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Emotional hybrids and Functional Cerebral Asymmetries: The role of the left and right hemispheres in processing unseen emotional content

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Abstract

Functional cerebral asymmetries have been demonstrated for emotional face perception but a conflicting pattern of results emerges from the literature. Previous studies suggest discrepancies may be driven by the spatial frequency content of emotional stimuli and also participant's awareness. The current study investigated this using emotional hybrid faces which are created by combining low spatial frequency content of an emotional face with high spatial frequency information of a neutral face. An affective priming paradigm was employed to investigate whether emotional content conveyed by low spatial frequencies was sufficient to affect identification of target emotional hybrids; when presented to each cerebral hemisphere using the divided visual half-field technique. In Experiment 1, participants viewed neutral or emotional primes followed by emotional targets on congruent trials or neutral targets on incongruent trials, presented in each visual half-field. Participants indicated whether the target face was emotional or neutral. Experiments 2 and 3 adopted an expression identification task, requiring participants to identify the emotion displayed. The results revealed fearful faces were identified more accurately by the left hemisphere in Experiment 1 and that emotional congruency of prime and target had a positive effect on performance. Experiments 2 and 3 however, showed a general advantage for the right hemisphere and an adverse effect of emotional congruency. It was concluded that contrast effects accounted for the adverse effects of congruency in the later experiments and differences between Experiments 1 and Experiments 2 and 3 were the result of increased task difficulty in the latter. The results also suggest a general RH dominance for emotion processing as the left hemisphere advantage for fear in Experiment 1 was concluded to result from a hemispheric advantage for processing changes in the white sclera of the eye region.

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Statement of Copyright

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Introduction

Definitions of emotion are heavily debated in both psychological and philosophical research but common conceptualisations include arousal, appraisal, experience, expression and goal-directed behaviour as components in the wider emotional system (Scherer, 2005; Plutchik, 1984). The appraisal component allows rapid and accurate identification of others' emotional states and enables humans to select context-appropriate behaviours in accordance with the inferred mood-state of the observed (Damasio, 1995). A wealth of nonverbal information is communicated by the face and efficient extraction of emotional information from facial expressions plays a large role in human social interactions (Uleman, Saribay & Gonzalez, 2008). A sub-set of six facial expressions (anger, fear, happiness, disgust, sadness and surprise) are reliably identified across different cultures, highlighting their social importance (Ekman & Friesen, 1976; Ekman, 1992).

An occipito-temporal region referred to as the Fusiform Face Area has been linked to face perception (Kanwisher, McDermott & Chun, 1997) but less is known about the diffuse neural networks sub-serving emotional expression perception. Activations in specific cortical regions and subcortical structures, including but not limited to the temporo-parietal/prefrontal cortices, amygdala and thalamus have been linked to emotion processing but their relationship is poorly understood (Fusar-Poli et al., 2009). Functional differences between the left (LH) and right cerebral hemispheres (RH) have also been reported for face and emotion perception. The RH, for example, is dominant for face processing in general (Burt & Perrett, 1997), relative to the LH. These inequalities in hemispheric contributions, termed Functional Cerebral Asymmetries (FCAs), have been documented across multiple cognitive domains (Lassonde, Bryden & Dermers, 1990) and also in other non-human species which has led some to suggest an evolutionary advantage to the lateralization of brain function (Lust et al., 2011). There is conflicting evidence regarding the pattern of FCAs in emotional expression processing however, and three main hypotheses receive most support from the broad literature.

Firstly, the Right Hemisphere hypothesis (Gainotti, 1969; 1972) states the RH is dominant for all emotional tasks and therefore processes all six basic emotional expressions. Other models suggest a more complex pattern of asymmetry and state that FCAs are determined by the emotional valence of stimuli, which generally refers to a positive/negative dichotomy. The Valence-Specific hypothesis postulates the LH preferentially processes positive emotional expressions (happiness and surprise) whilst the RH processes negative expressions (anger, sadness, fear and disgust) (Perria, Rosadina & Rossi, 1961; Ahern & Schwartz, 1979; Wedding & Stalans, 1985). The Approach-Avoidance hypothesis highlights motivational drive in response to emotionally salient stimuli as a determining factor for FCAs (Harmon-Jones, 2004). The Approach-Avoidance hypothesis groups emotional expressions as invoking approach or avoidance behaviours and differs from the Valence-Specific hypothesis only by the conceptualisation of anger. According to the Approach-Avoidance hypothesis, anger is related to approach tendencies and is therefore grouped with other positive/approach emotions.

Much of the early evidence for FCAs in emotion processing stems from studies of brain-damaged individuals and deficits in emotional processing have been reported after damage to the RH, which led to the suggestion of a dominant RH for emotional processing in general. A number of experiments have reported poorer performance following RH damage in facial expression perception tasks for example (Borod et al., 1998; Kucharska-Pietura et al., 2003; DeKosky, Heilman, Bowers & Valenstein, 1980; Anderson et al., 2000). One such study of patients with unilateral RH and LH brain damage showed participants photographs of all six basic emotional expressions (Adolphs et al., 1996). Participants were tasked with indicating how similar target expressions were to corresponding labels (i.e., how happy is this face?) and the results showed the LH group was unimpaired for all emotional expressions. In contrast, the RH group was selectively impaired for fearful and sad faces. Due to normal performance of the LH group, Adolphs and colleagues concluded the RH plays a dominant role in the perception of all emotional facial expressions.

Evidence for valence-specific deficits in brain-damaged patients performing perceptual tasks, however, is less abundant. Deficits in perceiving negative expressions have commonly been reported after RH damage (Borod et al., 1998; Mandal, Tandon & Asthana, 1991; Adolphs et al., 1996), which is in accordance with both the RH and Valence-Specific hypotheses, but there is little evidence of impaired perception of positive expressions following LH damage. Findings from studies with neurologically damaged individuals therefore tend to support the RH hypothesis (Kucharska-Pietura et al., 2003; DeKosky, Heilman, Bowers & Valenstein, 1980). The results from a recent investigation conducted by Laeng et al. (2010) suggest, however, that the LH and left amygdala play a vital role in processing sadness and fear. In this study, a patient with widespread resection of the LH and underlying subcortical structures was shown sad and fearful hybrid faces, which present emotional content below the threshold of conscious awareness, and asked to rate how friendly they appeared. Control participants showed a significant reduction in friendliness ratings for these two emotions but the neurologically damaged patient demonstrated no such effect which implicates the LH in the processing of these two emotions. These findings are not accounted for by the RH, valence-specific or Approach-Avoidance hypotheses.

However, many of these studies with brain-damaged participants were conducted using highly heterogeneous patient populations (Borod et al., 1986; Adolphs et al., 1996) which may partially explain the discrepant findings. Due to the fact that neuroplastic reorganisation following stroke is thought to contribute to recovery of cognitive function (Hochstenbach, den Otter, & Mulder, 2003; Murphy & Corbett, 2009), failure to control for time since injury and aetiology may confound these findings. A recent comprehensive study applied strict inclusion criteria to address these issues (Abbot et al., 2014). In this study, unilateral stroke patients completed expression identification and discrimination tasks but no significant performance differences were reported between right brain-damaged and left brain-damaged patients on either task. Importantly, participants also completed a facial recognition task to rule out a general face processing deficit resulting from RH damage. In light of these findings, retention of function evidenced in neurologically damaged participants may reflect post-injury adaptation or synaptic reorganisation as opposed to FCAs for emotional expression perception (Abbott et al., 2014).

The advancement of neuroimaging techniques, including Electroencephalography (EEG) and functional Magnetic Resonance Imaging (fMRI), has presented an alternative method of investigating the contributions of each hemisphere to emotional processing. In fMRI studies for example, greater activations in one hemisphere relative to the other during presentation of specific emotional stimuli or during emotional processing tasks are then interpreted as evidence of FCAs (Canli et al., 1998). Narumoto et al. (2001) reported findings in support of the RH hypothesis in an fMRI study using a match-to-sample emotional facial expression task. Specifically, selective activation of the right superior temporal sulcus was recorded in response to happy, sad and fearful expressions which suggests a general RH dominance but the majority of neuroimaging tend to support the Valence-Specific hypothesis.

Much of the neuroimaging evidence for valence-driven FCAs has been obtained by EEG studies whereby greater activations in the LH and RH, relative to the opposing hemisphere, are recorded in response to positive and negative expressions respectively (Balconi & Mazza, 2010; Breiter et al., 1996). A recent EEG study, for example, reported greater alpha activations in the RH in response to angry, fearful and surprised expressions and in the LH in response to happiness (Balconi & Mazza, 2010). The poor spatial resolution of EEG renders localisation of activation origin difficult however but Magnetoencephalography (MEG) provides superior spatial resolution in comparison (da Silva, 2004). This technique has recently been applied to the study of FCAs in emotional face processing by Nakamura, Maess, Knosche and Friederici (2014). In this experiment, participants were required to categorise centrally presented faces as happy or neutral and reported greater activity in left temporal regions during presentation of happy compared to neutral faces. Although negative emotional facial expressions were not tested, greater activations in the LH during presentations of positive expressions are in accordance with the Valence-Specific hypotheses. Davidson (1987) has highlighted that greater activations in one hemisphere may not represent specialisation of that hemisphere for a specific task or indicate superior performance however. It is therefore important to consider evidence from behavioural studies to supplement neuroimaging data and thus, comprehensively evaluate the three models.

A widely used behavioural paradigm for the study of FCAs in emotional face processing is the divided visual half-field technique which presents stimuli tachistoscopically to the left and right of fixation (Ley & Bryden, 1979; Hugdahl, Iversen, Ness & Flatten, 1989; Suberi & McKeever, 1977; McClaren & Bryson, 1987; Buchtel, Campario, De Risio & Rota, 1978;

Hugdahl, Iversen & Johnson, 1993; Strauss & Moscovitch, 1981; Landis, Assal & Perrett, 1979; Alves, Aznar-Casanova & Fukusima, 2009; Everhart & Harrison, 2000; Ladavas, Umiltà & Ricci-Bitti, 1980; Safer, 1981). Due to the arrangement of retinal projections to the lateral geniculate nucleus, stimuli presented in the nasal region of each visual half-field are initially processed by the contralateral hemisphere (Mishkin & Forgays, 1952; van de Pol, 2009). Early divided visual half-field experiments using positive and negatively valenced cartoon stimuli have reported superior accuracy for targets shown in the LVF, corresponding to the RH, regardless of emotional valence (Ley & Bryden, 1979; Hugdahl et al., 1989). This is supportive of the RH hypothesis as both positive and negative emotional expressions were identified more accurately in the LVF.

The LVF advantage has also been replicated in studies recording participant's reaction times (RTs) whereby emotional expressions are correctly identified faster in the LVF (Suberi & McKeever, 1977; McClaren & Bryson, 1987). Shorter RTs are thought to represent faster processing which suggests an RT advantage in one VF is indicative of superior performance by the contralateral hemisphere (Bourne, 2008). Faster RTs have been reported for LVF presentations of sadness (Buchtel et al., 1978), happiness (Hugdahl et al., 1993), surprise (Strauss & Moscovitch, 1981) and for all six basic emotional expressions collectively (Ladavas et al., 1981; Safer, 1981). LVF advantages for all six basic emotional expressions suggest the RH is dominant for emotion processing, but conflicting evidence from other divided visual half-field studies suggest a valence-driven pattern of FCAs (Davidson et al., 1987; van Strien & van Beken, 2000; Jansari et al., 2000). RVF advantages, for example, have been reported for happy (Reuter-Lorenz & Davidson, 1981; Reuter-Lorenz, Givis, & Moscovitch, 1983) and sad expressions (Stafford & Brandaro, 2010) whilst superior accuracy and faster RTs have been documented for LVF presentations of fearful, sad and angry expressions (Alves et al., 2009; Stafford & Brandaro, 2010). The fluctuations in FCAs reported by these studies suggest the LH is specialised for processing positive expressions whilst the RH preferentially processes negative expressions, in accordance with the Valence-Specific hypothesis.

Studies using the divided visual half-field technique often report conflicting findings with regards to the pattern of lateralisation for emotion processing. The broad range of experimental tasks used in the literature may partially explain these discrepancies as FCAs have been evidenced for other cognitive functions involved in completing specific behavioural tasks. A number of studies supporting the Valence-Specific hypothesis, for example, have used an emotional label matching paradigm that required participants to match a target face to a verbal label (Burton & Levy, 1989; Rodway et al., 2003; Stafford & Brandaro, 2010; Jansari et al., 2011; Nijboer & Jellema, 2012). Given that language is lateralized to the LH in ~90% of right handers (Knecht et al., 2000), potentially confounding involvement of the LH in these tasks cannot be ruled out (Najt, Bayer, & Hausmann, 2013). Some studies that used this match-to-label paradigm have reported results in favour of the RH hypothesis (Ladavas et al., 1980) which indicates other confounding factors are involved. Bourne (2006) highlighted that presentation times of 150 ms or lower are required to prevent saccades away from fixation in the divided visual half-field paradigm. Saccades towards the periphery may allow stimuli to be viewed in regions other than the nasal portion of the visual half-field and therefore allow processing by the other hemisphere. Findings from studies presenting stimuli for longer than 150 ms (Reuter-Lorenz et al., 1983) that did not use an eyetracker to exclude trials in which saccades were made away from fixation, cannot guarantee processing by the contralateral hemisphere. Suggested FCAs in emotional processing may therefore be the result of confounding processing by the other hemisphere.

Other behavioural tasks also take advantage of the projections of the visual system to investigate functional lateralization of the cerebral hemispheres. One such task, termed the chimeric faces task, measures perceptual bias and reveals participant's tendency to respond to stimuli presented in one VF (Levy, Trevarthen & Sperry, 1972). The most often used variation of the task presents a face composed of an emotional expression on one side, and a neutral expression on the other (see Figure 1). Participants indicate which side of the chimera is more emotional or displays a target emotion and a laterality quotient (LQ) is calculated with left and right hemiface biases indicating a tendency to respond to the left and right sides of the chimera, respectively. A number of studies have reported left hemiface bias in accordance with the predictions of the RH hypothesis (Christman & Hackworth, 1993; Moreno, Borod, Welkowitz & Alpert, 1990; Asthana & Mandal, 2001; Ashwin, Wheelwright & Baron-Cohen, 2005; Bourne, 2010; Drebing, Federman, Edington & Terzian, 1997). Left hemiface bias has been reported under free viewing conditions for a subset of emotions (Christman & Hackworth, 1993; Moreno et al., 1990; Asthana & Mandal, 2001) and also in experiments using all six emotional expressions (Bourne, 2010). Participant's bias for responding more often or more accurately to emotional information in the left hemiface suggests the RH preferentially processes all emotional expressions. Only one study, to the author's knowledge, has reported a valence-driven bias in the chimeric faces task. In this experiment, participants rated the right hemiface and left hemifaces as more negative and positive, respectively (Natale, Gur & Gur, 1983). A bias towards negative evaluation by the RH and positive evaluation by the LH is suggestive of FCAs driven by valence and is in accordance with the Valence-Specific hypothesis.

Figure 1. A chimeric face displaying a happy expression in the left hemiface and a neutral expression in the right hemiface (from Innes, Kentridge & Hausmann, submitted).

In studies using the chimeric faces task and the divided visual half-field technique however, only a sub-set of the six basic emotional expressions have usually been included as testing stimuli (e.g., Buchtel et al., 1978; Stafford & Brandaro, 2010). It is important to note that without including all emotional face expressions it is difficult to discern whether FCAs are representative of processing differences for each individual emotion in a specific task or, an overall pattern of lateralization as predicted by the Right Hemisphere, Valence-Specific or Approach-Avoidance hypotheses. Similarly, experiments that excluded angry expressions cannot compare the Valence-Specific and Approach-Avoidance hypotheses as they differed only in their interpretation of FCAs for the processing of anger. There are few studies that have directly investigated hemispheric contributions to processing angry facial expressions and as a result, the majority of evidence for the Approach-Avoidance hypothesis is reported from studies manipulating participant's motivational states (Harmon-Jones & Allen, 1998; Harmon-Jones & Sigelman, 2001; Harmon-Jones, Sigelman, Bohlig & Harmon-Jones, 2003). Of the previous studies that have tested the full range of emotional expressions, some also failed to include neutral expressions (Ladavas et al., 1980; Safer, 1981). The inclusion of neutral expressions as a control condition is required as the RH has been demonstrated as dominant for face processing in general (Prete, Marzoli, & Tommasi, 2015). Superior performance in the LVF/RH for emotional tasks excluding neutral faces cannot therefore be dissociated from the RH dominance for face processing in general (Yin, 1970; Najt et al., 2013).

There are clear discrepancies in the literature and the three lateralised emotion processing hypotheses are neither fully confirmed nor discounted by findings from behavioural or neurophysiological studies. Despite this, a consistent pattern of RH specialisation for processing negative emotional expressions can be observed whilst FCAs for positive expressions have proven less consistent throughout the literature (Najt et al., 2013). It has been suggested however, that lateralisation of basic visual processes may underlie the conflicting pattern of results. Emotional facial stimuli are composed of featural and configural information which is represented in high and low spatial frequencies (HSFs/LSFs), respectively (Goffaux et al., 2005). The Spatial Frequency hypothesis (Sergent, 1982; 1983) suggests that whilst the LH and RH are equally sensitive in terms of detecting HSFs and LSFs, they differ in their ability to efficiently conduct higher-order cognitive operations based on the outputs of specifically tuned SF channels. The RH is suggested as dominant for LSFs and the LH for HSFs in this model. The time-course of processing LSFs is shorter than

HSFs as the former are conveyed rapidly by primarily subcortical, magnocellular channels and the latter more slowly by cortical, parvocellular channels (Derrington & Lennie, 1984; Livingstone & Hubel, 1988). Previous authors have highlighted the trend of valence-specific lateralization or RH dominance and presentation times (Innes, Kentridge, & Hausmann, 2016). Specifically, those using longer presentation times generally report results in favour of the Valence-Specific hypothesis whilst shorter duration studies support the RH hypothesis. Only two studies supporting the Valence-Specific hypothesis presented stimuli for 200 ms or less (Burton & Levy, 1989; van Strien & van Beken, 2000) in comparison with seven studies that favoured the RH hypothesis (Ley & Bryden, 1974; Suberi & McKeever, 1989; Ladavas et al., 1980; Safer, 1981; Alves et al., 2009; Everhart & Harrison, 2000; Kilgore & Yurgulen-Todd, 2007). A number of experiments supporting the Valence-Specific hypothesis also used a free-viewing paradigm that presents stimuli until participants give a response. Longer presentation times may therefore result in a greater degree of HSF information being processed and result in involvement of the LH whilst shorter durations restrict SF processing to the lower bands and may implicate the RH.

The predictions of the Spatial Frequency hypothesis have been ratified by a number of studies using an image manipulation technique known as filtering. This technique presents SFs above or below a specific threshold and creates a stimulus composed entirely of LSFs (approx. < 8 cycles per face) or HSFs (approx. > 8 cycles per face) (Costen, Parker & Craw, 1996). Low-pass filters produce stimuli composed of LSFs and high-pass filters produce HSF stimuli. A recent fMRI study showed participants low-pass, high-pass and broadband (normal SF content) natural scenes in an attempt to clarify the contributions of each hemisphere to the processing of specific SF bands (Musel et al., 2013). Their analysis revealed greater activations in RH occipito-temporal areas during presentation of LSF scenes and in LH temporal regions for HSF, which is in accordance with the Spatial Frequency hypothesis. Importantly, these findings have been replicated in studies with facial stimuli. Keenan, Whitman and Pepe (1989) used square wave gratings of HSF and LSFs to mask unilaterally presented neutral faces. Participants were required to discriminate a target face from a group of five and significantly more errors were made when LSF masked faces were presented to the LVF and HSF masked faces to the RVF. An LVF advantage for faces composed of HSF and RVF advantage for LSF faces, respectively, is in accordance with the RH specialisation for LSF and LH specialisation for HSF processing predicted by the Spatial Frequency hypothesis.

The LH and RH appear differentially involved in processing LSF and HSFs, which may itself contribute to the discrepant literature but there is also debate in the literature regarding the relative importance of each SF band for the accurate perception of individual emotional expressions and emotion processing in general (Whalen et al., 2004; for review, see de Cesarei & Codispoti, 2012). For example, Aguado, Serrano-Pedraza, Rodriguez and Roman (2010) found low-pass emotional faces were identified significantly slower than high-pass faces which suggest HSFs are necessary for accurate expression categorisation. Happy and angry expressions were used in this experiment but they were grouped as emotional for the purpose of analysis which means that differences in diagnostic SF bands for happiness and anger may have been hidden. On the other hand, another study reported a differential pattern of lateralisation with low-pass happy faces and high-pass sad faces were identified significantly faster than their filtered counterparts, suggesting a reliance on LSF and HSF information for happy and sad expression identification, respectively (Kumar and Srinivasan, 2011). FMRI data has shown activity in the amygdala, thalamus and superior colliculus in response to low-pass fearful faces (Vuilleumier, Armony, Driver & Dolan, 2003) and the authors suggested that LSFs are therefore most important for the accurate recognition of fearful faces due to LSF-specific activations in these areas. Similarly, findings from an EEG study also showed modulation of the P1 component, which is associated with attention (Mangun & Hillyard, 1992), during presentation of low but not high-pass fearful faces (Pourtois et al., 2005).

Findings from studies using other image manipulation techniques have also indicated differential involvement of SF bands in perceiving individual emotional expressions. The “bubbles” technique (Gosselin & Schyns, 2001; Smith, Cottrell, Gossellin & Schyns, 2005) isolates small areas of the face to present either HSF or LSFs. One study using bubbled stimuli asked participants to identify the expression of target faces (Smith & Schyns, 2009). Participants were more accurate at identifying sadness and fear when HSFs were isolated compared to better recognition of happiness, surprise, disgust and anger when LSF information was available. HSFs or LSFs appear to be diagnostic for identifying specific emotional expressions which, viewed in the context of FCAs for SF predicted by the SFH (Sergent, 1982), may explain the opposing findings regarding emotion processing lateralisation.

The studies discussed thus far, however, have used emotional facial stimuli that present a single SF band in isolation. Due to the fact that accurate emotional face perception requires configural and featural processing, and therefore both LSF and HSF information (Goffaux et al., 2005), the removal of one band of SFs results in an abnormal, degraded facial stimulus and may not reflect the cognitive processes involved in normal emotional expression perception. However, Schyns and Oliva (1999) developed “hybrid” faces which present emotional content in one SF band but still maintain the appearance of a coherent facial stimulus. LSF information extracted from an emotional face and HSFs from a neutral face are combined and the resulting stimulus contains “hidden” emotional content conveyed by LSFs. In previous experiment, participants were unable to explicitly identify the emotion of these hybrid faces but the hidden emotional content influenced participant’s subsequent decisions of friendliness and emotional content (Laeng et al., 2010; Leknes et al., 2013).

The creation of a coherent facial stimulus with hidden emotional content comprising both HSFs and LSFs provides a unique tool for investigating implicit emotion processing. The finite resources available to the visual system restrict higher processing to only the most salient of inputs (Miller, 1956).However, previous studies suggest that observer awareness is not a prerequisite for emotionally salient stimuli to modulate behavioural and physiological responses (Merikle, Smilek, & Eastwood, 2001; Batty & Taylor, 2003). Laeng and colleagues (2010) demonstrated this with hybrid faces by showing participants angry, happy, fearful and sad hybrids with the emotional content displayed in the LSF band. Participants gave a friendliness rating for each hybrid and it was found that angry expressions were considered the least friendly, followed by sadness and fear with happy expressions rated the friendliest. Friendliness rating scales do not, however, directly measure emotional processing and may reflect different cognitive processes to those involved in emotional facial expression perception. Another study conducted by Leknes and colleagues (2013) did apply a direct measure of emotional content however. Participants were required to rate faces for attractiveness as well as emotionality and the results showed a significant effect of hidden emotional content for judging angry and happy hybrid faces. Specifically, angry hybrids were perceived as angrier, less happy and less attractive than happy hybrids, which suggests emotion processing can occur outside of awareness and that emotional content, conveyed by LSFs only, is sufficient to facilitate this.

Alternatively, priming paradigms offer a substitute technique for investigating implicit emotion processing. Priming effects are thought to represent implicit processing and prove a useful tool for investigating the functioning of cognitive networks in the absence of conscious awareness (Öhman, 1988). Brief presentations of an emotional prime can affect both early and late ERP components (Werheid et al., 2005) and have been shown to significantly improve RTs in a valence classification task (Fazio et al., 1986). Emotional facial expressions can also influence participant's social decisions when presented for very short durations. One study showed participants positive and negative facial expressions for durations of 2 ms and observed that more negative traits were ascribed to cartoon characters after negatively valenced priming expressions and more positive traits following positive primes (Niedenthal, 1990). Although this study only demonstrates a general valence priming effect, a more recent report has recorded category-specific priming effects for emotional facial expressions (Carroll & Young, 2005). In this experiment, participants were shown unrelated primes or one of the five basic emotional expressions (excluding surprise but including neutral) and had to vocalise the emotion of a target face. Faster RTs were reported in congruent, related conditions and this effect was specific to each expression whereby fearful primes had the largest positive effect on fearful targets etc. Priming effects have also been reported in experiments using filtered emotional facial expressions, whereby the emotional content is presented in the LSF band only (Phaf, Wendte, & Rotteveel, 2005) and this suggests LSFs are sufficient to facilitate performance in priming paradigms. Taken together, the results from these priming experiments are in accordance with previous studies using hybrid faces indicating performance can be affected by the presence of unseen emotional content.

Although there is evidence of emotional, valence-driven lateralization in explicit emotion processing, studies presenting stimuli below the threshold of consciousness largely support the RH hypothesis (Pegna, Khateb, Lazeyras & Seghier, 2005; Pegna et al., 2005; Whalen et al., 1998; Ladavas et al., 1993). Gainotti (2012) proposed that the RH is dominant for unconscious emotional processing and a right-lateralised subcortical route termed the “low” road (Vuilleumier et al., 2003) facilitates implicit emotional processing. Previous research has demonstrated that conscious, top-down processing can affect patterns of lateralisation which may have a confounding effect on research on FCAs (Yamaguchi, Yamagata & Kobayashi, 2000). The dichotic listening task has previously been used to demonstrate this effect. In this task, auditory stimuli are presented to both ears simultaneously and participants are tasked with reporting the word or syllable they heard most clearly (Hugdahl, 1995; Hugdahl et al., 2009). Due to the dominant contralateral projections from the right and left ears to the opposing hemispheres, a right ear advantage is consistently reported as stimuli are processed by the language dominant LH (Kimura, 1967). The right ear advantage can be reversed, however, when participants are instructed to attend to stimuli heard in the left ear (Hugdahl et al., 1999) and this reflects a reversal of FCAs by top-down cognitive processing. In light of this, the apparent degree to which accurate identification of emotional facial expressions is dependent on either cerebral hemisphere may in fact be driven by top-down attentional biases rather than FCAs for emotional facial processing. Findings from previous studies that have used experimental paradigms to present stimuli below the threshold of conscious awareness lend support to this assumption, and generally report results in line with Gainotti’s suggestion of a RH dominant for implicit emotion processing.

The backwards masking paradigm, which presents an irrelevant stimulus after a briefly shown target to inhibit participant’s awareness of the target, has provided evidence for a dominant RH in implicit emotion processing (Esteves & Öhman, 1993; Rolls, Tovee, & Panzeri, 1999). This technique reduces activity in primary visual cortex and ventral occipito-temporal regions which have been linked to visual awareness and attention (Macknick & Livingstone, 1998; Noguchi & Kagigi, 2005). Two Positron Emission Tomography (PET) studies used backwards masked stimuli in a classic emotional conditioning paradigm. Morris, Öhman and Dolan (1998) showed participants angry faces and, although they were unable to detect the masked angry faces, comparison of the conditioned and unconditioned faces revealed greater activations in the right amygdala for masked faces. A second experiment by the same authors used a similar conditioning paradigm but compared covariance in PET data from masked and unmasked conditions to investigate connectivity in this region (Morris, Öhman & Dolan, 1999). They reported increased connectivity between the right amygdala and midbrain regions in masked, but not unmasked conditions, which was interpreted by the authors as evidence of connections in the subcortical low road. These studies also demonstrate selective activation of the RH during implicit emotion tasks, which is in accordance with the predictions of a dominant RH for implicit emotion processing (Gainotti, 2012).

A number of lateralised, affective priming experiments have also reported an RH advantage for processing unseen emotional content. In one experiment (Sato & Aoki, 2006), angry, happy and irrelevant primes were backwards masked and presented unilaterally. Participants indicated their level of preference for irrelevant target Korean characters. Their findings showed a negatively driven pattern of lateralization as participants reported reduced preference during LVF presentation of negative primes relative to RVF, happy and control prime conditions. Sato and Aoki suggested positive implicit processing may not be sufficiently salient to elicit significant visual half-field differences. These results specifically implicated the RH in implicit emotion processing as there was no LVF advantage for any expression. It should be noted, however, that the relationship between participant's preference for irrelevant characters and emotional facial primes may not provide a direct measure of affective, facial priming effects.

On the other hand, LVF advantages have been reported in priming studies using expression identification tasks (Tamietto and de Gelder, 2008). In this experiment, three different trial types were used including a unilateral unmasked face, bilateral presentation of emotionally congruent masked and unmasked faces and a bilateral display with emotionally incongruent masked and unmasked faces. Importantly, Signal Detection Theory (SDT) measures (Macmillan & Creelman, 2004) were used in a pilot study to establish detection thresholds for the target stimuli independent of response bias and a presentation time of 20 ms was found to consistently prevent detection above chance levels. A significant RT advantage was reported when fearful faces were presented to the LVF, in accordance with suggestions of the RH being dominant for emotional facial processing. Moreover, RTs were faster when unmasked and masked fearful faces were shown in opposing visual half-fields which demonstrated a positive influence of unseen emotional content.

The consistency with which backwards masking prevents conscious awareness of masked stimuli has, however, been called into question (for review see Hedger, 2016). Pessoa, Japee and Ungerleider (2005) calculated SDT measures in a task that briefly presented participants with a fearful or happy target face (17 ms, 33 ms or 83 ms), followed by a neutral mask and asked to identify whether the target was fearful and then provide a confidence rating of their response. In contrast with previous studies (Whalen et al., 1998), 64% of participants could reliably detect the target at 33 ms and two were above chance levels when the target was presented for only 17 ms, despite reporting they were unaware of the presence of any faces. Receiver Operatic Characteristic (ROC) curves also revealed large variation between participants suggesting that there is no universal objective, detection threshold for backwards masked emotional stimuli. This highlights the importance of using SDT as an objective measure of perceptual sensitivity as participants can report unawareness despite being able to detect ambiguous stimuli in forced-choice paradigms (Whalen et al., 1998) and the effectiveness of masking may fluctuate between participants.

In light of this, hybrid stimuli provide an alternative to the backwards masking paradigm as Laeng et al. (2010) previously demonstrated with objective SDT measures that participants were unaware of the emotional content of the hybrid faces. Recently, hybrid faces have been presented with divided visual half-field technique to investigate FCAs for implicit emotion processing. To date, only a small number of studies have adopted this approach (Prete, Laeng & Tommasi, 2013a; 2013b Prete, Laeng, Fabri, Foschi & Tommasi, 2015; Innes, Kentridge & Hausmann, 2016). Prete, Laeng and Tommasi (2013a) conducted the first of these experiments and unilaterally presented angry and happy hybrid faces for 125 or 250 ms. Participants completed a friendliness rating task, similar to Laeng et al.'s. (2010) experiment. Their findings showed a significant effect of hidden emotional content with participants rating happy hybrids as friendlier than neutral faces and neutral faces as friendlier than angry hybrids. A visual half-field effect was also reported with emotional hybrids rated less friendly in the LVF, compared to the RVF. Prete and colleagues interpreted this finding as supportive of the Valence-Specific hypothesis which predicts the RH is specialised for negative emotion processing. As faces presented in the LVF were perceived as more negative than in the RVF, they suggest this represents a bias in the RH for negative processing and therefore a valence-specific pattern of lateralisation.

A later experiment by Prete and colleagues (2013b) used the same friendliness rating scale to assess implicit and explicit processing of hybrid and normal faces in neurologically intact and split brain participants. Angry and happy hybrids were presented both unilaterally and bilaterally for 250 ms. In contrast with their previous findings, control participants and a partially sectioned split brain participant, with the splenium spared, showed a RH dominance in bilateral presentation conditions. Specifically, participants evaluated happy and angry hybrids in the LVF as more and less friendly compared to RVF presentations. The bias towards extreme friendliness ratings for both positive and negative expressions in the LVF is in accordance with the RH hypothesis and a dominant RH for all emotional processing. These results must be interpreted with some care however, as previous studies have demonstrated the occurrence of saccades at durations lower than 200 ms (Carpenter, 1988; Bourne, 2008). Participants may therefore have initiated saccades away from fixation and towards unilateral targets which could mean stimuli were not primarily processed by the intended hemisphere.

A final study by Prete and colleagues (2015) used hybrid faces, hybrid chimeric faces and inverted faces in an attempt to reconcile their previous conflicting findings. The paradigm of their first experiment was identical to that used in their previous studies but presentation times of less than 150 ms were used which rules out the possibility of confounding saccadic movements. A valence-driven pattern of lateralization was reported with shorter presentation times as faces shown in the LVF were judged as less friendly than those in the RVF. However, when hybrid chimeric faces were presented foveally in a second experiment, those with happy expressions in the left hemiface were evaluated as friendlier than all other combinations which is supportive of the RH hypothesis. A third experiment identical to experiment one tested an anterior callosotomised patient, A.P., who evaluated hybrid faces presented in the LVF as less friendly than those in the RVF, again lending support to the Valence-Specific hypothesis. Finally, A.P. completed the task from Experiment 2 with hybrid chimeric faces and showed a bias towards basing friendliness judgements on the emotional content of the left hemiface. As presentation time, eccentricity of stimuli and task demands were similar across all studies, the authors concluded that heightened cognitive load may drive these conflicting findings. Specifically, superior performance of the RH occurred during bilateral presentation as a result of increased cognitive load whilst a valence-specific pattern of lateralisation is observed when facial stimuli are presented in isolation. A theoretical approach in which the RH and Valence-specific hypotheses are considered coexistent rather than mutually exclusive is therefore suggested by the authors and may partially explain the discrepant literature. The focus on a subset of the six basic emotional expressions means that observed differences between positive and negative emotions could represent differences between individual emotions rather than general FCAs for emotional face processing however. In addition, friendliness-rating tasks are an indirect measure of perception as friendliness is a complex social construct and may therefore engage different processes to those responsible for emotional expression perception. One study to date has attempted to address these issues.

Innes, Kentridge and Hausmann (submitted) presented all six basic emotions as low pass, high pass and hybrid faces with the divided visual half-field technique and asked participant's to categorise faces as emotional or neutral. Their results showed superior RTs for unfiltered emotional, compared to neutral faces in the LVF which is consistent with the RH hypothesis. Hybrid conditions again showed support for the RH hypothesis with significantly higher hit rates reported for emotional faces presented in the LVF. This effect, however, was observed in male participants only which the authors highlighted is in accordance with previous reports of reduced asymmetry in females (Proverbio et al., 2006). Fewer errors were also made for happy hybrids compared to the other emotional expressions and this replicates previous findings of faster identification of happy expressions (Everhart & Harrison, 2000) and suggests LSFs are important for identifying this emotion. As some participants failed to correctly identify any hybrid faces in some conditions, the authors concluded that there was an insufficient pool of correct trials upon which a robust analysis of RT data could be conducted. This highlights a general issue with previous studies as RT data can reveal subtle processing differences between stimuli (Pisoni & Tash, 1974) and, in the study of FCAs, patterns of lateralization (Bourne, 2008). In some experiments, RTs have proven a more sensitive performance measure than accuracy or response bias data alone with some authors reporting significant hemispheric differences in RT data only (Everhart & Harrison, 2000; Welsh & Elliot, 2001; Bourne, 2005; Bourne & Hole, 2006breiter). In addition, fluctuations in FCAs for processing each emotional expression may not be revealed by normal stimuli displaying emotions at full intensity due to floor (Innes et al., submitted) or ceiling effects (Law Smith et al.,, 2010). A previous study (Hoffman et al., 2010) reported better performance in females only at lower emotional intensities in a facial affect recognition task. Males and females, however, did not differ significantly when full intensity emotional expressions were used which highlights how presenting stimuli of varying intensities may clarify subtle differences between the LH and RH for processing individual emotional expressions.

The present study sought to investigate whether unseen emotional content is processed faster or more accurately by the cerebral hemispheres and how this pattern of lateralisation fluctuates with each emotional expression. To investigate this question, emotional hybrid faces are employed in a lateralised, affective priming paradigm. Firstly, by presenting emotional content in the LSF band only in the present experiments, the confounding effects of hemispheric differences in processing HSF and LSFs and different diagnostic SF bands for accurate identification of each expression are controlled for. Secondly, previous research has demonstrated that FCAs fluctuate as a result of top-down processing (Yamaguchi, Yamagata & Kobayashi, 2000), meaning apparent FCAs for processing emotional expressions may rather represent attentional biases. By presenting emotional content below the threshold of conscious awareness with backwards masking, FCAs can be investigated independently of top-down bias and to this end; SDT measures were calculated to objectively assess participant's awareness in experiments two and three. Thirdly, a priming paradigm is used to investigate whether emotional content conveyed by LSFs only is sufficient to improve detection or categorisation of ambiguous emotional hybrids. Fourthly, as RTs have been demonstrated as a more sensitive measure of FCAs (Bourne & Hole, 2006; Welsh & Elliot, 2001; Everhart & Harrison, 2000) and previous studies using hybrid stimuli have been unable to collect RT data due to floor effects (Innes et al., submitted), stimuli of different emotional intensities were used in the present experiments.

The RH has been implicated in the processing of both positive and negative emotions in a number of behavioural studies (Borod et al., 1998; Hugdahl et al., 1993; Safer, 1981) and in negative emotion processing in neurophysiological studies (Adolphs et al., 1996). Support for the Valence-Specific hypothesis and the role of the LH, however, is less consistent (Laeng et al., 2010; Breiter et al., 1996; Alves et al., 2009). It is therefore predicted in the current experiments that a general LVF performance advantage will be reported across all experiments and emotional expressions. Similarly, evidence from backwards masking paradigms suggests the RH is dominant for implicitly processing emotional expressions (Esteves & Öhman, 1993; Rolls, Tovee, & Panzeri, 1999) and that the LSF band conveys this information through a specialised subcortical route (Vuilleumier et al., 2003; Gainotti, 2012). In light of this, emotionally congruent primes are predicted to have a positive effect on performance across all emotion. Finally, this phylogenetically old, subcortical network is thought to be specialised for threat detection (Morris et al., 1998; Morris et al., 1999) and it is predicted that the congruency effect will be greater for fearful expressions than happy or fearful faces.

Experiment 1

Previous studies have shown that emotional content conveyed by the LSF band can affect performance in both emotional expression identification and categorisation tasks (Sergent, 1982; Smith & Schyns, 2009; Vuilleumier et al., 2003). There is also evidence that FCAs in emotion processing fluctuate as participant's awareness of the stimuli changes (Gainotti, 2012). This experiment sought to specifically investigate whether unseen emotional content, conveyed by LSFs, could improve participant's ability to correctly identify emotional target hybrids as emotional. It was hypothesised that all three emotional expressions would be identified faster and more accurately in the LVF due to a suggested RH dominance for emotional, LSF and implicit processing in general (Borod et al., 1998; Keenan, Whitman & Pepe, 1989; Gainotti, 2012). Secondly, it was predicted that participants would perform better when the priming and target stimuli were emotionally congruent. This congruency effect, however, was expected to be most pronounced for fearful expressions as evidence suggests accurate identification of fear in particular is reliant on LSF information (Almeida et al., 2013; Sato & Aoki, 2006; Yang, Cao, Xu, & Chen, 2012). Thirdly, participants were predicted to correctly identify fearful faces faster than happy or angry faces as the low road specialised for fear detection is thought to process this expression more rapidly than other emotions (Morris et al., 1999; Vuilleumier et al., 2003).

Method

Subjects

Thirteen individuals right-handed individuals recruited from the Durham University student population took part in experiment one (8 females, 5 males). Participants ages ranged from 21-42 years (*Mean* ± *Standard Deviation* = 25.30 years ± 5.39) and all had normal or corrected to normal visual acuity. Participant's hand preference was measured using the short version of the Edinburgh Handedness Inventory (Oldfield, 1971) and a Laterality Quotient (*LQ*) calculated by subtracting the total number of tasks completed with the left hand from the total number of those completed with the right hand. This score was then divided by the total number of tasks (10) and multiplied by 100 to give an LQ value. Positive values (+100) indicate a right hand bias and negative values (-100) a left hand bias with 0 representing no directional bias (*LQ* = 86.82 ± 13.52). Participants with an LQ value above 0 were classified as right handers and those with a value below 0, left handers.

Apparatus

The experiment was presented on a Dell notebook at a resolution of 740 x 680 pixels with a screen refresh rate of 60 Hz and DMDX software was used to present experimental trials and record participant's responses and RTs. The presentation time of all stimuli were precisely measured using a light-sensitive diode connected to a millisecond accurate clock.

Stimuli

Grayscale photos of four males and four females from the Ekman and Friesen (1976) set displaying angry, happy and fearful expressions were used in the present experiment. These stimuli were morphed to 5% increments of emotional intensity with 0% representing neutral and 100% displaying the full intensity expression using Psychomorph software (Tiddeman, Burt, & Perrett, 2001). Intensities of 0%, 25%, 50% and 100% were selected for further image manipulation and cropped to remove inconsistent or salient vignettes. In MatLab software, 0% stimuli were then subjected to high-pass filtering (>7 cpi) to create a neutral face displaying only HSFs and the 25%, 50% and 100% intensity stimuli from the same individual were low-pass filtered (<7 cpi) to create stimuli displaying emotional content in the LSFs. The high-pass neutral and low-pass emotional faces for each individual were then combined in the Fourier domain and transformed to create a hybrid face (Figure 2). This process was repeated for all individual posers and emotions at all intensities, resulting in 72 hybrid faces and 8 neutral faces (Mean luminance 219.23 ± .68). A masking stimulus composed of visual noise at middling spatial frequencies (~7 cpi) and a null stimulus were also created. The null stimulus was a grey rectangle that was matched in luminance to the average background luminance of all facial stimuli.

Figure 2. An angry hybrid target at 50% emotional intensity.

Design

Experimental trials followed the same structure throughout experiment one (Figure 3), beginning with a central fixation cross, measuring 0.3 x 0.3 degrees of visual angle at a viewing distance of 57 cm, presented for 750-1250 ms. The fixation cross was replaced by a central prime presented for 50 ms which was immediately followed by the masking stimulus, presented for 150 ms. The final frame consisted of a target hybrid or neutral face in the LVF or RVF, a central fixation cross and the null stimulus in the contralateral VF, presented for 180 ms. The inside edge of all lateralised stimuli was presented 2.5 degrees of visual angle from the edge of the fixation cross. Participants responded after this frame and indicated whether the target face was emotional by depressing the ‘H’ key or neutral by depressing the ‘G’ key. The facial, null and masking stimuli all measured 4.2 x 5.3 degrees of visual angle at a viewing distance of 57 cm. Congruent trials were categorised by the prime and target stimulus displaying the same emotional expression and incongruent trials by a neutral prime and an emotional target. The priming stimuli, when emotional, were hybrid faces at 100% intensity whilst target emotional hybrids were evenly distributed between 25%, 50% and 100% intensities. The prime and target stimulus always represented the same individual, regardless of whether trial was congruent or incongruent. 576 unique trial combinations were created so that each individual was shown in each VF, displaying each emotion at every intensity in congruent and incongruent trials at least once. Participants completed each full set of trials twice, resulting in 1152 overall test trials. Experimental trials were preceded by 10 practice trials, selected randomly from the pool of experimental trials to allow participants to familiarise themselves with the task demands and response keys. Specifically, participants responded using only one hand at any time. The overall testing time for each participant was approximately two hours. Trials were presented in a pseudo-randomised order with no expression or individual presented in the same VF in succession and participant's starting response hand was also counterbalanced which meant half of participants began responding with their right hand and half with their left hand.

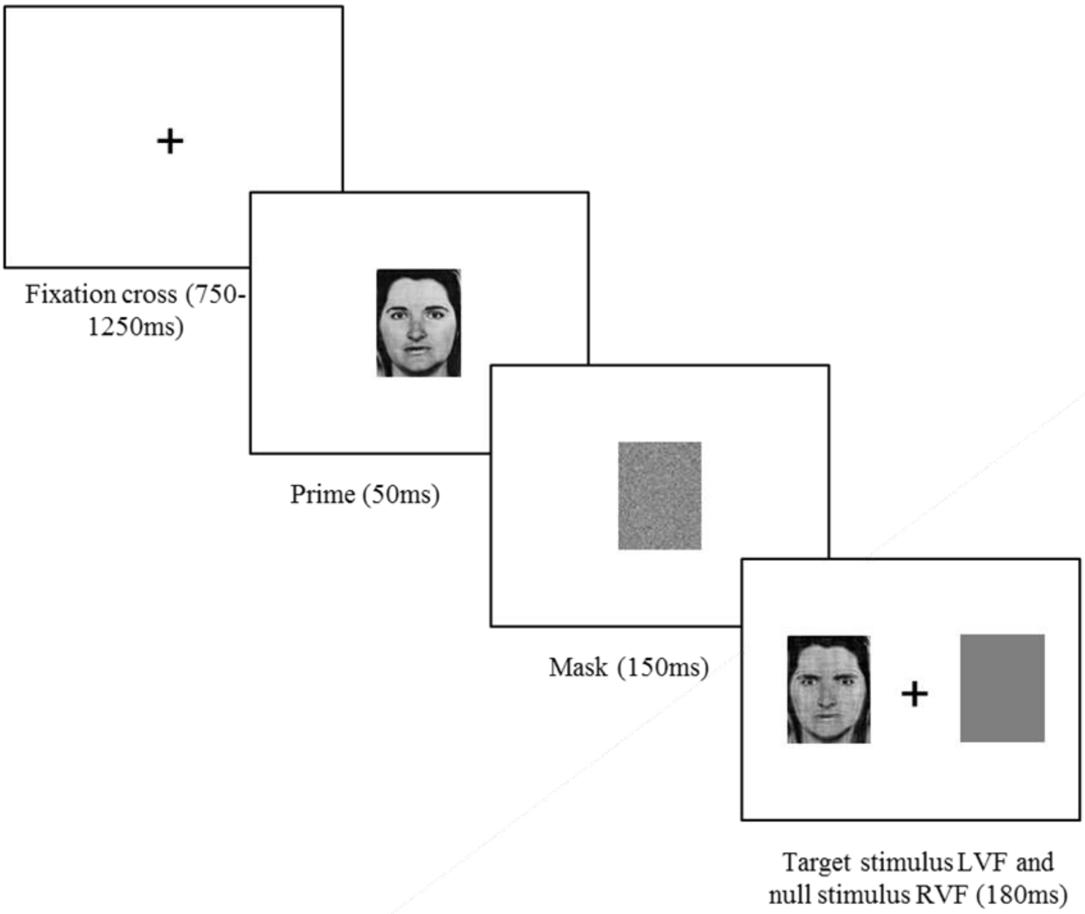

Figure 3. The structure of a standard trial, specifically depicting an incongruent trial where an angry emotional hybrid at 50% intensity is presented in the LVF and primed by a neutral expression.

Procedure

The present experiment was conducted in a quiet testing room and upon arrival; participants were given an information sheet to read that provided details of the experimental methodology and investigative aims. Participants were then offered the opportunity to ask any questions and, if willing, completed the consent form and Edinburgh Handedness Inventory (Oldfield, 1971). Following this, participants were given an instruction sheet that detailed the task demands throughout and were instructed to sit in a comfortable position at the testing station. A tape measure was then used to approximate a viewing distance of 57 cm and participants were reminded to try and refrain from moving their head or distorting their vision during the experiment. The experiment commenced with an initial instruction screen that informed participants of the response keys and instructed them to press the spacebar to begin the practice trials. After the practice trials were completed, the experiment informed them that the experimental trials would commence once they pushed the spacebar. When participants had completed a block of 288 trials, the experiment would pause and inform them that this was a scheduled rest period and to press spacebar when they were ready to continue. Overall, three rest periods were provided. At the second rest period, once participants had completed half of the experimental trials, an instruction screen informed them to switch their response hand for the remainder of the experiment. Upon completion of all experimental trials, they were informed by the program that the experiment had ended. Participants then read through the debriefing sheet and were given the opportunity to ask any questions.

Results

Four participants were excluded from the analyses as their performance did not significantly differ from chance in at least 24 out of 36 conditions. The Greenhouse-Geisser correction was applied to degrees of freedom where the assumption of sphericity was violated and all post hoc tests were Holm-bonferroni corrected.

Hit rates

Hit rates were subjected to a 3x2x2x3 repeated measures analysis of variance (ANOVA) with target emotion (Anger,Fear,Happiness), visual half-field (Left Visual Field,Right Visual Field), emotional congruency (Congruent,Incongruent) and emotional intensity (25%/50%/100%) as within-subjects factors. Analysis revealed significant main effect of target emotion ($F(2,16) = 17.47$, $p < .001$, $\eta_p^2 = .686$) with significantly fewer errors made for happy targets compared to fear ($p = .002$) and anger ($p = .002$) and also for fear compared to anger ($p = .036$). Main effect of visual half-field ($F(1,8) = 7.77$, $p = .024$, $\eta_p^2 = .493$) also reached significance and fewer errors were made for targets presented in the RVF compared to LVF. A significant main effect of Intensity ($F(1.24,9.94) = 44.243$, $p < 0.001$, $\eta_p^2 = .847$) was also reported and 100% targets were identified more accurately than 50% and 25% intensity targets ($p \leq .001$) and also 50% targets compared to 25% ($p < .001$). There was a significant emotion × VF interaction ($F(2,16) = 4.903$, $p = 0.045$, $\eta_p^2 = .380$) and paired-samples *t*-tests (Figure 4) revealed significantly fewer errors were made for RVF presentations of fearful faces (56.71 ± 16.33), compared to LVF (45.02 ± 16.31), ($t(8) = 3.86$, $p = .005$) which was not in accordance with the experimental hypothesis that predicted an LVF advantage.

To further investigate any differences in the emotion X VF conditions, a series of one sample *t*-tests were conducted to establish if any emotions were correctly identified as emotional above the 50% chance level. Analysis revealed that no emotion was identified correctly in any VF above chance level ($p > 0.05$).

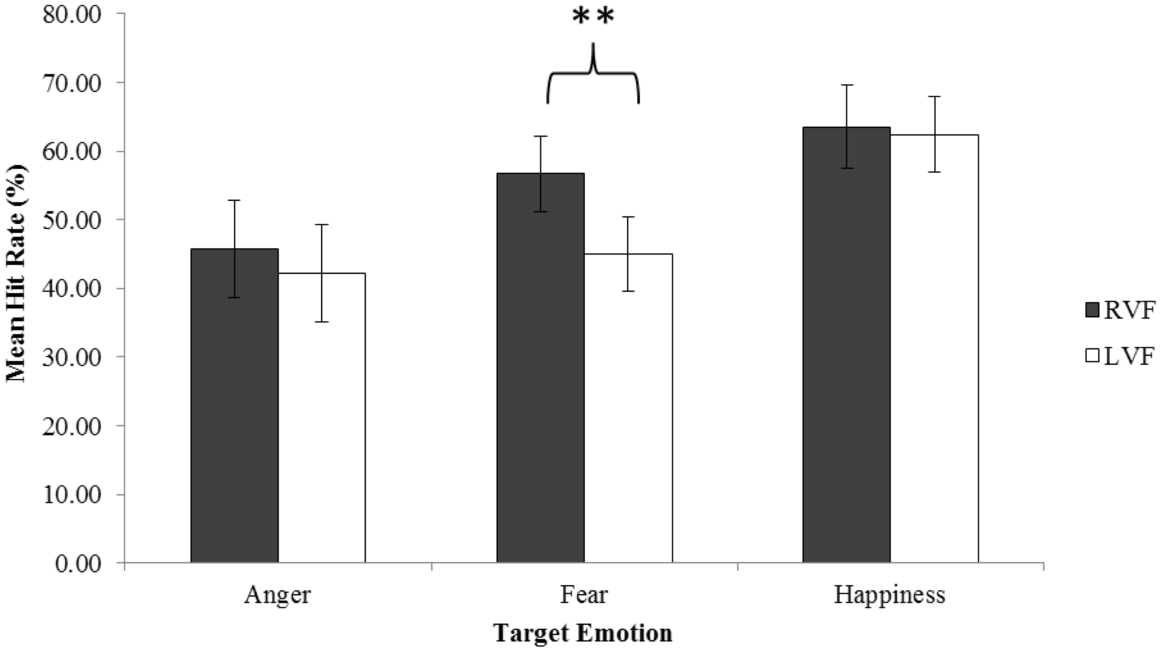

Figure 4. Mean accuracy scores (Error bars represent one standard error of the mean) for presentation of each target emotion in the visual half-fields. (****** = $p \leq .005$ derived from a paired-samples *t*-test, two-tailed and Holm-Holm-bonferroni-corrected).

Response times

RTs from incorrect trials and outside the 200-2000 ms window were excluded from analysis. Three more participants were also excluded from this analysis due to 0% hit rates in at least one condition[1]. Corresponding analysis revealed significant main effects of congruency

($F(1,5) = 7.69$, $p = .039$, $\eta_p^2 = .606$) with significantly faster RTs recorded for emotionally congruent trials compared to incongruent trials (Figure 5) and intensity ($F(2,10) = 9.64$, $p = .05$, $\eta_p^2 = .658$) with fastest response times recorded for 100% targets compared to 50% ($p = .020$) and 25% ($p = .022$) targets. Faster RTs on emotionally congruent trials is in partial concordance with the predicted outcome as it was hypothesised that fearful faces would be identified significantly faster than happy and angry faces on congruent trials. No other main effects or interactions reached statistical significance.

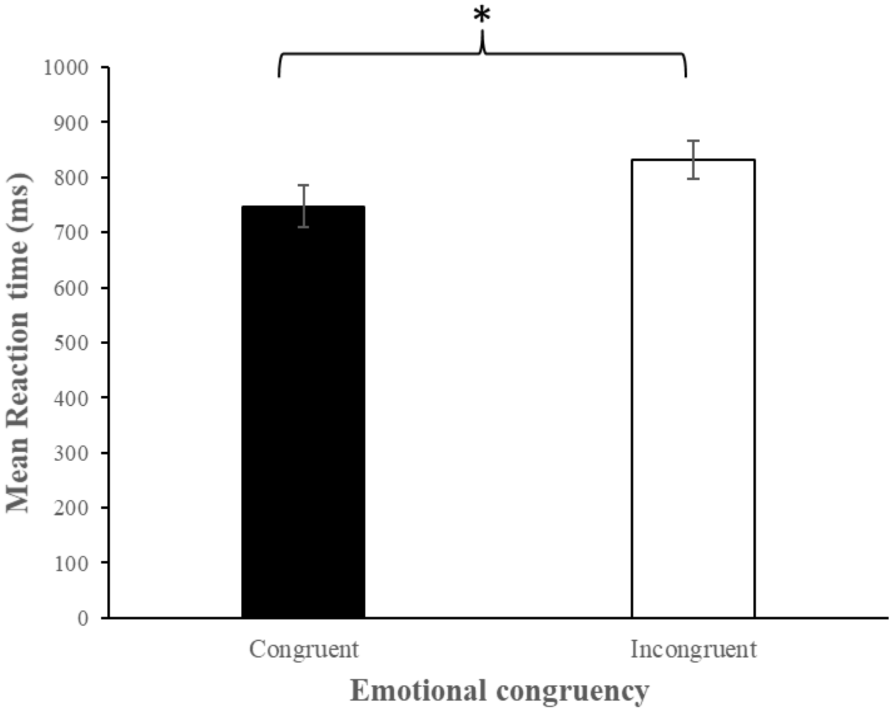

Figure 5. Mean reaction times (ms) (error bars represent one standard error of the mean) for trials with emotionally congruent and incongruent primes and targets.

Control Analyses

A separate ANOVA was also computed to assess performance for neutral targets to establish whether congruency effects were the result of emotional content or other, general facial characteristics. A 2x2 repeated measure ANOVA was conducted on hit rates with VF (RVF,LVF) and congruency (Congruent,Incongruent) as within-subjects factors, using the same sample as the previous hit rate analysis[2]. Main effect of VF reached significance ($F(1,8) = 6.961$, $p = .030$, $\eta_p^2 = .465$) and participants made significantly fewer errors for neutral targets presented in the LVF compared to RVF which indicates superior performance of the RH for identifying faces in general as this effect was specific to neutral faces. No other main effects or interactions reached significance.

An identical analysis performed on RT data revealed significant main effects of VF ($F(1,5) = 11.014$, $p = .021$, $\eta_p^2 = .688$) with neutral targets identified significantly quicker in the LVF and congruency ($F(1,5) = 8.192$, $p = .035$, $\eta_p^2 = .621$) with neutral targets on congruent trials identified significantly faster than on incongruent trials.

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[1] Unequal samples for the RT and hit rate analysis were caused by floor effects and an identical ANOVA was conducted on hit rates using the same participant sample as used in the RT analysis. Main effect of VF was not significant in this analysis but the emotion × VF interaction remained significant and post hoc tests revealed fear was still identified significantly more accurately in the RVF compared to LVF. All other significant main effects remained the same.

[2] As with the previous analysis, an identical ANOVA was conducted on the sample used in the RT data. In this analysis however, the main effect of VF did not reach significance.

Interim Discussion – Experiment 1

Participants made significantly fewer errors when fearful targets were presented in the RVF, compared to LVF which contrasts the predictions of hypothesis one and a general RH advantage for processing all emotional expressions. Previous PET (Morris et al., 1996) and fMRI studies (Vuilleumier, Armony, Driver, & Dolan, 2001), however, have reported selective activation of the left amygdala in response to fearful expressions and it may be that under the current task constraints, the LH is dominant for processing fear. The predictions of a RH advantage for processing LSFs made by the Spatial Frequency hypothesis are also conflicted by the RVF advantage for fear as emotional content was conveyed in the LSF band only (Vuilleumier et al., 2003; Pourtois et al., 2005). As these findings violate all predictions, an alternative post hoc explanation is presented by the phenomenon of categorical perception. Categorical perception references participant's ability to correctly identify stimuli of different conceptual categories better than those within the same category (Etcoff & Magee, 1992). Rather than FCAs for emotional processing, an RVF advantage for fearful expressions may be a by-product of the LH dominance for language which has been proposed to underlie categorical perception (Roberson et al., 2010).

The significant effect of emotional congruency reported in the RT analysis partially supports the second hypothesis as participants were significantly faster at correctly identifying targets when prime and target were emotionally congruent. There was no difference in the magnitude of priming for each expression however, which may suggest unseen emotional content conveyed by LSFs facilitates performance non-discriminately across happy, angry and fearful expressions. Participants revealed during debriefing that they were aware of the presence of the priming stimulus and, as the structure of the present experiment did not allow SDT measures to be calculated as the priming stimuli were not presented in isolation, it cannot be concluded that the congruency effect represents a positive performance effect of unseen emotional content processed below the threshold of conscious awareness. Despite this, presentation durations of 25-200 ms have previously been used in affective priming experiments (Sato & Aoki, 2006; Carroll & Young, 2005) and timings used in the present experiment are consistent with this. Participant's subjective awareness of the priming stimuli may also not equate to conscious processing of the emotional content. The significant effect of congruency revealed by the control analysis on RT data suggests that general facial characteristics play a role in the priming effect observed in the hit rate analysis and previous studies have indeed reported face priming with neutral faces (Burton et al., 2005).

The prediction of an RT advantage for fear, representing faster preferential processing, was not supported by the results of the present experiment as fearful faces were detected more accurately than angry faces, but overall performance was better for happiness compared to the other two emotional expressions. Greater accuracy for happy, relative to fearful and angry expressions has been reported by other authors (Everhart & Harrison, 2000; Ashwin et al., 2005; Alves et al., 2009) but is in conflict with the suggestion of a rapid subconscious route specialised for threat detection. The categorisation task used in the present experiment may only provide an indirect measure of expression identification however. Studies have shown that the smiling mouth is the most salient feature of all facial expressions and diagnostic changes around the mouth region are represented mainly by LSFs (Smith & Schyns, 2009; Calvo, Fernandez-Martin, & Nummenmaa, 2014). These results suggest happy faces are more representative of emotional faces as a category due to the emotional vs. neutral categorisation task used in the present experiment but this task did not directly measure differences in participant's ability to correctly identify each emotional expression. Therefore, the present results may indicate that salient happy faces are the most emotional in appearance but it cannot be concluded that this also represents an advantage for explicitly identifying happy expressions as happy when compared to other emotions.

Experiment 2

Debriefing from Experiment 1 revealed participants were aware of the presence of the priming stimulus, meaning that unconscious processing of the emotional content of the prime could not be assumed. This experiment included a second experimental block that presented the priming stimuli in isolation to allow SDT measures to be calculated and therefore objectively measure participant's degree of awareness. It was expected, based on the previous debriefing, that participants would be able to identify the emotion of the priming stimulus and that this would be reflected in *d'* values significantly above chance levels. In addition, the emotional vs. neutral categorisation task of Experiment 1 provided only an indirect measure of participant's ability to identify individual emotional expressions as it could only be assumed that superior performance for an expression was indicative of that emotion being more readily identified as emotional. To provide a more direct measure of this and investigate the advantage for happy faces reported in Experiment 1, an expression identification task was used in this experiment that required participants to indicate which expression they believed a target face displayed. A previous study using hybrid faces also found that the diagnostic SF band for accurate performance varied between a categorisation and identification task where, specifically, HSF information was more important in the former task, and LSF information in the latter (Schyns & Oliva, 1999). As LSF information has been shown to be more important for accurate performance in this type of task, it was adopted for the present experiment in an attempt to obtain more consistent results. The hypotheses for the present experiment were identical to Experiment 1 and it was therefore predicted that participants would be faster at correctly identifying fearful faces relative to angry and happy faces as the advantage for happy faces in Experiment 1 was thought to represent this expression being more representative of emotional faces in general. Secondly, performance was expected to be better on trials where the priming and target stimuli were emotionally congruent and thirdly, emotional and neutral stimuli were expected to be identified more accurately and faster when presented in the LVF.

Method

Participants

Seven individuals (6 females, 1 male) recruited from the Durham University student population took part in the current experiment with an age range of 21-41 years (26.43 years ± 6.92). Five participants were classified as right-handers whilst one participant demonstrated no hand preference and, one participant was classified as a left-hander (*LQ* = 55 ± 77.51). All participants had normal or corrected to normal visual acuity.

Apparatus

The current experiment was presented on the same Dell laptop in the same software as experiment 1. A Logitech Dual Action gamepad was used to record participant’s responses in place of the keyboard used in Experiment 1.

Stimuli

Identical masking, null, neutral and emotional hybrid stimuli were used in the present experiment as in Experiment 1 but 25% intensity emotional hybrid targets were excluded. These stimuli were removed as participant's hit rates were significantly below chance in Experiment 1 and they were therefore consistently misidentified as neutral.

Design

The current experiment was divided into two experimental blocks and the structure of experimental trials in the first block was identical to Experiment 1. Participants completed an expression identification task in both blocks that required them to decide whether a target face displayed happy, fearful, angry or no (neutral) emotional content. This was indicated by pressing response keys on the gamepad with left bumper, left trigger, right bumper and right trigger corresponding to happiness, anger, neutral and fear respectively. In the second block, however, the structure of trials was slightly different with the initial fixation cross, prime and mask stimuli presented identically to block one but without the final, lateralised target frame. Block one consisted of 768 unique experimental trials that represented every combination of emotion, VF, congruency, intensity and individual. Neutral targets were categorised as one of four emotions in the present experiment which resulted in an even number of trials with happy, fearful, angry and neutral targets. Incongruent trials with neutral expressions were primed by each emotional expression an even number of times whilst emotional targets on incongruent trials were always primed by neutral expressions. Block one began with 30 practice trials that were randomly selected from the overall pool of trials and which were excluded from all subsequent statistical analyses. In block two, every combination of each individual and emotion created 144 unique trials. To calculate *d'* and therefore assess participant's sensitivity to the emotional content of the priming stimuli, these 144 trials were completed four times to obtain a large number of trials upon which a robust SDT analysis could be conducted. This resulted in an overall total of 576 experimental trials in block two. Trial presentation order was pseudo-randomised in an identical fashion to Experiment 1 so that no emotion, individual or intensity was presented in the same VF in succession. The location of the response buttons was also counterbalanced whereby neutral and fear were assigned to the left bumper and left trigger respectively whilst happiness and anger were assigned to the right bumper and right trigger for four out of seven participants. Testing took approximately 2 hours to complete.

Procedure

The procedure adopted in block one was identical to Experiment 1 but upon completion of the first block of trials in Experiment 2, participants were instructed by the software that they would now only see one face presented very briefly for the rest of the experiment. They were also informed that they were to perform the same task as in block one and that the response keys were also identical. Rest periods were provided after completion of 192 cumulative trials in block one and after 288 trials in block two.

Results

Hit Rates

One participant was excluded from analyses due to a 0% hit rate in one or more conditions. Hit rates were subjected to a 3x2x2x2 repeated measures ANOVA with emotion (Anger, Fear, Happiness), visual half-field (LVF, RVF), emotional congruency (Congruent,Incongruent) and emotional intensity (50%, 100%) as within-subjects factors. Analysis revealed a significant main effect of emotion ($F(2,10) = 4.864$, $p = .033$, $\eta_p^2 = .493$) with significantly fewer errors made for fear compared to anger ($p = .009$). Main effect of intensity also reached significance ($F(1,5) = 204.188$, $p < .001$, $\eta_p^2 = .976$) with 100% targets identified significantly better than 50%. The interaction of emotion × VF reached significance ($F(2,10) = 6.007$, $p = .019$, $\eta_p^2 = .546$) and paired-samples *t*-tests showed that fewer errors were made when happy targets were presented in the LVF (66.67 ± 13.85) compared to RVF (61.11 ± 17.02) although this was not significant post correction. It was predicted that all emotional expressions would be identified more accurately in the LVF and this finding therefore is in only partial accordance with the stated hypothesis. The interaction of emotion × congruency also reached significance ($F(2,10) = 7.281$, $p = .011$, $\eta_p^2 = .593$) and paired-samples *t*-tests revealed happy targets were identified significantly less accurately when primed with happy (58.85 ± 17.13), compared to neutral faces (68.92 ± 13.98) , ($t(5) = -3.932$, $p = .011$) (Figure 6). Contrary to the expectation of a positive effect of emotional congruency, this interaction demonstrates a negative effect of congruency whereby similar priming stimuli resulted in decreased accuracy.

A series of one sample *t*-tests were conducted on the mean hit rates of each emotion x VF condition to further explore any differences in performance for identifying each emotion in each VF. Chance level was set at 25% as this task was an identification task with four possible responses. The results revealed that each emotion was identified significantly above chance in both the RVF and LVF ($p < 0.05$).

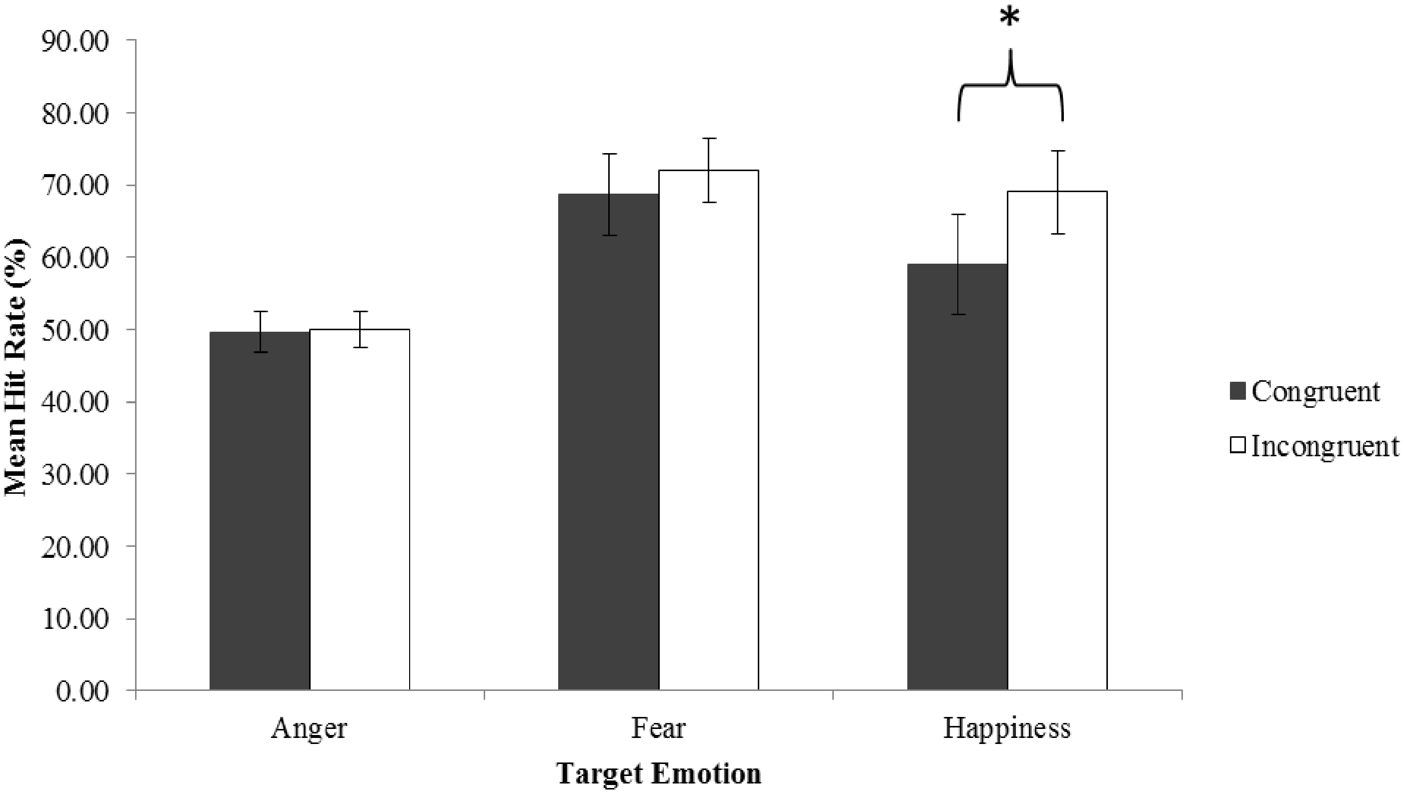

Figure 6. Mean hit rates (%) for each target emotion on trials where they were primed with an emotionally congruent stimulus and an incongruent, neutral stimulus (Error bars represent one Standard error of the mean).

Response times

Response times from incorrect trials and outside of the 200-2000 ms window were excluded from analysis. Corresponding analysis revealed significant main effects of congruency ($F(1,5) = 83.576$, $p <.001$, $\eta_p^2 = .944$) with significantly faster response times recorded on emotionally incongruent trials compared to congruent trials and intensity ($F(1,5) = 19.797$, $p = .007$, $\eta_p^2 = .798$) with faster response times recorded for 100% targets compared to 50%. A significant interaction of congruency × intensity was also revealed ($F(1,5) = 41.557$, $p < .001$, $\eta_p^2 = .893$). Paired-samples *t*-tests (Figure 7) showed that RTs for 50% intensity targets on emotionally congruent trials were significantly slower (1103.53 ms ± 110.53) than incongruent trials (945.75 ms ± 107.67), (*t*(6) = 7.278, *p* <.001) which is not in accordance with predictions of a positive congruency effect.

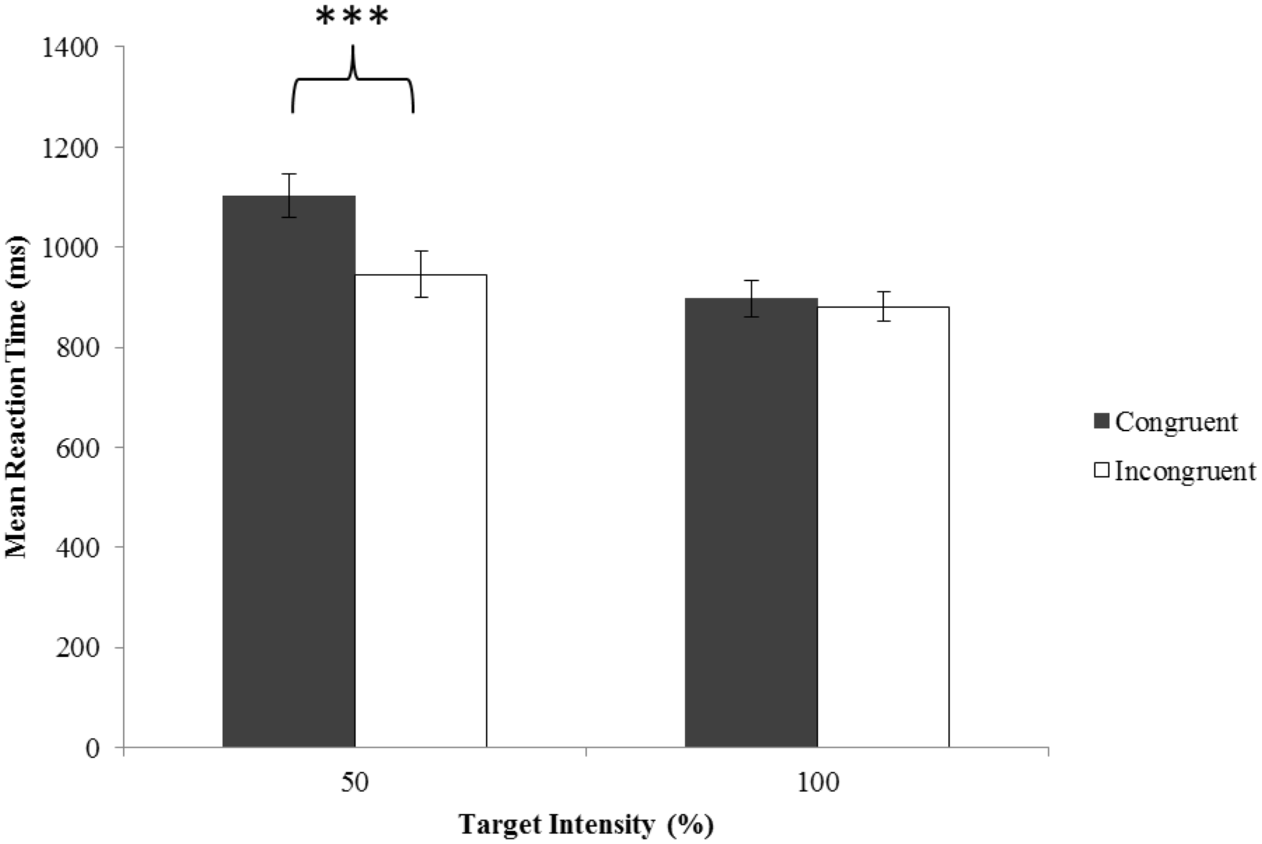

Figure 7. Mean reaction times (ms) for 50% and 100% intensity emotional targets on congruent and incongruent trials (Error bars represent one Standard error of the mean).

Control analyses

An identical analysis to experiment one was performed on hit rate and RT data. Neither the hit rate (Maximum *F* = .493, *p* > .514) or RT analysis (Maximum *F* = 2.268, *p* > .192) produced any significant main effects or interactions.

Signal detection measures

To objectively investigate participant's sensitivity to the emotional content of the priming stimuli, independently of response bias, *d'* values were calculated for each participant based on their results from block two. *d'* was calculated using Equation 1 (Macmillan & Creelman, 2004) and for the purpose of analysis, trials presenting emotional primes were treated as signal trials and those presenting neutral primes were treated as noise trials.

$$d' = [\, z(\text{Hit Rate}) - z(\text{False Alarm Rate}) \,] \quad \text{(Equation 1)}$$

A one sample *t*-test was conducted to assess whether *d*' values differed significantly from zero, as zero indicates performance at chance levels. The results showed that *d*' values (2.25 ± .50, Minimum *d'* = 1.86, Maximum *d'* = 3.13) were significantly greater than zero ($t(6)$ = 12.993, p <.001) which suggests participants could reliably detect the emotional content of the priming stimuli.

Interim Discussion – Experiment 2

There was evidence of FCAs in the present experiment but after Holm-Bonferronni corrections were applied, these were not significant. Definitive conclusions cannot therefore be drawn from these results but there is evidence of a trend in the data. Specifically, happy faces were identified better when they were presented in the LVF compared to RVF. This is in line with the predictions of hypothesis one, that predicted a general RH advantage for all emotions and also with the RH hypothesis that predicts the RH is dominant for processing all emotional expressions (Borod et al.,1998). As the LVF advantage was limited to happy faces, the predictions of the Valence-Specific and Approach-Avoidance hypotheses are contrasted here as both of these models predict the LH would preferentially process happiness due to specialisation for positive and approach emotions, respectively (Wedding & Stalans, 1985; Harmon-Jones, 2004).

In contrast with the predicted positive effect of emotionally congruent priming and target stimuli, happy primes shown before happy targets had an adverse effect on participant's accuracy. Participant's performed significantly worse on congruent trials displaying happy targets compared to incongruent trials, which is in conflict with previous affective priming studies (Sato & Aoki, 2006). Importantly, no significant results were obtained from the control analysis for neutral faces which suggests that this effect is driven by emotional content as opposed to priming by general facial characteristics. A possible explanation for this can be found from studies demonstrating contrast effects, which refer to unrelated primes facilitating identification of unambiguous targets due to the increased perceived salience of a target when compared with an incongruent prime (Herr, Sherman, & Fazio, 1983). The finding that adverse performance effects of congruency were limited to happy expressions also lends support to this idea as happiness is considered the most salient emotional expression due to the characteristic smiling mouth and may therefore be considered most different from neutral expressions.

The prediction of an advantage for identifying fearful faces is partially supported as the hit rates demonstrated a significant advantage for processing fear compared to anger. Although this indicates advantageous processing of fearful faces, it was specifically predicted that fearful expressions would be processed faster than all other emotional expressions as previous authors have suggested a subcortical route is specialised for rapidly detecting this emotion specifically (Vuilleumier et al., 2003). Superior accuracy may still indicate an advantage for processing fear relative to other emotional expressions and previous findings lend support to this assumption (for review, see Vuilleumier, 2005).

The analysis of *d'* values revealed that participants could reliably identify the emotional content of the priming stimuli. This confirms assumptions from Experiment 1 insofar as the paradigm used in the present experiment did not prevent participant's awareness of the prime. It also indicates that sufficient processing occurred for accurate identification of priming expressions As a result, the effect of the priming stimuli on participant's performance cannot be attributed to implicit processing but this does align with previous studies reporting rapid processing of affective information in backwards masking paradigms (Pessoa et al., 2005). Participants may have been more proficient at identifying the emotional content of the primes in block two compared to block one however. Trials in block one presented target stimuli after the prime and participants were required to respond to this target. In block two however, the target stimuli were absent. It is speculated that the conditions for detecting emotional content were therefore optimised in block two as there was no interference from target stimuli and participant's sensitivity to the primes may have been reduced in block one as a result. An alternative explanation for participant's above chance *d'* values may be presented from previous studies investigating rates of luminance decay on different types of computer monitors. The timings and masking procedures were consistent with previous priming studies so the finding that LCD Dell monitors are prone to inconsistent timings when displaying different colours (Ghodrati, Morris & Price, 2015), this may have resulted in stimuli being displayed longer than anticipated in the present experiment.

Experiment 3

Based on the findings from the SDT analysis in Experiment 2, it was confirmed that participants were able to detect the emotional content of priming stimuli. As a result, Experiment 3 aimed to present the priming stimuli below the threshold of conscious awareness by creating a new masking stimulus and reducing the presentation duration of the priming stimulus whilst increasing the duration of the masking stimulus. In light of the findings from Experiment 2, the present experiment was also conducted to evaluate any performance differences when participants are aware and unaware of a prime in the same expression identification task. The adverse effect of emotional congruency in experiment two was suggested as being caused by contrast effects resulting from visible priming stimuli, and it was therefore predicted that a positive priming effect would be observed for all three emotional expressions. In addition, it was again predicted that participants would be faster at correctly identifying fearful, compared to happy and angry, emotional hybrid targets and that all emotions would be identified better in the LVF.

Method

Participants

Six right-handed individuals (3 females, 3 males) recruited from the Durham University student population took part in experiment two with an age range of 19-31 years (24.33 years ± 5.35). Participants all displayed a right hand preference (*LQ* = 87.71 ± 30.08) and had normal or corrected to normal visual acuity.

Apparatus

The same Dell Laptop was used to present the current experiment in the same software as in Experiments 1 and 2.

Stimuli

In order to investigate whether a masking stimulus more similar to the priming stimulus would be more efficient at preventing participant's awareness, a new masking stimulus was created for the present experiment. The mask used in Experiments 1 and 2 was composed of middling spatial frequencies and as emotional content was conveyed in the LSFs only by the testing stimuli, the middling range of SFs may have failed to prevent awareness of the emotional content in the emotional primes. Also, it has been suggested that the more similar a masking stimulus is to the stimulus presented before it, the more effective the perceptual disruption (Hedger, 2016). A new mask was therefore created which was formed from a template of other neutral faces to more closely match the low-level features of the priming stimulus. The mask used in the present experiment was created in MatLab by swapping 20x20 pixel areas of each individual displaying a neutral expression (Figure 8). These areas were rotated and placed randomly on the template and the edges of the overlain sections blurred to prevent hard, salient sections of the face being visible. The average luminance of the mask was also then matched to the average luminance of all priming stimuli. All other experimental stimuli were identical to those used in Experiment 2.

Figure 8. Masking stimulus created through combining sections of all individuals displaying a neutral expression.

Design

The design of the present experiment was identical to Experiment 2 apart from the presentation durations of the prime and masking stimuli. Specifically, the duration of the prime was reduced from 50 ms to 32 ms and the duration of the masking stimulus was increased from 150 ms to 180 ms.

Procedure

An identical experimental procedure was followed in the present experiment as detailed for Experiment 2

Results

The analyses computed in the present experiment were identical to Experiment 2.

Hit rates

Analysis revealed a significant main effect of emotion ($F(2,8) = 7.096$, $p = .017$, $\eta_p^2 = .640$) with significantly more errors made for angry targets compared to happy ($p = .025$) and fearful targets ($p = .009$) (Table 1). This effect was partially predicted by the experimental hypothesis as fear was identified more accurately than anger but identification of fearful faces was also expected to be significantly more accurate than happy faces. Main effect of intensity ($F(1,4) = 483.765$, $p <.001$, $\eta_p^2 = .992$) also reached significance with 100% targets identified significantly more accurately than 50%. The interaction of VF × intensity ($F(1,4) = 28.316$, $p <.006$, $\eta_p^2 = .876$) reached significance and paired-samples *t*-tests were conducted to further explore this interaction. It was revealed that 50% intensity targets presented in the RVF (30.17 ± 9.29) were identified worse than 50% targets presented in the LVF (34.48 ± 7.11) although this was not significant post correction.

An analyses identical to that described in experiment 2 was conducted on the emotion x VF conditions to explore differences in identifying each emotion in each VF. A series of one sample *t*-tests were computed and chance was again set at 25%. The analysis revealed that fear was identified significantly above chance in both the RVF ($t(4) = 10.806$, $p < 0.001$) and LVF ($t(4) = 8.089$, $p = .001$). Happiness was also identified above chance level in both the RVF ($t(4) = 3.921$, $p = .017$) and LVF ($t(4) = 6.520$, $p = .003$). Anger, however, was identified above chance in the LVF ($t(4) = 2.860$, $p = .046$) but not in the RVF ($t(4) = 2.488$, $p = .068$) which suggests the RH is more accurate in the identification of anger.

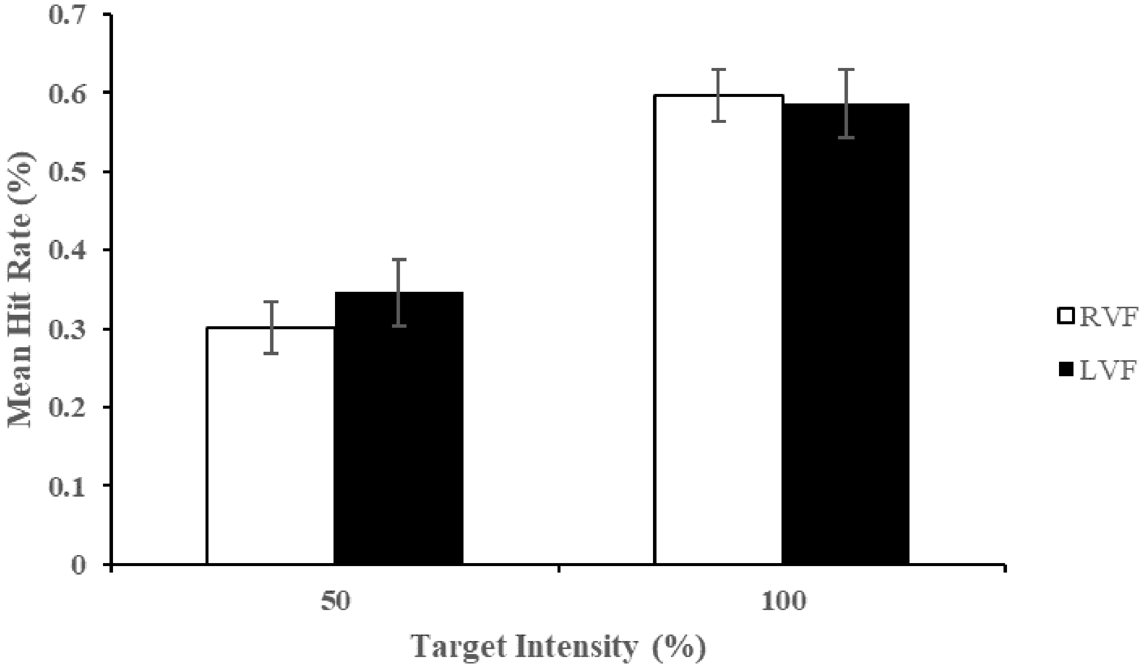

Figure 9. Mean hit rate (% correct) for 50% and 100% intensity emotional targets presented in the LVF and RVF (error bars represent one standard error of the mean).

Response times

Corresponding analysis revealed significant main effects of emotion ($F(2,8) = 23.196$, $p <.001$, $\eta_p^2 = .853$) and congruency ($F(1,4) = 13.460$, $p = .021$, $\eta_p^2 = .771$). Pairwise comparisons revealed happiness was correctly identified significantly faster than anger ($p = .002$) or fear ($p = .017$) (Table 1) and RTs were also significantly faster on emotionally incongruent trials compared to congruent trials which was not in accordance with predictions of reduced RTs on emotionally congruent trials. A significant interaction of emotion × intensity was also revealed ($F(2,8) = 23.059$, $p <.001$, $\eta_p^2 = .852$) and paired-samples *t*-tests showed that angry targets at 50% intensity (891 ms ± 73.87) were identified faster than angry targets at 100% intensity (957.83 ms ± 71.14) but this was not significant post correction.

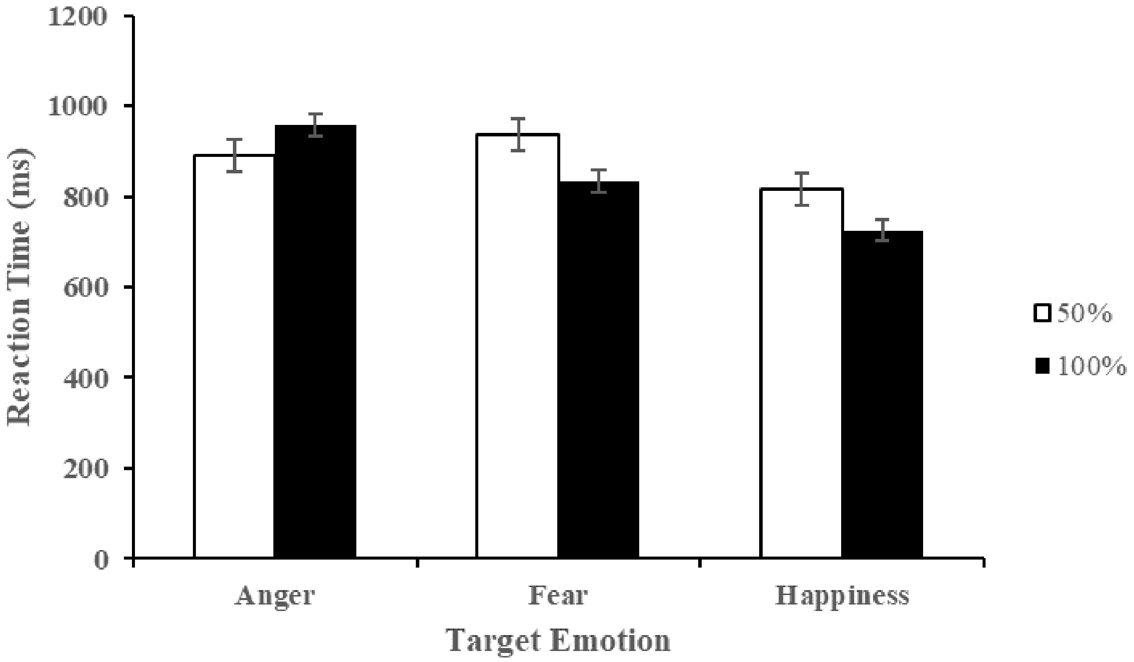

Figure 10. Mean reaction times (ms) for trials with each target emotion and at 50% and 100% intensities (error bars represent one standard error of the mean).

Control analyses

The hit rate analysis revealed no significant main effects or interactions (Maximum $F = .590$, $p > .485$). The RT analysis, however, revealed a significant main effect of congruency ($F(4,1) = 11.542$, $p = .027$, $\eta_p^2 = .743$) and neutral targets were correctly identified significantly faster when primed with emotional (785.20 ms ± 63.53) compared to neutral faces (860.62 ms ± 50.82).

Signal detection measures

To investigate the effectiveness of the altered priming and masking procedures adopted in the present experiment and therefore participant's awareness of the priming stimuli, *d'* values were calculated for each participant. Participants *d'* values (.59 ± .62, Minimum *d'* = -.33, Maximum *d'* = 1.33) did not differ significantly from chance (*t*(5) = 2.143, *p* >.05) which indicates, on average, participants were not able to detect the emotional content of the priming stimuli and were therefore not aware of its presence.

Interim Discussion – Experiment 3

Firstly, the analysis of *d'* values revealed that the procedural adaptations made to the current experiment based on the *d'* values obtained in Experiment 2 being significantly above chance were sufficient to prevent participant's awareness of the priming stimulus. Specifically, *d'* values in the current experiment did not significantly differ from chance levels which means participants were unable to detect the emotional content of the priming stimuli. As a result, any effects of congruency are likely to represent modulation of performance by implicit processes.

The prediction that all emotional expressions would be identified significantly better when presented in the LVF was not supported after Holm-bonferroni corrections were applied and no VF advantages were reported in either the hit rate or RT analyses. Despite this, a trend was revealed by the significant VF × intensity interaction whereby 50% targets were identified more accurately in the LVF compared to RVF. 50% targets were emotionally ambiguous and therefore, the greater accuracy of the RH for correctly identifying the emotional content of these stimuli regardless of valence is in accordance with the predictions of the RH hypothesis. Similarly, angry expressions were identified significantly above chance in the LVF only. Previous studies have suggested the RH may be more sensitive to emotional expressions in general (Natale, Gur, & Gur, 1983) and these results are in line with this suggestion.

Hit rate analysis revealed participants made significantly fewer errors for fearful and happy expressions compared to angry. No differences between fear and happiness processing were evidenced however and this conflicts with predictions of superior identification of fearful, relative to happy and angry targets. Similarly, this advantage was predicted for RT data but there were no significant differences between fear and the other emotional expressions. There is however, a significant advantage in both accuracy and RT data for happy expressions which suggests this expression, rather than fear, is identified faster using emotional information conveyed in the LSFs. Previous studies have also reported an advantage for processing happy expressions (Kirouac & Doré, 1983; Ladavas et al., 1980) and this may be driven by salient, configural changes specific to happy faces (Calvo, Fernandez-Martin, & Nummenmaa, 2014).

The third hypothesis that predicted a positive effect of emotionally congruent primes was also rejected in the current experiment as emotional congruency had an adverse effect on participant's performance. Specifically, participants were significantly faster at correctly identifying emotional targets when they were primed with neutral faces. This suggests that participant's awareness of the emotional content of the priming stimuli does not modulate the adverse effect of emotionally congruent information. It should be noted, however, that the control analysis conducted on RT data revealed an adverse congruency effect as well. It is therefore possible that poorer performance on emotionally congruent trials is resultant from general facial characteristics such as gender or perceptual configurations, which have previously been shown to elicit priming effects (Vanmarcke & Wagemans, 2017; Bowers, 2000).

General Discussion

The present experiments sought to investigate whether unseen emotional content conveyed by LSFs could improve subsequent performance in an emotional identification or categorisation task. Facilitation in this fashion would imply that emotional expressions can be processed in the absence of awareness and are therefore an important category of stimuli prioritised for rapid, unconscious processing. Secondly, FCAs for emotional face processing have been suggested to fluctuate as a function of awareness with the current study predicting the RH to be dominant due to receiving the most consistent support in the literature. The present experiments therefore manipulated the visibility of testing stimuli to clarify the contributions of each hemisphere to processing individual emotional expressions. Thirdly, it was predicted that fearful expressions would demonstrate a performance advantage as it has been suggested they are processed preferentially compared to other emotional expressions by a subcortical visual pathway specialised for LSF information. The current experiments presented emotional information confined to this SF band to further investigate this claim.

Fearful expressions were identified more accurately than angry expressions in the identification task used in Experiments 2 and 3, which is in line with the current experimental hypothesis and previous studies (Juncai, Jing, & Rongb, 2016), but performance for identifying anger and fear has most commonly been equivalent (Innes et al., submitted; Alves et al., 2009). This discrepancy between the current study and a similar experiment conducted by Innes et al. may be driven by the experimental stimuli used. In Innes et al.'s experiment, stimuli were gender-averaged and visually manipulated to remove imperfections and noise, whereas the current experiments used the original gendered individuals from the Ekman and Friesen (1976) set. A recent study demonstrated that female and male posers displaying the same emotion are evaluated differently and specifically, male faces are perceived as angrier and female faces as happier (Harris, Hayes-Skelton, & Ciaramitaro, 2016). It is important to note that results from studies using emotional hybrid faces have also reported a bias for identifying male faces as angrier and female faces as more positive (Prete et al., 2015; 2013a). In light of these findings, male posers used in the current experiment may have been misidentified as angry, causing the significant advantage for fear whilst the gender-averaged stimuli used in Innes et al.'s study were not subject to this bias.

The categorisation task of Experiment 1 however, revealed that happiness was identified more accurately than both fear and anger which is not in accordance with the experimental hypothesis. Similarly, there were no significant differences between identification of happy and fearful expressions in Experiments 2 and 3. Superior accuracy for identifying happy expressions has been documented in other studies (Everhart & Harrison, 2000; Ashwin et al., 2005; Alves et al., 2009; Innes et al., submitted) and may not conflict with the suggestion of a subcortical route, specialised for rapid detection of fearful stimuli as it is assumed the processing advantage would be reflected in RT data (Vuilleumier et al., 2003).

The RT data does not support this assumption as significant differences between emotions were observed in Experiment 3 only and happiness was identified significantly faster than both fear and anger. An RT advantage has been demonstrated for happy faces in previous studies (Hugdahl et al.,1993; Harrison & Corelczenko, 1990; Wells, Gillespie, & Rothstein, 2016) and a recent meta-analysis also reported a general advantage for processing happy faces in studies that used both RT and accuracy as dependent measures (Nummenaa & Calvo, 2015). This advantage may be driven by the salience of diagnostic changes around the mouth region that are specific to this expression (Calvo & Nummenmaa, 2008; Calvo, Fernandez-Martin, & Nummenmaa, 2014). Importantly, this configural change is represented in the LSF band and as emotional content was isolated to LSFs in all emotional facial stimuli in the current study, this suggests the RT advantage for happiness was resultant from salient changes conveyed by LSFs (Fernandez-Martin, & Nummenmaa, 2014). In accordance with this, LSFs have been consistently reported as diagnostic for identifying happy expressions (Kumar & Srinivasan, 2011; Srinivasan & Hanif, 2010; Srinivasan & Gupta, 2010) whilst HSF and middling SFs have been implicated for accurate identification of fear and anger (Smith & Schyns, 2009; Comfort et al., 2013). This finding has recently been replicated using an adaptation paradigm (Prete, Laeng, Tommasi, 2016). In this study, emotional faces and emotional hybrids underwent spatial frequency filtering. Participants were presented with filtered, unfiltered or hybrid adapting stimuli and then asked to rate the friendliness of a neutral face. The findings were concordant with the aforementioned studies (Kumar & Srinivasan, 2011; Comfort et al., 2013) as angry faces were shown to exert stronger aftereffects when filtered to preserve only middling-HSF information which implicates this band in the processing of fearful expressions. These results contrast with a proposed subcortical low road specialised for rapid detection of threat-related stimuli conveyed by LSFs and rather suggests perceptual salience, represented in the LSFs, may be the determining factor in processing differences between emotions.

Although the perceptual salience of happy faces may contribute to the processing advantage observed in the current and previous experiments, a study by Svärd, Wiens & Fischer (2012) observed an advantage for detecting happy faces at 7 different presentation durations ranging from 17-267 ms. It is assumed that rapid, low-level processing at shorter durations is reliant on processing salient configural changes but that the degree of high-level processing increases with the presentation duration (Svard et al., 2012). Happy faces are encountered more regularly than other expressions in daily life and this exposure has been suggested to result in a general detection advantage (Öhman et al., 2001; Calvo et al., 2014). The parallel distributed processing model conceptualised by McClelland & Rumhelhart (1981; 1982) suggests accurate perception is driven by an inter-related, distributed network of processing nodes that are specialised for detecting specific classes of stimuli. Accurate identification of stimuli requires matching a visual percept with stored semantic knowledge and these diverse stores form the basis of the processing nodes in parallel distributed processing model (Warrington & Taylor, 1978). Processing nodes are thought to operate as a function of neuronal activation thresholds whereby accurate detection is achieved once sufficient visual inputs are processed to exceed this threshold. Importantly, these activation thresholds are variable and can be lowered as the connections between nodes are strengthened, a process which is driven by repeated exposure to stimuli (McClelland & Rumelhart, 1981). The superior performance for identifying happy faces in the current experiments may therefore be driven by a greater degree of exposure to happy, relative to angry and fearful, expressions and consequently lower activation thresholds for processing nodes in the semantic network (Rumelhart, Hinton, & McClelland, 1986).

The congruency of the prime and target stimuli also significantly affected performance across all three experiments and specifically, RTs were significantly faster in Experiment 1 when primes and targets were emotionally congruent which conforms to the experimental hypothesis. This demonstrates a positive effect of emotional content conveyed by LSFs in the priming stimulus which is consistent with previous demonstrations of positive priming effects using expressive facial stimuli (Carroll & Young, 2005) and also LSF filtered expressions (Phaf, Wendte, & Rotterveel, 2005). The RT data for neutral faces however, revealed an identical congruency effect whereby neutral faces were correctly categorised as neutral significantly faster when primed with neutral faces, compared to emotional. This raises the possibility of priming by general, facial characteristics as opposed to affective information. Perceptual priming, for example, occurs when subsequent identification of a target is facilitated by primes that are similar in form and which are presented in the same sensory modality (Bowers, 2000). Alternatively, previous studies have also demonstrated a significant congruency effect of gender in priming paradigms (Vanmarcke & Wagemans, 2017). As the gender of the prime and target stimuli were always congruent and a control task was not used to explicitly test this, it is possible that congruency effects were facilitated by gender.

In contrast with Experiment 1, Experiments 2 and 3 revealed adverse priming effects in both RT and hit rate data. As *d'* values were significantly above chance for detecting the emotional content of the priming stimuli in Experiment 2 however, this may represent conscious processing of the prime. A previous study reported dissociation between positive and negative priming effects which fluctuated with participant's level of awareness of the prime. Specifically, negative priming was reported for participants who reported awareness whilst those who reported unawareness showed positive priming (Lombardi, Higgins & Bargh, 1987). The authors suggested participants who perceived the prime demonstrated flexibility in their categorisation decisions whilst those who were unaware showed automatic attention capture, resulting in inflexible categorisation that was in accordance with the priming stimulus. However, this explanation may not be sufficient as it was shown by analysis of *d'* values in Experiment 3 that participants were on average, not aware of the emotional content of the prime.

An alternative explanation is provided by the conceptualisation of contrast effects which refer to the same adverse effect of emotionally congruent information, but suggest implicit regulation of emotional responses underlies poorer performance in incongruent trials (Glaser

& Banaji, 1999). It is theorised that when priming stimuli are particularly representative of a specific category, in the case of the present experiments this would be the primes displaying 100% emotional intensity, an automatic correction response occurs (Strack et al., 1993). This correction response is thought to result from participants implicitly processing the potential bias of a salient priming stimulus which then affects subsequent appraisals of the target stimulus and correction responses are then overcompensated, leading to the contrast effect (Stapel et al., 1998). Glaser and Banaji (1999) claim that participant's motivation to perform accurately is a determining factor in the magnitude of contrast effects and this may explain the differences observed in congruency effects between Experiment 1 and Experiments 2 and 3. The difficulty of the expression identification task used in Experiments 2 and 3 was likely greater than the categorisation task of Experiment 1 as participants were only required to indicate the presence of emotional content, non-discriminately, in the latter task. The identification task, however, required participants to identify the specific emotional expression. It is speculated here that the increased task difficulty resulted in a greater degree of accuracy motivation in experiments two and three and therefore caused the observed pattern of contrast effects.

A pattern of differential performance between the categorisation and identification tasks was also observed in terms of visual half-field advantages and therefore, FCAs. An unpredicted RVF advantage was recorded in hit rates for fearful faces in the categorisation task which is not predicted by the RH, Valence-Specific or Approach-Avoidance hypotheses. This also contrasts with previous neurophysiological (Adolphs et al., 1996; Borod et al., 1986), divided visual half-field (Alves et al., 2011; Stafford & Brandaro, 2010) and chimeric faces studies (Bourne, 2010) that have reported a RH advantage for processing fearful expressions. Categorical perception may offer a rudimentary explanation of this RVF advantage as previous authors have suggested the LH may play a larger role than predicted by lateralised emotional processing models as a result of dominance for linguistic categories necessary for accurate identification (Etcoff & Magee, 1992; Roberson et al., 2010). Despite this, it is unclear why this phenomenon would manifest as an RVF advantage for fearful expressions alone in Experiment 1 as all emotional expressions should have been subject to the same degree of bias. Similarly, if the LH was exerting a confounding effect due to the involvement of language, it would be expected that an RVF advantage would be greater in magnitude in the expression identification tasks used in Experiments 1 and 2 as accurate performance in this task required matching the facial expressions to specific, linguistic subcategories.

Alternatively, there is evidence that the LH preferentially processes salient changes associated with fearful expressions and this may suggest the RVF advantage for fear is in fact driven by FCAs for processing specific facial changes. An fMRI study by Hardee, Thompson & Puce (2008) found that the left amygdala was selectively activated in response to fearful expressions and importantly, this effect was primarily driven by increases in the size of the white sclera of the eyes. This is in accordance with previous studies reporting modulation of amygdala activation in response to luminance changes in the eye region (Whalen et al., 2004). Following this, the RVF advantage documented in Experiment 1 may be representative of specialisation of the left amygdala for processing changes in the sclera of the eyes, rather than a LH dominance for processing fear. Laeng et al. (2010) reported that LH damage resulted in disrupted processing of fearful and sad emotional hybrids which further implicates the LH in processing fear.

In contrast, however, evidence of RH specialisation was reported in the categorisation task but post hoc tests were not significant after corrections were applied and further investigation is therefore required to clarify these trends. The hit rate data from Experiment 2 showed a trend of superior identification of happy faces in the LVF, which is consistent with previous divided visual half-field studies using shorter presentation (Alves et al., 2009; Everhart & Harrison, 2000; Innes et al., submitted). A trend was also observed in Experiment 3 whereby 50% intensity targets were identified more accurately in the LVF, than RVF which implicates the RH in emotion processing as performance for targets presented in each visual half-field did not fluctuate by emotional valence or motivational behaviours induced by target stimuli. In Experiment 3 the RH advantage for processing emotionally ambiguous stimuli may reflect a greater sensitivity of the RH to emotional expressions in general (Natale, Gur, & Gur, 1983). The opposing pattern of FCAs between Experiment 1 and Experiments 2 and 3 is likely driven by task demands as the methodologies of Experiment 1 and 2 differed in this aspect. The LH advantage for fearful expressions in Experiment 1 may therefore represent the greater importance of identifying salient changes in the sclera of the eye for categorising fearful expressions as emotional. An LH advantage for fear would be predicted across all three experiments if this hemisphere did preferentially process this emotion, but this was not evidenced.

A hypothesis proposed by Shobe (2014), however, may partially reconcile these findings. It is suggested in this review paper that the LH and RH are both capable of processing positive and negative emotions but the LH relies on information transferred via the corpus callosum from the RH and performs subsequent higher order operations on this information. On the other hand, the RH processes emotional stimuli at a lower, perceptual level. As the differences in patterns of lateralisation occur only between experiments using the categorisation and identification tasks, the separate tasks may have invoked different forms of processing which resulted in the opposing FCAs. The finding that 50% intensity targets trended towards more accurate identification when presented in the LVF is in keeping with this theory due to the suggested role of the RH in low-level analysis. Similarly, if superior recognition of happy faces specifically is driven by recognising familiar, salient changes, the RH would again be predicted to perform better. Insofar as the LH advantage observed for fear in the categorisation task, higher-order, linguistic operations may be implicated to a greater extent than in the identification task. Alternatively, general emotionality decisions may engage the LH through regulation of affective experiences as evidence suggests the LH is crucial in regulating emotional experiences (Greenberg, 2007).

Experiments 2 and 3 do, however, contribute to the trend observable in the literature whereby studies presenting stimuli for longer than 200 ms (Reuter-Lorenz & Davidson, 1981; Jansari et al., 2011) have generally reported results in favour of the Valence-Specific hypothesis compared to those using presentation times of less than 200 ms that generally support the RH hypothesis (Safer, 1981; Innes et al., submitted). The present findings are therefore in line with suggestions of rapid processing of LSF information underlying these observed patterns of lateralisation (Sergent, 1981). Other studies using hybrid faces and the divided visual half-field technique have reported a valence-specific pattern of lateralisation with tachistoscopic presentation times however (Prete et al., 2013; Prete et al., 2015). A possible explanation for this discrepancy may be the task used in these studies as participants were asked to rate the friendliness of hybrid faces whilst explicit measures of emotionality were used in the current study, and a previous study that also reported a RH advantage (Innes et al., submitted).

To compare the unconscious RH (Gainotti, 2012) and RH hypotheses (Borod et al., 1998), it is necessary to consider the effects of congruency and VF together. The unconscious RH hypothesis would be supported if congruency effects varied as a function of the visual half-field the target stimuli were presented in. Specifically, congruent or incongruent trials would have a greater effect on performance when targets were presented in the LVF as the prime was presented centrally and thus, the emotional content was available to both hemispheres. However, the results from Experiments 2 and 3 indicated the emotional content of the priming stimulus, which was presented below the threshold of awareness, did have a significant effect on performance, albeit not in a lateralised fashion. The RH hypothesis is instead supported as there was a trend of more accurate performance for targets presented in the LVF, regardless of the degree of emotional congruency between the prime and target. Many of the studies included in Gainotti's (2012) review used backwards masking paradigms (Morris et al., 1998; Morris et al., 1999) without objective measures of awareness and it is therefore possible that RH advantages observed in these studies are driven by conscious perception of stimuli.

The present experiments collectively demonstrate that emotional content conveyed by LSFs and presented below the threshold of conscious awareness are processed sufficiently to affect performance. These findings contribute to a growing literature suggesting emotional expressions (Leknes et al., 2013; Vuilleumier et al., 2013), and salient stimuli in general can be processed in the absence of awareness (Merikle et al., 2001). An interesting question is raised by these findings; what facilitates participant's ability to process emotional information when they are unaware of its presence? One proposal is the existence of a subcortical visual route, termed the "low road", although this is contested in the literature (for review, see Pessoa & Adolphs, 2008). The low road model posits that numerous subcortical structures including the pulvinar, superior colliculus and amygdala are anatomically connected to primary visual areas (Vuilleumier et al., 2003). A subcortical route for visual information proves interesting for the study of implicit emotion processing due to the different information conveyed by cortical and subcortical routes. Parvocellular pathways primarily convey HSF information rapidly whilst magnocellular pathways convey LSF information more slowly (Derrington & Lennie, 1984' Goffaux et al., 2011). Due to the fact that parvocellular channels are exclusive to cortical routes, the subcortical pathway would be facilitated by magnocellular channels (Vulleumier et al., 2003; Livingstone & Hubel, 1988) and would convey LSFs only. Relating this anatomical knowledge to the findings from the current and previous experiments, the low road offers a rudimentary, theoretical explanation for implicit emotion processing.

Early, indirect evidence for the low road is provided from previous studies with individuals who have undergone surgery to disconnect the corpus callosum fibre bundle that connects the two cerebral hemispheres as a treatment for severe epilepsy (Wagenen & Herren, 1940). Complete transection of the corpus callosum results in two, functionally independent hemispheres, providing a unique opportunity to investigate the individual contributions of the LH and RHs to a range of cognitive tasks. A number of experiments have shown that split-brain patients can complete tasks that require integration of information presented in both hemifields (Sergent, 1987; Corballis & Sergent, 1992; for review see Corballis, 1995). In the absence of communication between the cortices of the LH and RH, authors have suggested that intact subcortical structures located in both hemispheres and connections to visual areas could facilitate split-brain performance. The low road has also been proposed as a facilitator for the residual visual abilities observed in blindsight patients. These "blindsight" patients retain a degree of visual processing following damage to primary visual areas but report no conscious awareness of the stimuli being presented in their blind fields (Danckert & Goodale, 2000; Kentridge, Heywood, & Weiskrantz, 1999). Basic visual abilities, such as orientation discrimination and texture perception (Weiskrantz, Warrington, Sanders, & Marshal, 1974;

Sahraie et al., 2010), have been demonstrated in blindsight but evidence has shown that a degree of affective processing can also be preserved.

The term “affective blindsight” was coined by de Gelder, Vroomen, Pourtois and Weiskrantz (1999) in an experiment with patient G.Y. who suffered a large lesion in his left occipital lobe. G.Y. was shown video fragments of a woman vocalising a sentence whilst displaying either a happy, sad, angry or fearful expression. G.Y. performed significantly above chance in a forced-choice labelling task when stimuli were shown in his blind RVF. Conditions that used static stimuli, however, resulted in chance level performance but ERP recordings showed that these stimuli still elicited activity in higher visual areas. De Gelder and colleagues concluded that these residual abilities must be mediated by an alternative anatomical route that bypasses striate cortex. A subsequent fMRI study of patient G.Y. investigated whether the patient’s performance was wholly reliant on facial movement and the data revealed significant activations of the amygdala in response to static, masked fearful expressions presented in his blind RVF (Morris et al., 2001), which suggests there is significant activation in the absence of dynamic facial movement.

It is worth noting, however, that some authors question the validity of findings from the study of patient G.Y. due to the young age at which he sustained neural damage (Tamietto & de Gelder, 2008). The possibility of neuroplastic restructuring in visual pathways may facilitate his apparent ability to identify emotional facial expressions (Tamietto & de Gelder, 2008). Studies have shown that the number of functioning inferior collicular neurons in primate brains increase after striatal damage (Mohler & Wurtz, 1977) and G.Y.’s performance has indeed improved over time (Weiskrantz, 2000). Despite this, an fMRI study of another blindsight patient, case T.N., who sustained damage to both their left and right visual cortices much later in life also demonstrated emotion processing capabilities in their blind field (Pegna et al., 2005). Patient T.N. correctly identified the expression of happy and angry faces above chance levels. Right amygdala activations were also recorded in response to emotional faces, which is in keeping with previous findings from neuroimaging studies of implicit emotion processing. T.N. also completed two control tasks that required him to identify the gender of a face and indicate whether normal/jumbled faces were authentic faces and his performance was at chance levels in both tasks. This suggests that his residual visual processing capabilities are driven by the emotional content of the face rather than other facial characteristics. Upon consideration of the above evidence, the low road provides a possible route through which LSF information was conveyed by the priming stimuli in the current experiments, outside of the participant's awareness.

Limitations & Future directions

The main weakness of the current experiments was the small participant sample sizes which meant that the effect of participant's sex could not be investigated directly and this also increased the risk of type 2 errors. Previous studies have reported sex driven differences in FCAs for facial discrimination tasks (Hausmann & Günturkün, 1999) and more recently, in divided visual-half field studies with emotional hybrids (Innes et al., submitted). The current experiments combined hybrid faces and affective priming in the divided visual-half field and potential sex-differences in the current task may have been overlooked due to the sample size. Similarly, two participants in Experiment 2 did not demonstrate a consistent right-hand bias and it has been reported that participants demonstrating a consistent right-hand bias are more strongly lateralised, specifically to the RH, in emotional processing tasks (Bourne, 2008). Although there was no evidence of LH specialisation in Experiment 2, a reduction in the magnitude of lateralisation in the left-hand biased participants may have confounded results and follow-up studies should explicitly control for this factor.

Only Experiment 3 presented the priming stimuli below the threshold of conscious awareness and an interesting future experiment may assess the differences between emotional expression identification and categorisation priming paradigms where stimuli are also presented outside of awareness. Similarly, the design of the current experiments prevented objective measures of sensitivity from being calculated for detecting each emotional expression and rather were employed to assess participant's awareness of the priming stimulus. Recently, multidimensional SDT modelling has been used to evaluate detection sensitivity in more complex experimental models (King & Deheane, 2014) and its application to the current task would provide an objective measure of sensitivity to individual emotional expressions.

Conclusion

The current experiments are the first to combine affective priming with hybrid faces presented in the divided visual half-field and collectively demonstrate that emotional content conveyed by hybrid faces in the LSF band is sufficient for participants to correctly identify emotional expressions which highlights their usefulness for the study of emotion processing, whilst controlling for potential confounds of SF lateralisation. Emotional content presented below the threshold of conscious awareness was also shown to affect subsequent identification of ambiguous emotional hybrid targets, albeit in an unpredicted direction and interestingly, this pattern of priming effects differed between categorisation and expression identification tasks. Finally, there was some evidence of FCAs in all three experiments but again, dissociation was observed in the direction of lateralisation between the categorisation and identification tasks. The present results provide support for the RH hypothesis specifically as there was no evidence for either the Valence-Specific or Approach-Avoidance hypotheses. The subcortical low road seems a likely facilitator for the priming effects observed in this study but until conclusive evidence is provided with regards to its role in emotion processing, the conclusions drawn here remain purely correlative.

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