, SE = .04), p < .001, but not between happy and neutral faces, p = .329. There was also a significant main effect of hemisphere electrode site, F (2, 58) = 8.52, p = .001, η^2 = .23, whereby post

hoc comparisons with Bonferroni corrections for multiple comparisons showed that the mean

amplitude at the midline electrode sites (M = 0.34, SE = .04) was significantly greater than the

amplitude at LH electrode sites (M = 0.25, SE = .03), p < .001, but not at the RH electrode sites (M =

0.30, SE = .03), p = .079; additionally, there was no significant difference in amplitude between the

RH and the LH amplitudes, p = .272.

There was a significant interaction of emotion by hemispheric electrode site, F (2.41, 69.79) = 18.81,

p < .001, η_p^2 = .39, and a significant interaction of emotion by electrode region, F(1.50, 43.48) = 3.85,

p = .040, η_p^2 = .12. These two interactions were qualified by a three way interaction of emotion by

hemispheric electrode site by electrode region, F(2.52, 73.10) = 4.00, η_p^2 = .12 (see means in Table 1)

Simple effects analyses with Bonferroni corrections demonstrated that hemisphere electrode

amplitude patterns differed for neutral at the frontal region location, F (2, 28) = 9.26, p = .001, η_p^2 =

.40, and the central region location, F (2, 28) = 10.49, p < .001, η_p^2 = .43. Similarly, hemisphere

electrode amplitude patterns differed for happy at the frontal region location, F (2, 28) = 6.74, p =

.004, η_p^2 = .33, and the central region location, F (2, 28) = 8.61, p = .001, η_p^2 = .38. There was no

significant difference in hemisphere electrode amplitude patterns for sad at the frontal region

location, F (2, 28) = .33, p = .725, η_p^2 = .02, and the central region location, F (2, 28) = 1.33, p = .282,

η_p^2 = .09. For both the neutral and happy images amplitudes in the frontal region were higher in the

RH than the LH (p-values = .006 and .010, respectively), while in the central region there was no

significant difference between the LH and RH amplitudes (p-values = 1.00). Further, for both neutral

and happy trials in the frontal region, the amplitude at the central electrode site was higher than

that at the LH (p-values < .001 and .003, respectively) but not than that at the RH (p-values = .088

and .152, respectively). In the central region, for the neutral images the amplitude at the central

electrode site was higher than that at the LH (p = .003) and at the RH (p = .008), and for the happy

images the amplitude at the central electrode site was not significantly different than that at the LH

(p = .064) but was at the RH (p = .004).

Late temporal window (180-400ms), P300

In the time window most closely resembling the P300 effect, there was a significant effect of emotion, $F(2, 58) = 10.15$ $p < .001$, $\eta_p^2 = .26$, whereby post hoc comparisons with Bonferroni correction showed that there was greater amplitude for the happy ($M = .15$, $SE = .04$) than neutral faces ($M = .10$, $SE = .04$), $p = .020$, and for the sad ($M = .20$, $SE = .05$) than neutral faces, $p < .001$, but not for happy and sad amplitudes, $p = .307$. There was also a main effect of hemisphere electrode site, $F(2, 58) = 5.76$, $p = .005$, $\eta_p^2 = .17$. Post hoc comparisons with Bonferroni correction showed that amplitude was significantly lower at the midline electrodes than at the LH electrodes, $p = .002$, but not than at the RH electrodes, $p = .105$ (LH $M = .18$, $SE = .04$; midline $M = .11$, $SE = .05$; RH $M = .16$, $SE = .04$); further there was no significant difference between LH and RH amplitudes, $p = 1.00$.

Summary of the standard face findings

For early epochs amplitudes were significantly greater at the midline electrode sites than the LH and RH sites. Early in the epochs (N1) the amplitudes recorded were greater in the RH compared to the LH. The amplitudes were also sensitive to the emotional content of the standard faces presented. This was driven primarily by a significant difference between the responses to happy and sad faces. Midway through the epochs (VPP) amplitude differences were greater in the RH compared to the LH for the neutral faces and happy faces; although for the happy faces this was just in the frontal region. In the final period of the epoch (180-400ms) with the standard faces we primarily observed a generic target versus non-target effect. That is, the amplitudes distinguished both happy and sad faces from the neutral non-targets, but they did not distinguish the different emotions.

Chimeric faces

Table 2 shows the mean and standard error of the amplitudes within the three temporal windows, for each of the chimeric face conditions. We submitted the mean voltages for each of these windows to a set of repeated measures ANCOVA (as described in the methods section).

[Insert Table 2 about here]

Early temporal window (80-120ms), N1

In the time window most closely resembling the N1 effect, we observed a significant main effect of hemisphere electrode site, $F(1, 29) = 13.52$, $p = .001$, $\eta_p^2 = .32$, where there was greater amplitude in the RH (M = -.15, SE = .03) than the LH (M = -.10, SE = .02). Additionally, there was an interaction between hemisphere emotion and electrode site, $F(1, 29) = 6.08$, $p = .020$, $\eta_p^2 = .17$, and an interaction between electrode site and electrode region, $F(1, 29) = 7.79$, $p = .009$, $\eta_p^2 = .21$. These interactions were qualified by a three way interaction of emotion by electrode site by electrode region, $F(1, 29) = 5.14$, $p = .031$, $\eta_p^2 = .15$. Simple effects analyses with Bonferroni corrections demonstrated that whilst for both the happy and sad emotion processing there was higher amplitudes in the RH than the LH in the frontal electrode regions, this effect was stronger for the sad emotion than for the happy emotion, sad $F(1, 29) = 18.32$, $p < .001$, $\eta_p^2 = .39$ and happy $F(1, 29) = 5.748$, $p = .023$, $\eta_p^2 = .17$ (see Figure 3). There was no significant in the LH and RH amplitudes at the central regions for sad and happy chimeras, F-values < 1.

Middle temporal window (130-180ms), VPP

In the time window most closely resembling the VPP effect, there was a significant main effect of hemisphere electrode site and it approached significance, $F(1, 29) = 2.98$, $p = .095$, $\eta_p^2 = .09$, whereby there was greater positivity in the RH ($M = .14$, $SE = .03$) than in the LH ($M = .12$, $SE = .02$). There was a significant interaction of hemisphere electrode site by emotion, $F(1, 29) = 3.36$, $p = .077$, $\eta_p^2 = .10$, and of emotion by side of emotion presentation, $F(1, 29) = 8.24$, $p = .008$, $\eta_p^2 = .22$. Importantly, these two way interactions were qualified by a significant three way interaction between

hemisphere electrode location, side of emotion presentation, and emotion, $F(1, 29) = 5.51$, $p = .026$,

$\eta_p^2 = .16$. Simple effects analyses showed that for the sad emotion, amplitude was higher at the RH

than the LH locations when the emotion was presented on the left side of the chimeric images, $F(1,$

$29) = 7.02$, $p = .013$, $\eta_p^2 = .20$, while there was no difference when the emotion was presented on the

right side of the chimeric images, $F < 1$. Additionally, there was no difference between LH and RH

amplitudes for happy emotion when the emotion was presented on the left or on the right side of

the chimeric images, $F\text{-}value$s < 1 (see Figure 4).

[Insert Figure 4 about here]

Late temporal window (180-400ms), P300

In the time window most closely resembling the P300 effect, there were no significant main effects,

but there was a significant interaction of hemisphere site location by visual field of emotion

presentation, $F(1, 29) = 5.55$, $p = .025$, $\eta_p^2 = .16$. Simple effect analyses showed that when the

emotion information was presented on the left side of the chimeric faces there was difference

between RH and LH amplitudes that approached significance, $F(1, 29) = 3.25$, $p = .082$, $\eta_p^2 = .10$.

There was no significant effect when the emotion information was presented on the right side of the

chimeric faces, $F < 1$ (see Figure 5).

[Insert Figure 5 about here]

Summary of the chimeric face findings

Early in the epochs, the amplitudes that we recorded were sensitive to the emotional content of the chimeric faces presented; while the amplitudes were higher at the RH electrode sites than the LH electrode sites in the frontal regions, this was stronger when processing the sad images than the happy images. Midway through the epochs (130-180 ms) the chimeric face trials demonstrated that the effect of emotional content could be relatively lateralized, depending upon the visual field of the emotional content. Specifically with sad chimeras, when the emotional content was on the left we observed more positive amplitudes over the right hemisphere, whereas when the emotional content was on the right there was no difference between the two hemispheres. In the final period of the epoch (180-400 ms) with the chimeric faces, there was not a strong differential response to the two emotions. However, there was a different effect of visual field of emotion presentation over the two hemispheres: when the emotion was presented in the LVF there were greater amplitudes over the LH than the RH, while when presentation was in the RVF there was no difference in amplitudes between the LH and RH.

DISCUSSION

This study investigated the patterns of electrophysiological responses of early emotional processing at frontocentral sites and whether these are lateralised. The data show a pattern of waveforms consistent with previous EEG research for the processing of emotions, namely, the N1, the VPP and the P300. These potentials were modulated by emotional expressions which supports the idea that the recognition of emotion from faces and structural encoding of faces are parallel and independent mechanisms. Importantly, there is evidence of laterality for facial emotion processing using chimeras, particularly for the sad emotional chimeras. When the emotional information was presented on the left side of the image we see a significant asymmetry between the amplitudes of the two hemispheres, whereas when the same emotional information is presented on the right side of the image there is no significant different in the amplitudes of the two hemispheres.

Standard Faces

Within the standard face trials each temporal window (early, middle, and late) showed activation

patterns that differed depending on if the facial expression viewed was happy, sad, or neutral. This

supports earlier work that the processing of facial expression begins during the early stages of face

processing and that the processing of facial expression continues in the later stages at a time when

cognitive processing of faces occurs (Batty & Taylor, 2003; Campanella Quinet, Bruyer, Crommelinck

& Guerit, 2002; Eimer, Holmes, & McGlone 2003; Esslen, Pascual-Marqui, Hell, Kochi, & Lehmann,

2004; Marinkovic & Halgren, 1998; Vandeerploeg et al., 1987; Wong et al., 2009). In the early epoch

activation patterns showed higher amplitudes over the RH electrode sites than the LH electrode

sites, indicating processing occurring in the RH over that occurring in the LH. Specifically, across the

early and middle temporal windows the activation patterns for the neutral and happy faces did not

differ, while the amplitudes for sad emotional faces were lower than for the happy and the neutral

faces (N1 and VPP), albeit for the happy the differences in the middle temporal window only was

shown in the frontal electrode sites. Similar to the early temporal window, in the late temporal

window the amplitudes were greater when the happy and the sad faces were processed in

comparison to when the neutral faces were processed. Together, these findings indicated that early

in facial emotion processing happy and sad faces are processed differently. Later in processing

(P300) we simply observed differential processing for emotional faces relative to their neutral

counterparts. A number of studies have been consistent in finding an enhanced positivity (or

reduced negativity) at these later latencies within the frontocentral sites (e.g., Batty & Taylor, 2003;

Eimer & Holmes, 2007; Olofsson, Nordin, Sequeira, & Polich, 2008; Vandeerploeg et al., 1987),

where the later processing (>300ms) is thought to reflect a higher and more intensive level of

emotional processing, for instance, conscious evaluation of emotional information and memory

updating (Dolcos & Cabeza, 2002; Palomba, Angrilli, & Mini,1997).

Further to the differences in activation patterns depending on the emotional affect of the face

displayed, we saw that amplitudes were greatest at the midline electrodes during the N1 and VPP

temporal windows in comparison to activation over the left hemisphere electrodes and the right

hemisphere electrodes, but not during the P300 temporal window. The greater midline amplitudes at the start of processing could possibly be explained by physics; the dipoles in each hemisphere summate at midline. An alternative interesting view to explain the bilaterality early in the processing of the emotional stimuli, which was observed across participants in the present study (as indicated by significantly greater midline amplitudes), was presented by Kinsbourne (1982) who proposed an equilibration of the two hemispheres, where the corpus callosum (a large neural bundle of fibres which connects the two cerebral hemispheres and enables their interaction and integration of information between them) is concerned with excitation – inhibition balance between the two hemispheres. Therefore, depending upon the task demands the corpus callosum will either allocate activation to one hemisphere or will distribute activation between the hemispheres. Further, there may be a high degree of interhemispheric transfer occurring shortly after stimulus presentation; as one hemisphere which is specialized for a task becomes overtaxed more resources are recruited from both hemispheres (bilateral advantage) giving an increased processing capacity. Therefore, even when one hemisphere is less efficient in a task than the other it has the capacity to contribute when task difficulty increases (Banich, 1998).

While amplitudes were greatest over the midline electrodes, the amplitudes were greater at the right hemisphere electrode sites than at the left hemisphere electrode sites during this early temporal window; however, this finding was not moderated by emotion. In other words, within the first 400ms of the face presentation the facial emotion information does not appear to be lateralized when viewing full face stimuli. This finding is consistent with the laterality effects for facial recognition (Chung & Thomson, 1995; Bourne & Hole, 2006) and therefore would most likely be explained by the face recognition. It would be important to investigate in future research whether lateralization of facial emotional processing appears in a larger time window (after 400 ms and up to 1000 ms) than was investigated in this study to assess laterality effects for emotion processing for different facial emotional stimuli.

Chimeric Faces

Within the chimeric face trials we found early processing (N1) differences overall in the right hemisphere than in the left hemisphere, although in the frontal electrode sites this finding was stronger when sad images were viewed than when happy images were viewed. Furthermore, in the middle temporal window (VPP) we found that there was greater activation over the right hemisphere than the left hemisphere (approaching significance), regardless of whether the chimeric image was happy or sad. Taken together these findings are consistent with previous work (e.g., Bourne, 2005, 2010; Kucharska-Pietura & David, 2003; Nakamura et al., 1999), which suggests that emotive facial images are processed in the right hemisphere. Further, the finding that hemispheric processing is more differentiated for sad faces (negative emotions), is also consistent with previous work (e.g., Itier & Taylor, 2004; Pizzagalli, Lehmann, Hendrick, Regard, Pascual-Marqui, & Davidson., 2002).

Importantly, in the middle temporal window (VPP) amplitudes tended to be higher in the RH than in the LH. For sad this activation pattern differed further depending on the side of the chimeric face image that the emotion was displayed on. Specifically, when the sad emotion was displayed on the left side of the chimeric face images participants' amplitudes were greater over the right hemisphere than the left hemisphere. When the sad emotion was displayed on the right side of the chimeric face images there was no difference in amplitude between the right and left hemisphere electrode locations. This finding, where there was higher amplitude at the right hemisphere electrode locations when emotion is presented on the left side of the image, is a pattern that would be predicted based on previous literature (e.g., Bourne, 2010; Kucharska-Pietura & David, 2003; Levy, Heller, Banich, & Burton, 1983).

Different activation patterns continued in the late temporal window; however, the hemispheric differences were opposite to those seen in the VPP window. We saw that in the P300 window when the emotion was presented on the left side of the chimeric face (regardless of whether it was happy

or sad) that there was higher amplitude over the left hemisphere than the right hemisphere.

Consistent with the VPP findings, when the emotion was presented on the right side of the chimeric

face there was no difference in left and right hemisphere amplitudes. Greater amplitude over the

left hemisphere with presentation of emotion on the left side of the chimeric stimulus is interesting.

It is possible that this could be due to participants preparing for the next stimulus when they would

be required to decide which face is most emotional (the first or the second). In preparation, of the

decision they will be making, participants may be beginning to make predictions about what

stimulus is upcoming. Researchers have found that when making predictions in language (e.g., what

word will come up next) there is greater left hemisphere activation (Federmeier, 2007). It would be

important to follow this up in future work, varying the methods to remove the possible influencing

factor of a participant predicting the next image (e.g., rather than after every two images making a

judgement, make the judgement more randomly throughout the program).

The chimeric faces findings support our prediction that there would be differential activation,

depending on the visual field of presentation. Specifically, where the chimeras displayed the

emotion on the left side of the face there was greater amplitude over the RH and where the

chimeras displayed the emotion on the right visual field there was greater amplitude over the LH.

This adds to the support that already exists that the CFT is a test of hemispheric laterality (Bourne,

2010; Kucharska-Pietura & David, 2003; Levy et al., 1983). Further, there is support that the

processing of sad faces is stronger than for happy faces in the right hemisphere, but that early

processing occurs in the right hemisphere for both emotions.

Theories of emotion processing

This work presents some of the first findings exploring emotion processing in full faces and those in

chimeric faces. Both the standard face task and the chimeric face task point to early emotion

processing occurring in the RH when an early emotional versus non-emotion distinction is being

made. Interesting, from the standard face task, this distinction may be more than simply processing

if the image is emotional or not given that amplitudes were significantly higher for the happy emotion than for the sad emotion. It is possible that the brain is able to process positive valence and approach emotions more efficiently (discriminate quickly from neutral). Happy emotions are the earliest emotion to be recognised (Herba & Phillips, 2004) while emotions such as sadness have been found to have more errors in emotion recognition with age (e.g., Keightley, Winocur, Burianova, Hongwanishkul, & Grady, 2006). This is something that should be investigated further in future work with other forms of positive or approach emotions.

Theories of emotion recognition tend to support that sad emotional faces are processed in the RH, whereas there are conflicting views about whether the processing of happy emotional faces is completed in the right or in the left hemisphere. The valence hypothesis and the approach withdrawal hypothesis would argue that happy emotional faces are processed in the LH, whereas the right hemisphere hypothesis is that these faces are processed in the RH (for a discussion see Bourne, 2010; Watling, Workman, & Bourne, 2012; Workman et al., 2000). The evidence from this work supports the idea that emotions are processed in the RH, and there is not clear support that that is differentiated depending on the emotion. We did find that with the chimeric faces there were higher RH amplitudes for the sad than for the happy trials, but overall there was higher amplitudes in the RH than the LH. This supports previous work where there is evidence that happy emotional faces may be less strongly lateralised to the right hemisphere (e.g., Bourne, 2010). In general, the findings from this study indicate that early processing of emotions occurs more strongly in the RH.

Our findings indicated that hemispheric activation may differ depending on the timing post presentation of stimuli. We saw in early and middle temporal timings that the right hemisphere had greater amplitudes in the frontal electrode sites than in the central sites. As highlighted in the introduction, research that has explored emotion processing in the brain have found different regions that may play a role (see Adolphs, 2002). It may be that at different stages of emotion

processing different neural systems play a role. It would be important to explore how the temporal timing of emotion processing may relate to activation in neural systems.

Summary

Taken together, we found that there were differences in the findings for the standard and chimeric face trials, possibly reflective of the differences in the two tasks. For the standard face trials one image was emotive and the second was neutral, while for the chimeric face trials both images were emotive, which may influence how the participants attended to and processed the information. Having emotion information presented on one side of the face in the chimeric images was designed to assess differences in emotion processing in the LH and RH, which is a strength of the current study; however, this may impact how the faces were processed in comparison to how full faces are processed due to the stimuli not being one full face (e.g., two halves put together).

Taken together, the findings from the standard (full) faces and the chimeric faces tasks we see that emotion processing is present during the early phases of face processing in the frontocentral sites. In particular, sad emotional faces are processed differently than neutral and happy (including happy chimeras) faces in these early phases of processing. Further, whilst we know from the standard face trials that there was greater activation over the midline electrodes, there were still differences in the amplitudes from the electrodes at the left and right hemisphere electrode sites, particularly in the early temporal window. These hemispheric differences in processing were also found in the chimeric face trials. We saw differences between amplitudes for the happy and sad chimeric face trials, which supports that there is differential hemispheric activation that is being invoked by emotions. Importantly, the findings indicated of this work supports that emotions are processed first in the right hemisphere, supporting the right hemisphere hypothesis of emotion processing. More work is required to establish the temporal sequence of emotion recognition processing within the right and left.

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Table 1. Means (SE) of the amplitudes for each electrode region by site for each ERP component (N1,

VPP, and PS300) and type of emotional face (happy, sad, neutral)

		Electrode Site					
		Frontal M(SE)			Central M(SE)		
		F3	Fz	F4	C3	Cz	C4
		LH	Central	RH	LH	Central	RH
N1	Happy	-.10 (.03)	-.23 (.04)	-.19 (.03)	-.16 (.04)	-.30 (.05)	-.18 (.04)
	Sad	-.07 (.03)	-.17 (.04)	-.13 (.03)	-.14 (.04)	-.26 (.05)	-.14 (.03)
	Neu	-.08 (.03)	-.20 (.03)	-.15 (.03)	-.16 (.03)	-.26 (.03)	-.16 (.03)
VPP	Happy	.27 (.03)	.42 (.05)	.35 (.04)	.38 (.06)	.47 (.05)	.38 (.04)
	Sad	.15 (.03)	.17 (.04)	.16 (.03)	.20 (.04)	.18 (.04)	.21 (.03)
	Neu	.23 (.03)	.38 (.04)	.33 (.03)	.33 (.05)	.42 (.05)	.35 (.04)
P300	Happy	.13 (.04)	.11 (.05)	.13 (.04)	.22 (.06)	.13 (.05)	.21 (.04)
	Sad	.21 (.06)	.17 (.07)	.18 (.05)	.26 (.06)	.15 (.064)	.23 (.05)
	Neu	.12 (.04)	.05 (.05)	.09 (.04)	.14 (.05)	.04 (.06)	.14 (.05)

Table 2. Means (SE) of the amplitudes for each electrode region by site for each ERP component (N1, VPP, and PS300) and type of emotional face (happy, sad) by visual field of presentation (LVF or RVF)

			Frontal		Central	
			F3	F4	C3	C4
			LH	RH	LH	RH
N1	Happy	LVF	-.04 (.03)	-.11 (.03)	-.15 (.03)	-.12 (.03)
		RVF	-.06 (.03)	-.12 (.04)	-.15 (.04)	-.16 (.04)
	Sad	LVF	-.05 (.03)	-.17 (.03)	-.16 (.03)	-.17 (.03)
		RVF	-.05 (.02)	-.16 (.04)	-.17 (.04)	-.18 (.04)
VPP	Happy	LVF	.15 (.03)	.14 (.03)	.18 (.03)	.20 (.04)
		RVF	.10 (.03)	.11 (.04)	.12 (.04)	.13 (.04)
	Sad	LVF	0 (.002)	.10 (.04)	.11 (.03)	.16 (.05)
		RVF	.14 (.03)	.12 (.03)	.14 (.04)	.17 (.03)
P300	Happy	LVF	.29 (.05)	.25 (.06)	.27 (.04)	.24 (.05)
		RVF	.22 (.05)	.26 (.05)	.24 (.04)	.23 (.05)
	Sad	LVF	.27 (.05)	.22 (.05)	.27 (.05)	.25 (.05)
		RVF	.27 (.05)	.24 (.05)	.27 (.05)	.25 (.05)

Figure 1. Emotion recognition trial. A face (emotional or neutral) is presented for 500ms followed by a centrally presented dot for 1000ms, followed by a second face presented for 500ms, followed by a dot for 1000ms.
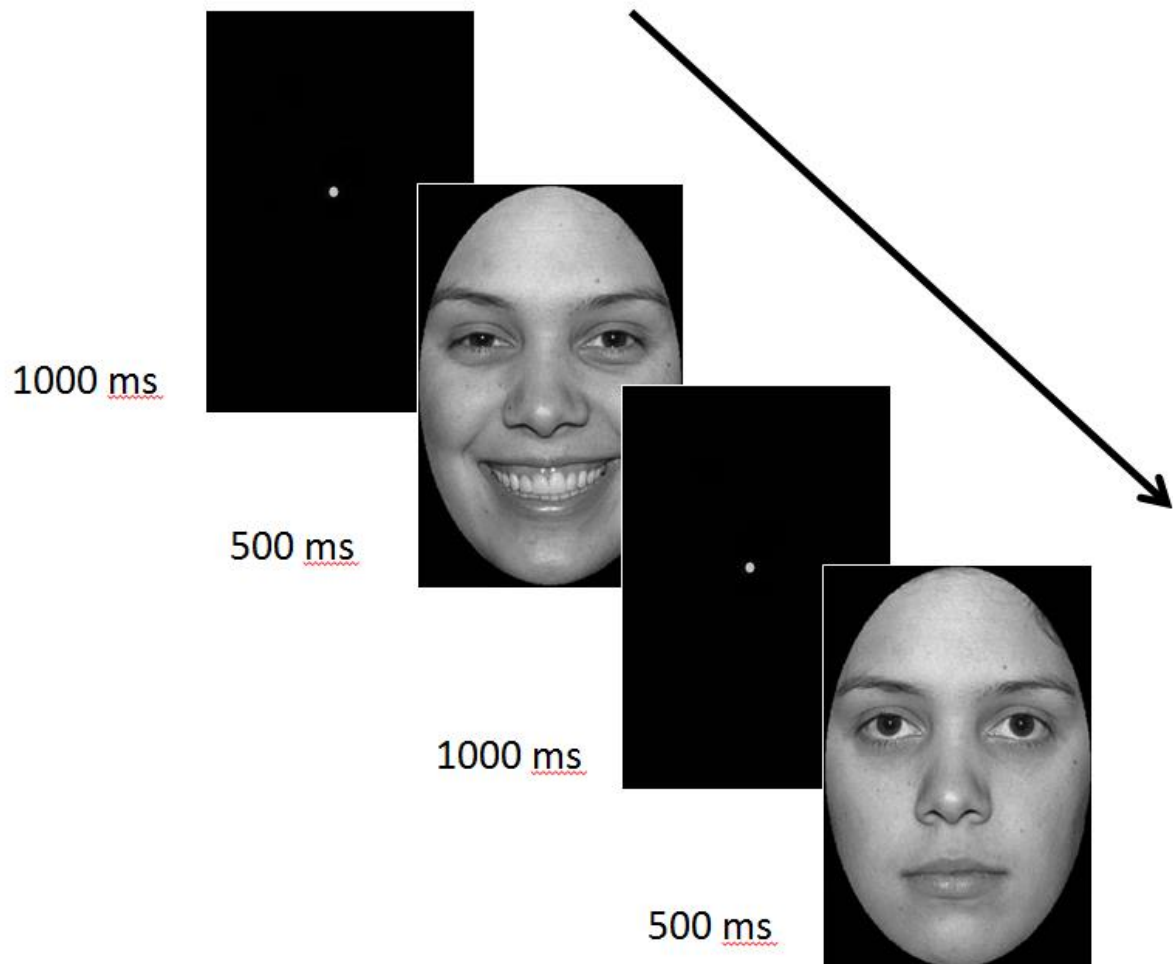
Figure 2. Chimeric face trial. A chimeric face (with the emotion being on the left or right side of the face) is presented for 500ms, followed by a centrally presented dot for 1000ms, followed by a second chimeric face (with the emotion being on the side of the face different to the first face) presented for 500ms, followed by a dot for 1000ms.

1000 ms

500 ms

1000 ms

500 ms
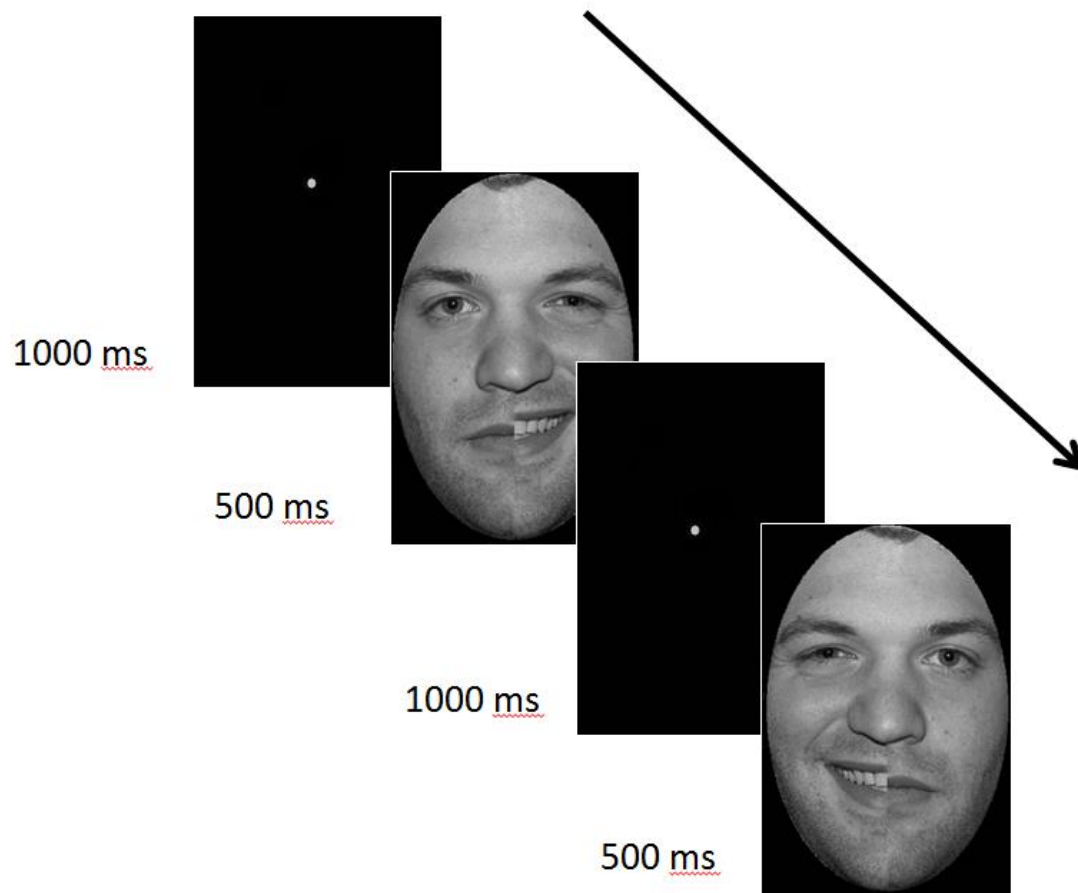
Figure 3. Grand averages of amplitudes of standard face images at the Frontal electrode sites (F3, Fz, and F4) and Central electrode sites (C3, Cz, and C4) for happy, sad, and neutral images
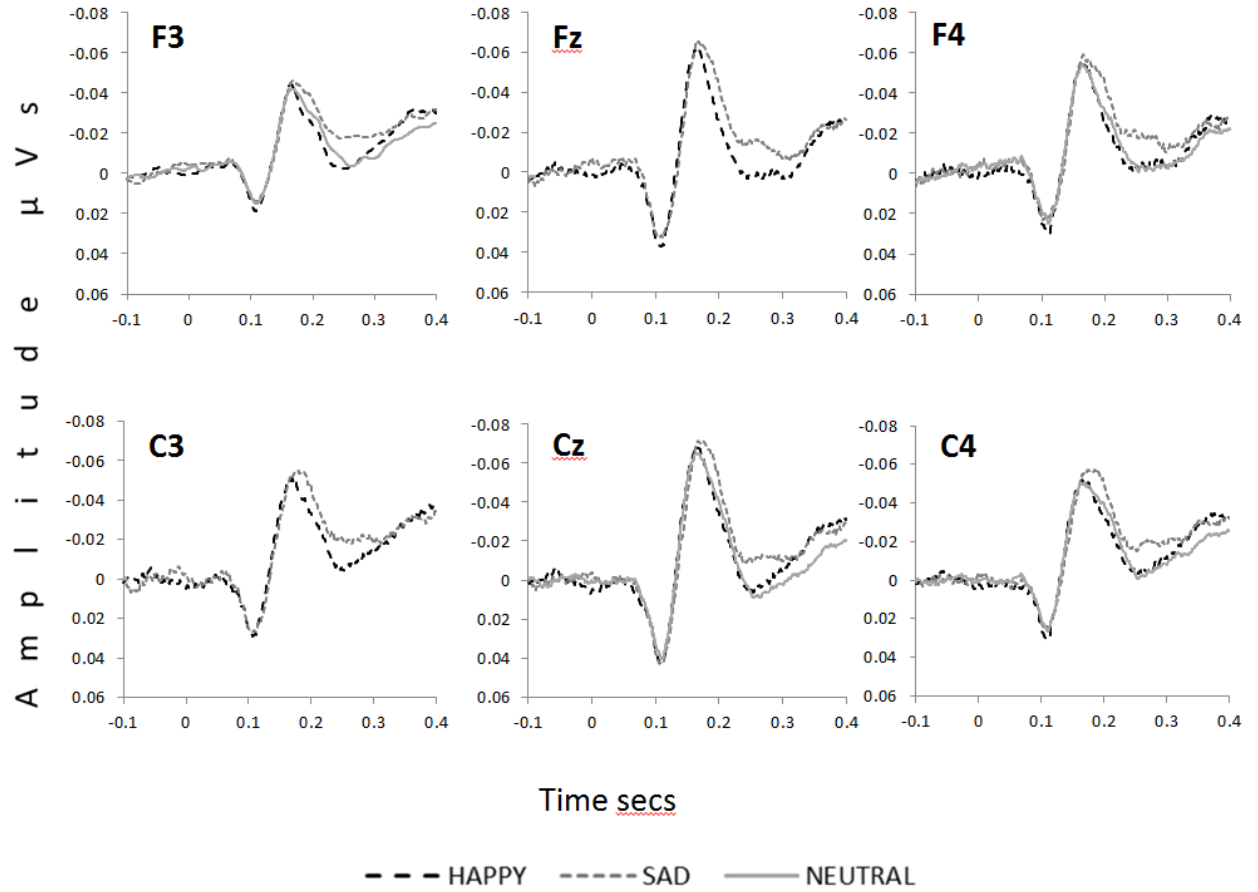
Figure 4a. Grand averages of amplitudes of happy chimeric face images at the Frontal electrode sites

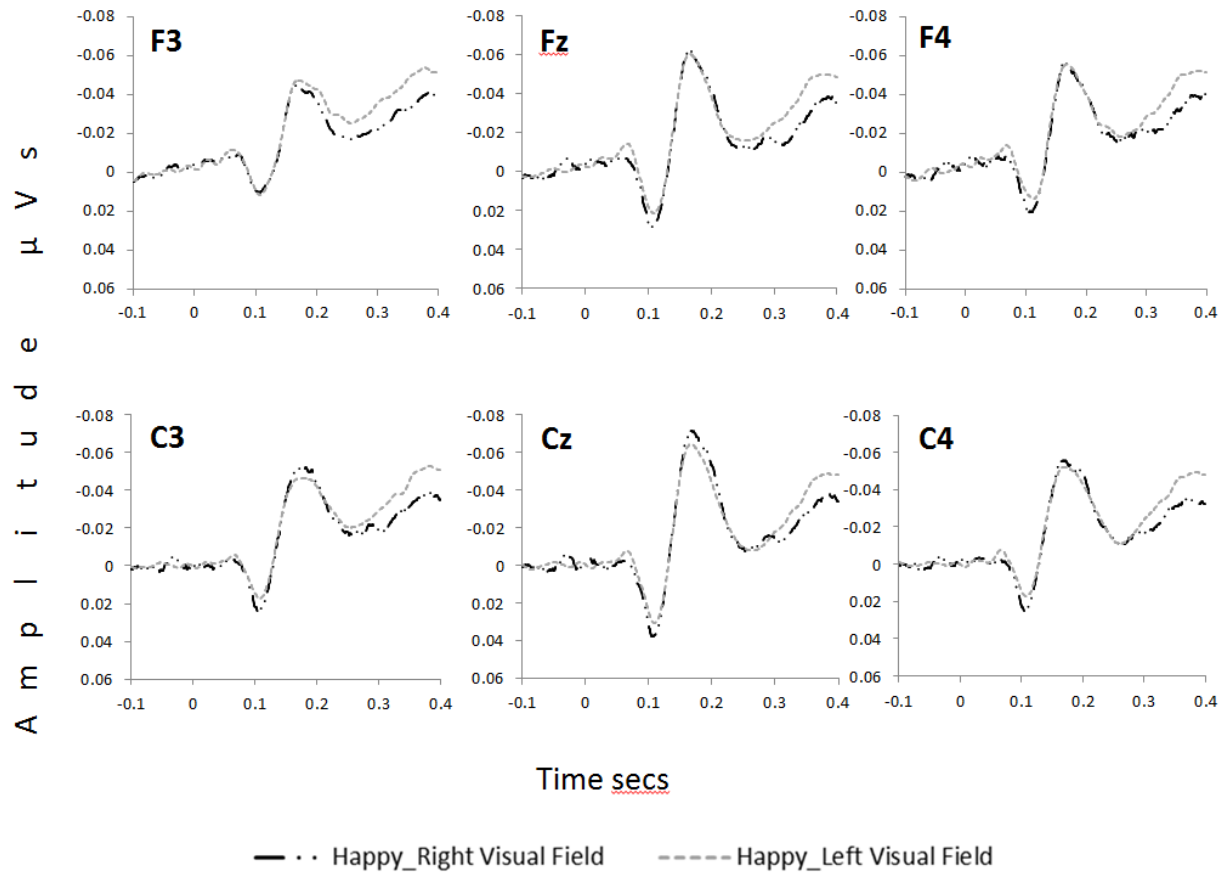(F3, Fz, and F4) and Central electrode sites (C3, Cz, and C4)

Figure 4b. Grand averages of amplitudes of sad chimeric face images at the Frontal electrode sites

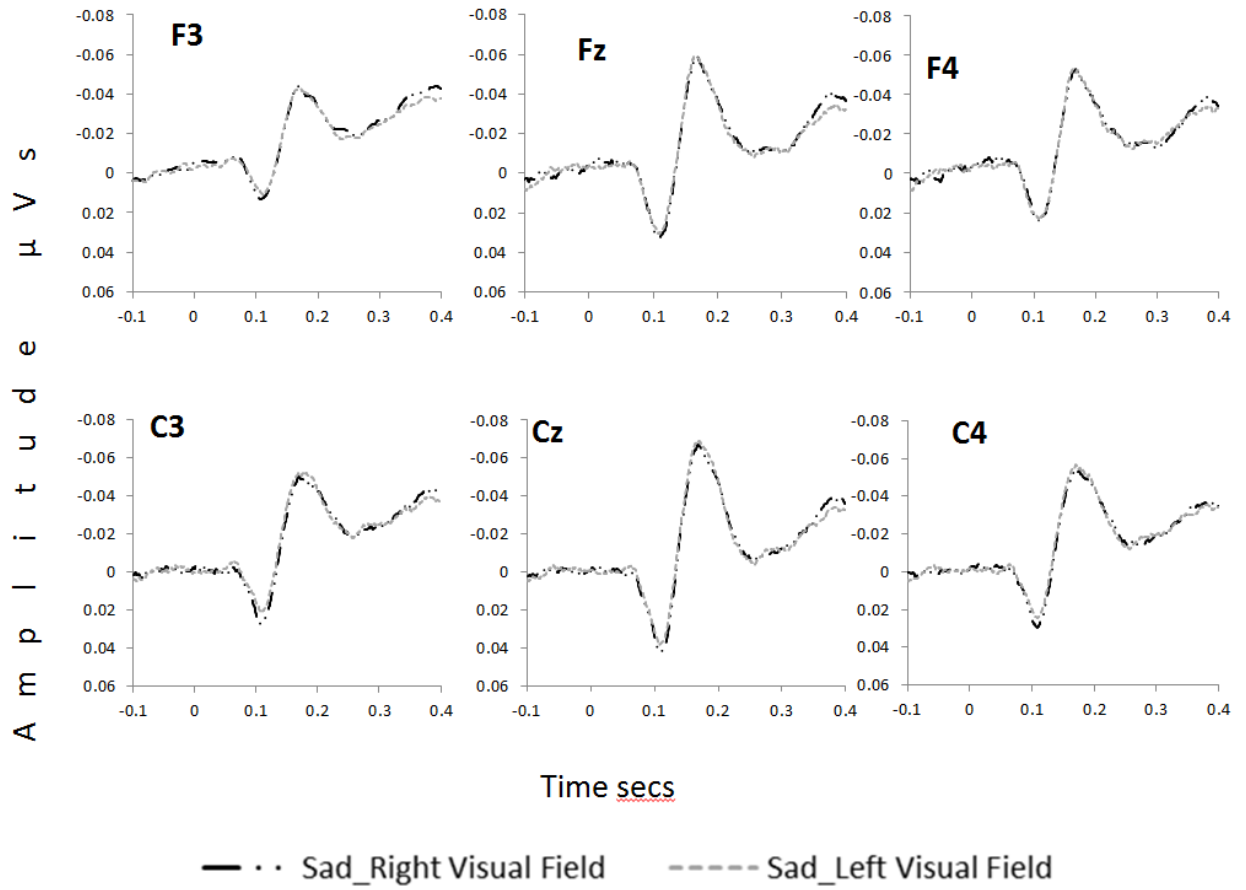(F3, Fz, and F4) and Central electrode sites (C3, Cz, and C4)

Figure 3. N1 mean amplitude and SE bars for each electrode region (frontal or central) by

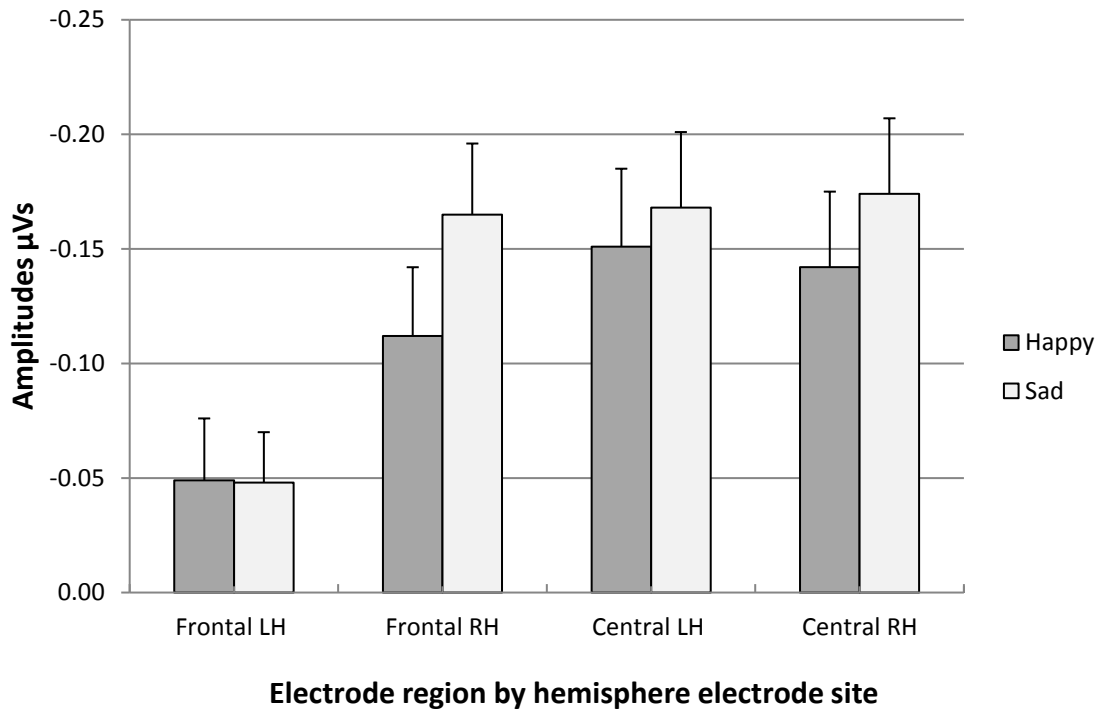hemisphere electrode site (LH or RH) by for happy and sad chimeric face trials

Figure 4. VPP mean amplitude and SE bars for each hemisphere electrode site (LH or RH) by visual

field of emotion presentation (LVF or RVF) for happy and sad chimeric face trials
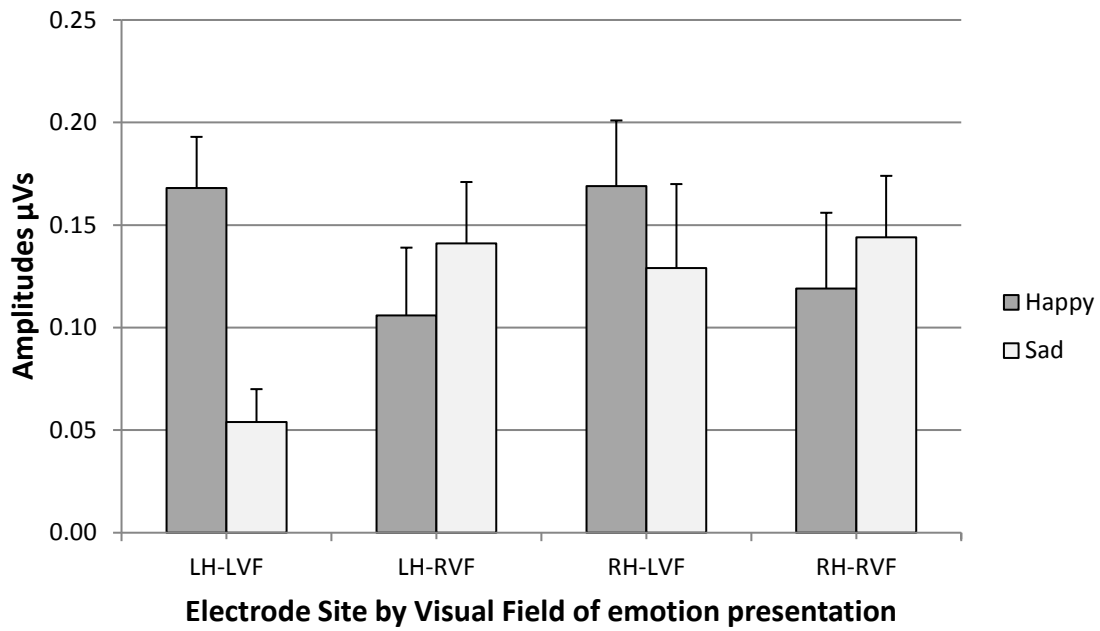
Figure 5. P300 mean amplitude and SE bars for each hemisphere electrode site (LH or RH) by visual

field of emotion presentation (LVF or RVF) for chimeric face trials