available at www.sciencedirect.com
ScienceDirect
journal homepage: www.elsevier.com/locate/cortex

Research report

Examining the effects of inversion on lateralisation for processing facial emotion

Victoria J. Bourne*

School of Psychology, University of Dundee, Dundee, UK

ARTICLE INFO

Article history:
Received 7 October 2009
Reviewed 20 January 2010
Revised 24 January 2010
Accepted 18 March 2010
Action editor Stefan Schweinberger
Published online xxx

Keywords:
Face processing
Emotional expression
Lateralisation
Hemispheric specialisations
Inversion

ABSTRACT

There is an increasing amount of evidence which suggests that each hemisphere is differently specialised for processing facial stimuli, with the right hemisphere specialised for the processing of configural information and the left hemisphere specialised for the processing of featural information. While there is evidence for this distinction from studies of face recognition, it has not been shown in studies of lateralisation for processing facial emotion. In this study the chimeric faces test was used with faces expressing anger, disgust, fear, happiness, sadness or surprise, presented in either an upright or an inverted orientation. When presented upright, a significant right hemisphere bias was found for all six emotions. However, when inverted, a significant left hemisphere bias was found for the processing of happiness and surprise, but not for the processing of negative emotions (although the analysis was approaching significance for anger). These findings support the hypothesis that each hemisphere is differently specialised for processing facial emotion, but contradicts previous work that examined the effects of inversion on chimeric face stimuli.

1. Introduction

It is quite widely accepted that there are hemispheric differences in the ability to process faces with the right hemisphere being specialised to a greater extent than the left hemisphere. In terms of processing facial emotion, this right hemisphere dominance has been shown in a wide range of studies using chimeric face stimuli. This behavioural paradigm presents vertically split half faces in which one hemi face is neutral and the other hemi face is expressive. Participants tend to rate a face as more emotive when the emotional expression is shown in the left hemi face (their left visual field) than when the emotional expression is shown in the right hemi face (their right visual field). This left visual field bias is interpreted as reflecting the right hemisphere superiority for face processing and has been shown in a large number of studies (e.g., Levy et al., 1983; Bourne, 2005, 2008, in press; Burt and Perrett, 1997).

Evidence for the left visual field bias found in the chimeric faces test reflecting right hemisphere superiority for the processing of faces has been shown in two studies of visual field biases in participants with unilateral brain lesions (Bava et al., 2005; Kucharska-Pietura and David, 2003). In both studies, participants with left hemisphere lesions showed the usual right hemisphere bias on the chimeric faces test, whereas those with right hemisphere lesions showed no clear visual field bias. Although there is considerable evidence for the right hemisphere being dominant for the processing of facial emotion, it is important to acknowledge that there are contrasting theories regarding the lateralisation of emotional face processing. The right hemisphere hypothesis suggests that the processing of all facial emotion is lateralised to the right

* School of Psychology University of Dundee, Park Place, Dundee, UK.
E-mail address: v.bourne@dundee.ac.uk

0010-9452/$ – see front matter © 2010 Elsevier Srl. All rights reserved.
doi:10.1016/j.cortex.2010.04.003

hemisphere (Borod, 1992) whereas the valence hypothesis proposes that the processing of positive emotion is lateralised to the left hemisphere and the processing of negative emotion is lateralised to the right hemisphere (Davidson, 1992). Overall there is more support for the right hemisphere hypothesis than the valence hypothesis (see Bourne, in press), but it is important to include both positive and negative emotions in any study of lateralisation for the processing of facial emotion to enable the comparison of these two theoretical standpoints.

Although the chimeric faces test tends to show a right hemisphere bias for the processing of emotion presented in the left visual field, it is important to note that this does not preclude the possibility of left hemisphere mechanisms being capable of processing facial stimuli. Indeed, a great deal of work examining the lateralisation of face recognition has shown that both hemispheres are able to process facial stimuli, but that processing is more efficient in the right hemisphere. For example, prosopagnosia (loss of the ability to effectively process faces) may occur as a result of unilateral damage to either the right hemisphere (e.g., De Renzi et al., 1968; Inoue et al., 2008; Schiltz et al., 2006; Yin, 1970) or the left hemisphere (e.g., Barton, 2008; Hamsher et al., 1979; Meadows, 1974; Wright et al., 2006). Further, it has been suggested that unilateral lesions only cause selective deficits to face processing and that bilateral lesions are necessary to entirely disrupt face processing (Boeri and Salmaggi, 1994; Warrington and James, 1967). This possibility indicates that each hemisphere makes a distinct contribution to the processing of faces.

One of the main accounts for the different hemispheric specialisations in face processing is that each hemisphere is specialised for processing distinct forms of facial information: the left hemisphere being specialised for processing featural information and the right hemisphere being specialised for processing configural (the relative distances between the features) information (see Bourne et al., 2009). A number of studies have examined this distinction using manipulations of one or both forms of information. One of the most frequently used manipulations is face inversion. Face inversion reduces the ability to effectively process a face and this impairment is of a greater magnitude than is found with other classes of stimuli (Yin, 1969). The generally accepted explanation for the face inversion effect is that, when presented in the upright orientation, faces are processed primarily on the configural information contained within them, while inverted faces are processed on the basis of their featural information (e.g., Yin, 1969; Bartlett and Searcy, 1993; Leder and Bruce, 2000).

Research on patients with prosopagnosia following right hemisphere lesions has shown that the face inversion effect is reduced (e.g., Yin, 1970; Boutsen and Humphreys, 2002; Farah et al., 1995; Rouw and de Gelder, 2002) and some have even shown a face inversion superiority effect (e.g., de Gelder et al., 1998; de Gelder and Rouw, 2000; Boutsen and Humphreys, 2002; Marotta et al., 2002; Rouw and De Gelder, 2002). That is that some patients with prosopagnosia are actually better at processing inverted faces than they are at processing upright faces. This research suggests that the processing of faces on the basis of the configural information contained within them is not possible due to the damage acquired and instead processing is reliant on the left hemisphere featural mechanisms. This pattern has also been shown in behavioural studies using the divided visual field paradigm (Leehey et al., 1978; Rhodes, 1993), event related potential studies (Jacques and Rossion, 2007; Rossion et al., 1999) and functional neuroimaging studies (Passarotti et al., 2007). It therefore seems that the typical right hemisphere dominance for face processing is eliminated or reversed when faces are inverted.

While a large number of studies using the chimeric faces test have found right hemisphere superiority for processing facial emotion, few have considered how inversion might change this pattern of lateralisation. Two studies used happy/neutral chimeras (the most typical two-face version of the chimeric faces test) in both upright and inverted orientations and found that inversion reduced the right hemisphere bias, but there was still a significant right hemisphere bias for inverted faces (Luh, 1998; Coolican et al., 2008). However, using an identity version of the chimeric faces test in which left–left or right–right chimeric faces have to be matched to the original face, Coolican et al. (2008) found that inversion did not reduce the right hemisphere bias. The effect of inversion on chimeric face stimuli has also been considered in two studies using a one face gender version of the chimeric faces test in which the chimeric faces are formed from one male half face and one female half face (Butler and Harvey, 2005; Parente and Tommasi, 2008). Butler and Harvey found that the right hemisphere bias was significantly reduced with inversion. Their initial analysis showed no right hemisphere superiority for the processing of inverted faces, but the removal of two outliers revealed a significant right hemisphere bias. In contrast Parente and Tommasi found no significant difference in the laterality bias between upright and inverted faces with both showing a right hemisphere bias.

Predictions about the lateralised effects of face inversion seem to differ between the face recognition and the chimeric faces test literature. The research using whole faces, which typically use identity recognition tasks, show that inversion either eliminates the right hemisphere bias or reverses it and shows left hemisphere superiority. In contrast, the work using chimeric faces tends to show that inversion reduces the strength of the right hemisphere bias, but does not eliminate it. This study provides a more detailed examination of the effects on inversion on the chimeric faces test by examining the lateralised bias for chimeric faces across all six of the basic emotions (anger, disgust, fear, happiness, sadness and surprise) for upright and inverted chimeric faces. It is important to examine both positive and negative facial expressions of emotion as there are contrasting theories regarding their lateralisation (see Bourne, in press). It is predicted that inversion will reduce the magnitude of the right hemisphere dominance, but it is unclear whether right hemisphere superiority will remain, whether no clear lateralisation pattern will be found, or whether the processing of inverted chimeric faces will elicit a left hemisphere bias.

2. Methods

2.1. Participants

There were 40 participants in this study (15 males) with a mean age of 25 years (SD = 8.5, range 18–49 years). All were

Fig. 1 – Example upright chimeric face stimuli. From left to right, the emotion expressed is: anger, disgust, fear, happiness, sadness and surprise. In all examples the top face is showing the emotional expression in the left half face. Inverted stimuli were identical but flipped on the horizontal axis.

right handed by self report and this was confirmed with a handedness questionnaire (adapted from Dorthe et al., 1995). All had normal or corrected-to-normal vision and none reported either having had a head injury or psychiatric diagnosis. Ethical approval for this study was granted by the Ethics Committee of the School of Psychology, University of Dundee.

2.2. *Stimuli and procedure*

The chimeric faces were formed using the Ekman stimuli (taken from Workman et al., 2006; see Fig. 1) with one male and one female poser. Neutral half faces were paired with emotive half faces. One stimulus was made using the poser's left half face and another made using the posers right half face. Individuals face subtended approximately 4.5° horizontally and 7° vertically at a viewing distance of 52 cm. Faces were presented in greyscale on a white background. Pairs of faces were presented, one above the other, with one showing emotion in the left half face and the other showing emotion in the right half face. Consequently there were eight different stimuli within each emotion (male or female, left or right half face, left face emotion stimuli shown at the top or bottom of the display) and each stimulus pair was seen three times, giving 24 trials. In half of the trials the top face showed emotion in its left half face and in the remaining trials the top face showed emotion in its right half face. This placement was randomised across participants. Each emotion was presented in a separate block of 24 trials and the order of these blocks was randomised. The inverted stimuli were simply flipped on the horizontal axis. Inverted trials were completed in separate blocks, again with each emotion in a block of 24 trials. There were a total of 12 blocks with each of the six emotions shown once in an upright block and once in an inverted block. Within each block, there were a total of 24 trials: 12 trials in which the top face showed emotion in its left half face and 12 in which the top face showed emotion in its right half face.

Pairs of faces were presented centrally on a computer screen. Participants were asked to decide which of the two faces looked more emotive (e.g., happier within the happy block of trials). If they thought the upper of the two faces was more emotive they pressed the upper button on a response pad. If they thought the lower of the two faces was more emotive they pressed the lower button on a response pad. Faces remained onscreen until the participant responded and they were asked to respond as instinctively as possible. For each condition a laterality quotient was calculated {laterality quotient = [number of LVF choices − (24 − number of LVF choices)]/24}. Positive scores significantly above 0 indicate a left visual field (right hemisphere) bias, whereas negative scores significantly below 0 indicate a right visual field (left hemisphere) bias.

3. Results

Initial analyses used one-sample *t* tests to compare laterality quotients to 0 (see Table 1). All six upright versions of the chimeric faces test had laterality quotients significantly above 0, showing a left visual field (right hemisphere) bias for processing facial emotions. All six inverted versions of the chimeric faces test had laterality quotients below 0, showing a right visual field (left hemisphere) bias for processing facial emotions. However, this was only significant for happiness and surprise and approaching significance for anger. To consider the overall pattern of lateralisation for upright and inverted chimeric stimuli, mean laterality quotients were calculated across the six emotions. Overall, there was a significant left visual field (right hemisphere) bias for upright

Please cite this article in press as: Victoria J. Bourne, Examining the effects of inversion on lateralisation for processing facial emotion, Cortex (2010), doi:10.1016/j.cortex.2010.04.003

Table 1 – Laterality quotients across the different versions of the chimeric faces test and one-sample *t* tests comparing quotients to 0 (no bias).

	Upright				Inverted			
	Mean	SD	*t*	*p*	Mean	SD	*t*	*p*
All emotions	.25	.44	3.5	<.001	−.10	.26	−2.6	.007
Anger	.25	.51	3.1	.002	−.08	.35	−1.5	.073
Disgust	.16	.48	2.1	.020	−.05	.34	−1.0	.159
Fear	.33	.55	3.7	<.001	−.07	.38	−1.2	.117
Happiness	.29	.56	3.2	.002	−.14	.47	−1.9	.035
Sadness	.17	.30	3.6	<.001	−.03	.21	−1.0	.157
Surprise	.30	.62	3.1	.002	−.24	.48	−3.2	.002

chimeras and a significant right visual field (left hemisphere) bias for the processing of inverted chimeras.

A 6(emotion) × 2(orientation) repeated measures ANOVA was conducted on the laterality quotients. There was no significant difference across the six emotions [$F(5, 195) = 1.3$, $p = .138$, partial $\eta^2 = .032$]. There was a significant effect of inversion [$F(1, 39) = 11.4$, $p = .001$, partial $\eta^2 = .032$] with inversion reducing the laterality quotients. As can be seen in Table 1, overall upright faces elicit a significant right hemisphere bias whereas inverted faces elicit a significant left hemisphere bias. There was a significant interaction between emotion and orientation [$F(5, 195) = 3.1$, $p = .005$, partial $\eta^2 = .073$], which suggests that the magnitude of the inversion effect varied across the six emotions. For all of the emotions inversion caused a significant reduction in laterality quotient, but the extent of this reduction varied. From the largest inversion effect through to the smallest inversion effect in terms of the mean difference in laterality quotient: surprise ($p = .001$), happiness ($p = .003$), fear ($p = .004$), anger ($p = .003$), disgust ($p = .025$) and sadness ($p = .001$).

4. Discussion

The main finding of this experiment was right hemisphere superiority for the processing of upright chimeric faces, but left hemisphere superiority for the processing of inverted chimeric faces. The strength of the right hemisphere bias for upright faces was stronger than the strength of the left hemisphere bias for inverted faces .25 *vs* −.10), however both showed significant but opposite patterns of lateralisation. This finding is not consistent with the small amount of previous work looking at the effects of inversion on the chimeric faces test, which tends to show a reduced but still significant right hemisphere bias. The finding of opposite patterns of lateralisation for upright and inverted chimeric faces is more consistent with the findings of research using whole face stimuli, particularly that from populations with prosopagnosia. In a study that contrasted the effects of face inversion in patients with left or right hemisphere, Yin (1970) found that patients with right hemisphere lesions were significantly worse at the processing of upright faces whereas patients with left hemisphere lesions were significantly worse at the processing of inverted faces. This dichotomous finding is consistent with the finding from this study, showing right hemisphere dominance for processing upright faces and left hemisphere dominance for processing inverted faces. The findings of this study therefore support the idea that each hemisphere is differently specialised for processing distinct forms of facial information, with the right hemisphere specialised for processing configural facial information and the left hemisphere specialised for processing featural facial information.

The suggestion that each hemisphere is specialised for processing different forms of facial information has been supported by a wide range of evidence from varying methodologies. Patients with prosopagnosia following right hemisphere lesions often have impaired configural processing of faces, but intact featural processing (e.g., Bliem, 1998; Uttner et al., 2002). Further, an fMRI study of a patient with prosopagnosia following a unilateral right hemisphere lesion showed that the remaining face processing abilities were associated with activation in the left hemisphere (Marotta et al., 2001). It was suggested that this left hemisphere activation reflected the featural processing of facial stimuli. Similar findings have been reported in non-clinical participants. For example, behavioural studies using the divided visual field methodology have shown that manipulations of configural information disrupt right hemisphere processing of faces, whereas manipulations of featural information disrupt left hemisphere processing (e.g., Bourne et al., 2009). Event related potential studies have also shown that inversion, which disrupts configural processing, reduces the N170 component to a greater extent in the right hemisphere than in the left hemisphere (Jacques and Rossion, 2007; Rossion et al., 1999). Similarly, functional magnetic resonance imaging studies have shown that inversion reduces activation in the right fusiform face areas to a greater extent than in the left fusiform face area (Passarotti et al., 2007). Taken together all of these sources of evidence provide support for the suggestion that the right hemisphere is specialised for processing configural facial information and the left hemisphere is specialised for processing featural facial information.

Although a left hemisphere bias was found for the processing of inverted chimeric faces, this did vary across the six emotions. The left hemisphere superiority was significant for the processing of happiness and surprise, approaching significance for the processing of anger and not significant for the processing of disgust, fear or sadness. If surprise is assumed to be a positive emotion, this finding suggests, when a face is inverted, a left hemisphere bias is found for the processing of positive emotions, but no clear pattern of lateralisation is found for negative emotions. Previous work examining the effects of configural manipulations on the processing of facial emotion has shown that negative emotional expressions are more affected by the manipulations than positive emotions (Chambon et al., 2006; Durand et al., 2007; Prkachin, 2003). This suggests that positive emotions can be processed well on the basis of both configural (when upright) and featural (when inverted) information, whereas the processing of negative emotions is more reliant upon the configural information contained within a face.

This evidence can be used to clearly explain the findings of the present study. If upright positive faces are processed using the right hemisphere configural mechanisms and inverted positive faces are processed using the left hemisphere featural

Please cite this article in press as: Victoria J. Bourne, Examining the effects of inversion on lateralisation for processing facial emotion, Cortex (2010), doi:10.1016/j.cortex.2010.04.003

mechanisms, opposite patterns of lateralisation would be expected. However, the processing of negative emotions seems to be far more reliant on the right hemisphere configural mechanisms and neither hemisphere seems to be able to adequately process negative emotion in inverted faces. In future work, it would be of interest to combine these two areas of research in an attempt to further understand the neuropsychological mechanisms underlying the processing of facial stimuli. For example, it might be predicted that individuals who show only a small face inversion effect would be more bilateral for the processing of facial emotion as they would have access to both the configural and the featural processing mechanisms in each hemisphere. In contrast, individuals who show a large face inversion effect might be more strongly lateralised to the right hemisphere and be more reliant upon the configural information contained within faces.

The findings of this study may also help to inform the current debate regarding the lateralisation of emotion processing (Bourne, in press). There are two key competing theories: the right hemisphere hypothesis (Borod, 1992), which suggests that the processing of all emotion is lateralised to the right hemisphere, and the valence hypothesis (Davidson, 1992), which suggests that the processing of positive emotion is lateralised to the left hemisphere and the processing of negative emotion is lateralised to the right hemisphere. In the upright condition, the right hemisphere hypothesis is clearly supported with a significant right hemisphere bias across all of the emotions. However, in the inverted condition there is more evidence for there being hemispheric differences in the processing of positive and negative emotions with the positive emotions showing a left hemisphere bias, but the negative emotions showing no clear bias.

Whether the findings of this experiment support the right hemisphere hypothesis or the valence hypothesis seems to depend on the orientation of the face. One possible explanation for this might be found by attempting to disentangle the lateralisation effects for the processing of facial stimuli and the processing of emotional stimuli. It is possible that the processing of upright faces is dominated by the facial processing mechanisms, which are primarily lateralised to the right hemisphere. However, when inverted, faces are processed using the more featural information contained within them, which may not elicit the face processing mechanisms as strongly and may consequently reflect the lateralised processing of emotion, rather than the lateralised processing of facial emotion. This suggestion may indicate that work using the chimeric faces test reflects face processing rather than emotion processing, however, such an extreme conclusion is unlikely to be true. First, studies using chimeric faces across a range of studies have found differences across different tasks, such as identity and emotion decisions (Coolican et al., 2008) or lip reading and age judgements (Burt and Perrett, 1997). If the processing of chimeric faces was dominated by the face processing mechanisms, the same lateralisation effect should be found across all tasks. Second, right hemisphere processing of emotional stimuli has been shown even for linguistic stimuli, which would typically elicit left hemisphere processing (Smith and Bulman-Fleming, 2006; Wildgruber et al., 2005). Clearly attempting to distinguish between asymmetry for processing emotion and asymmetry for processing the stimuli (e.g., words or faces) is important for future research.

Although the findings of the present study are consistent with the predictions from earlier face recognition research, it shows a rather different finding from the small amount of work that has previously examined the effects of inversion on the processing of chimeric faces. Two studies using happy/neutral chimeric face pairs, which are essentially identical to the happy condition in this study, found a reduced but still significant right hemisphere bias (Coolican et al., 2008; Luh, 1998). In contrast, the present study found that inversion actually reversed the asymmetry in the happiness condition and elicited a significant left hemisphere bias. There is no clear explanation for this difference methodologically; however each study used different faces to form their chimeric stimuli. For example, the sex of the poser (Parente and Tommasi, 2008) or the intensity of the emotional expression (Bourne, in press) may have influenced patterns of lateralisation.

The findings of this study provide support for the hypothesis that each hemisphere is differently specialised for processing of facial information, with the left hemisphere being specialised for the processing of featural information and the right hemisphere being specialised for the processing of configural information. While this pattern has been supported in studies of face recognition, this is the first study to support this distinction for the processing of facial emotion.

REFERENCES

Bartlett JC and Searcy JH. Inversion and configuration of faces. *Cognitive Psychology*, 25: 281–316, 1993.

Barton JJS. Prosopagnosia associated with a left occipitotemporal lesion. *Neuropsychologia*, 46(8): 2214–2224, 2008.

Bava S, Ballantyne AO, May SJ, and Trauner DA. Perceptual asymmetry for chimeric stimuli in children with early unilateral brain damage. *Brain and Cognition*, 59(1): 1–10, 2005.

Bliem HR. Experimental and clinical exploration of a possible neural subsystem underlying configurational face processing. *Brain and Cognition*, 37(1): 16–18, 1998.

Boeri R and Salmaggi A. Prosopagnosia – Commentary. *Current Opinion in Neurology*, 7(1): 61–64, 1994.

Borod JC. Interhemispheric and intrahemispheric control of emotion: A focus on unilateral brain damage. *Journal of Consulting and Clinical Psychology*, 60(3): 339–348, 1992.

Bourne VJ. Lateralised processing of positive facial emotion: Sex differences in strength of hemispheric dominance. *Neuropsychologia*, 43(6): 953–956, 2005.

Bourne VJ. Examining the relationship between degree of handedness and degree of cerebral lateralization for processing facial emotion. *Neuropsychology*, 22(3): 350–356, 2008.

Bourne VJ. How are emotions lateralised in the brain? Contrasting existing hypotheses using the chimeric faces test. *Cognition and Emotion*, in press, doi:10.1080/02699930903007714.

Bourne VJ, Vladeanu M, and Hole GJ. Lateralised repetition priming for featurally and configurally manipulated familiar faces: Evidence for differentially lateralised processing mechanisms. *Laterality*, 14(3): 287–299, 2009.

Boutsen L and Humphreys GW. Face context interferes with local part processing in a prosopagnosic patient. *Neuropsychologia*, 40(13): 2305–2313, 2002.

Please cite this article in press as: Victoria J. Bourne, Examining the effects of inversion on lateralisation for processing facial emotion, Cortex (2010), doi:10.1016/j.cortex.2010.04.003

Burt DM and Perrett DI. Perceptual asymmetries in judgements of facial attractiveness, age, gender, speech and expression. *Neuropsychologia*, 35(5): 685–693, 1997.

Butler SH and Harvey M. Does inversion abolish the left chimeric face processing advantage? *NeuroReport*, 16(18): 1991–1993, 2005.

Chambon V, Baudouin JY, and Franck N. The role of configural information in facial emotion recognition in schizophrenia. *Neuropsychologia*, 44(12): 2437–2444, 2006.

Coolican J, Eskes GA, McMullen PA, and Lecky E. Perceptual biases in processing facial identity and emotion. *Brain and Cognition*, 66(2): 176–187, 2008.

Davidson RJ. Emotion and affective style – Hemispheric substrates. *Psychological Science*, 3(1): 39–43, 1992.

De Renzi E, Faglioni P, and Scotti G. Tactile spatial impairment and unilateral cerebral damage. *Journal of Nervous and Mental Disorders*, 146(6): 468–475, 1968.

Dorthe NJ, Blumenthal TD, Jason DR, and Lantz PE. The use of next-of-kin in assessing handedness. *Perceptual and Motor Skills*, 81(1): 203–208, 1995.

Durand K, Gallay M, Seigneuric A, Robichon F, and Baudouin JY. The development of facial emotion recognition: The role of configural information. *Journal of Experimental Child Psychology*, 97(1): 14–27, 2007.

Farah MJ, Wilson KD, Drain HM, and Tanaka JR. The inverted face inversion effect in prosopagnosia – Evidence for mandatory, face-specific perceptual mechanisms. *Vision Research*, 35(14): 2089–2093, 1995.

de Gelder B and Rouw R. Structural encoding precludes recognition of face parts in prosopagnosia. *Cognitive Neuropsychology*, 17(1–3): 89–102, 2000.

de Gelder B, Bachoud-Levi AC, and Degos JD. Inversion superiority in visual agnosia may be common to a variety of orientation polarised objects besides faces. *Vision Research*, 38(18): 2855–2861, 1998.

Hamsher K, Levin HS, and Benton AL. Facial recognition in patients with focal brain lesions. *Archives of Neurology*, 36(13): 837–839, 1979.

Inoue S, Kondoh T, Nishihara M, Hosoda K, and Kohmura E. Transient prosopagnosia after removal of a tumor in the right occipito-temporal cortex: A case report. *Neurological Surgery*, 36(11): 1023–1027, 2008.

Jacques C and Rossion B. Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans. *NeuroImage*, 36(3): 863–876, 2007.

Kucharska-Pietura K and David AS. The perception of emotional chimeric faces in patients with depression, mania and unilateral brain damage. *Psychological Medicine*, 33(4): 739–745, 2003.

Leder H and Bruce V. When inverted faces are recognised: The role of configural information in face recognition. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, 53A: 513–536, 2000.

Leehey SC, Carey S, Diamond R, and Cahn A. Upright and inverted faces: The right hemisphere knows the difference. *Cortex*, 14: 411–419, 1978.

Levy J, Heller W, Banich MT, and Burton LA. Asymmetry of perception in free viewing of chimeric faces. *Brain and Cognition*, 2: 404–419, 1983.

Luh KE. Effect of inversion on perceptual biases for chimeric faces. *Brain and Cognition*, 37(1): 105–108, 1998.

Marotta JJ, Genovese CR, and Behrmann M. A functional MRI study of face recognition in patients with prosopagnosia. *NeuroReport*, 12(8): 1581–1587, 2001.

Marotta JJ, McKeeff TJ, and Behrmann M. The effects of rotation and inversion on face processing in prosopagnosia. *Cognitive Neuropsychology*, 19(1): 31–47, 2002.

Meadows JC. The anatomical basis of prosopagnosia. *Journal of Neurology, Neurosurgery and Psychiatry*, 37(5): 489–501, 1974.

Parente R and Tommasi L. A bias for the female face in the right hemisphere. *Laterality*, 13(4): 374–386, 2008.

Passarotti AM, Smith J, DeLano M, and Huang J. Developmental differences in the neural bases of the face inversion effect show progressive tuning of face-selective regions to the upright orientation. *NeuroImage*, 34(4): 1708–1722, 2007.

Prkachin GC. The effects of orientation on detection and identification of facial expressions of emotion. *British Journal of Psychology*, 94: 45–62, 2003.

Rhodes G. Configural coding, expertise, and the right hemisphere advantage for face recognition. *Brain and Cognition*, 22: 19–41, 1993.

Rossion B, Delvenne JF, Debatisse D, Goffaux V, Bruyer R, Crommelinck M, et al. Spatio-temporal localisation of the face inversion effect: An event-related potentials study. *Biological Psychology*, 50(3): 173–178, 1999.

Rouw R and de Gelder B. Impaired face recognition does not preclude intact whole face perception. *Visual Cognition*, 9(6): 689–718, 2002.

Schiltz C, Sorger B, Caldara R, Ahmed F, Mayer E, Goebel R, et al. Impaired face discrimination in acquired prosopagnosia is associated with abnormal response to individual faces in the right middle fusiform gyrus. *Cerebral Cortex*, 16(4): 574–586, 2006.

Smith SD and Bulman-Fleming MB. Hemispheric asymmetries for the conscious and unconscious perception of emotional words. *Laterality*, 11(4): 304–330, 2006.

Uttner I, Bliem H, and Danek A. Prosopagnosia after unilateral right cerebral infarction. *Journal of Neurology*, 249(7): 933–935, 2002.

Warrington EK and James M. An experimental investigation of facial recognition in patients with unilateral cerebral lesions. *Cortex*, 3: 317–326, 1967.

Wildgruber D, Riecker A, Hertrich I, Erb M, Grodd W, Ethofer T, et al. Identification of emotional intonation evaluated by fMRI. *NeuroImage*, 24(4): 1233–1241, 2005.

Workman L, Chilvers L, Yeomans H, and Taylor S. Development of cerebral lateralisation for recognition of emotions in chimeric faces in children aged 5 to 11. *Laterality*, 11(6): 493–507, 2006.

Wright H, Wardlaw J, Young AW, and Zeman A. Prosopagnosia following nonconvulsive status epilepticus associated with a left fusiform gyrus malformation. *Epilepsy and Behavior*, 9(1): 197–203, 2006.

Yin RK. Looking at upside-down faces. *Journal of Experimental Psychology*, 81(1): 141–145, 1969.

Yin RK. Face recognition by brain injured patients: A dissociable ability? *Neuropsychologia*, 8: 395, 1970.

Please cite this article in press as: Victoria J. Bourne, Examining the effects of inversion on lateralisation for processing facial emotion, Cortex (2010), doi:10.1016/j.cortex.2010.04.003