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Lateralised repetition priming for featurally and configurally manipulated familiar faces: Evidence for differentially lateralised processing mechanisms

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Although early research suggested that the right hemisphere was dominant for processing faces, more recent studies have provided evidence for both hemispheres being involved, at least to some extent. In this experiment we examined hemispheric specialisations by using a lateralised repetition-priming paradigm with selectively degraded faces. Configurally degraded prime faces produced negative priming when presented to the left visual field (right hemisphere) and positive priming (facilitation) when presented to the right visual field (left hemisphere). Featurally degraded prime faces produced the opposite pattern of effects: positive priming when presented to the left visual field (right hemisphere) and negative priming when presented to the right visual field (left hemisphere). These results support the proposal that each hemisphere is differentially specialised for processing distinct forms of facial information: the right hemisphere for configural information and the left hemisphere for featural information.

Keywords: Hemispheric specialisations; Face recognition; Repetition priming.

Prosopagnosia was originally thought to result from unilateral right hemisphere lesions (e.g., De Renzi & Spinnler, 1966; Marotta, McKeeff, & Behrmann, 2002). However, Damasio, Damasio, and VanHosen (1982) suggested that prosopagnosic patients typically suffer from bilateral lesions. This is supported in a number of more recent case studies (e.g., Barton, Press, Keenan, & O'Connor, 2002; Boutsen & Humphreys, 2002; Farah, Rabinowitz, Quinn, & Liu, 2000). Cases of prosopagnosia have also been reported following unilateral left hemisphere lesions (e.g., Benke, 1988; McNeil & Warrington, 1993; Meadows, 1974). Consequently it has been

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suggested that unilateral lesions only cause selective impairments and that bilateral lesions are necessary to cause complete disruption to face processing and recognition abilities (Boeri & Salmaggi, 1994; Warrington & James, 1967). Each hemisphere may be specialised for processing different types of facial information, the right hemisphere being dominant and specialised for processing configural (or holistic) facial information, and the left hemisphere more subordinate and being specialised for processing featural (or piecemeal) facial information. This is consistent with the suggestion that faces are processed more on the basis of their configural information than their featural information (Collishaw & Hole, 2000).

The idea that each hemisphere is specialised for processing different types of information is supported by data from prosopagnosic patients. Yin (1970) compared recognition of upright and inverted faces in patients with unilateral lesions and non-clinical controls. He found that only patients with unilateral right hemisphere lesions showed impaired performance when recognising upright faces, which would typically be processed on the basis of the configural information contained within them. Furthermore, patients with unilateral right hemisphere lesions typically show a greater reliance on featural information within faces (Marotta et al., 1999; Uttner, Bleim, & Danek, 2002), which suggests the recruitment of left hemisphere mechanisms. Additionally, Marotta et al. (1999) showed atypical left hemisphere activation in one such patient when viewing faces.

Behavioural studies on non-clinical participants also support a dual-route interpretation. A number of studies have used the divided visual field methodology (see Bourne, 2006) to present faces that have had either their configural or featural information degraded. Studies using face inversion, which encourages featural processing, have shown reduced left visual field (right hemisphere) superiority for the task (e.g., Leehey, Carey, Diamond, & Cahn, 1978; Rhodes, 1993). Studies that manipulated the featural information within a face have found that featural substitution disproportionately impairs left hemisphere processing, while featural displacement disproportionately impairs right hemisphere processing (e.g., Fairweather, Brizzolara, Tabossi, & Umiltà, 1982; Hillger & Koenig, 1991; Sergent, 1982).

Supporting evidence from non-clinical participants has also been acquired using neuroimaging methods. ERP studies have found greater activation in the right hemisphere when viewing upright faces and greater activation in the left hemisphere when viewing inverted faces (McCarthy, Puce, Belger, & Allison, 1999; Rossion et al., 1999). In a PET study, Rossion et al. (2000) found greater activity in the right hemisphere when processing the whole face and greater activity in the left hemisphere when processing individual features. ERP evidence with infants suggests that this hemispheric specialisation is evident from the age of 8 months (Scott & Nelson, 2006).

Overall, there seems to be a fair amount of evidence for the existence of two distinct and differently lateralised face-processing mechanisms: one in the right hemisphere, specialised for processing configural facial information, and one in the left hemisphere, specialised for processing featural information. In this paper we present an experiment that addresses this issue by considering the processing of both configurally and featurally manipulated faces using an alternative methodology: a lateralised repetition-priming paradigm. This paradigm has been used previously to confirm the right hemisphere superiority for face recognition (Bourne & Hole, 2006) and has been replicated by Cooper, Harvey, Lavidor, and Schweinberger (2007). We also consider the distinct specialisations of each hemisphere within the same experiment, whereas much of the previous research examines either left or right hemisphere processing. Here, we use Bourne and Hole's (2006) lateralised repetition priming paradigm, but also include prime faces that have been manipulated. In one condition prime faces were blurred to reduce the featural information contained within them, while leaving the configural information relatively intact. It is predicted that right hemispheric priming will occur, whereas left hemisphere priming should be reduced. In the other condition a featural displacement manipulation was used so that the featural information contained within the face remained relatively unimpaired but the configural properties were disrupted. It is predicted that this manipulation should reduce the right hemisphere priming effect, but not the left hemisphere priming effect.

METHOD

Participants

A total of 70 students (22 males) from the University of Sussex participated (mean age = 22.5 years, $SD = 4.7$). All were right-handed by self-report and this was confirmed by a handedness questionnaire (adapted from Dorthe, Blumenthal, Jason, & Lantz, 1995).

Design

This experiment was completed in two phases: the prime phase and the target phase. There was a delay of approximately 3 minutes between phases, and the participants were not aware that the two phases were associated. In the prime phase participants were presented with 40 faces (20 famous and 20 unfamiliar), half of which were unmanipulated and half of which were manipulated. Half of the participants saw featurally manipulated (blurred) primes and the other half saw configurally manipulated (displaced features) primes. An equal number of faces were presented to the left visual field and the right visual field. In the target phase participants were presented with all 40 faces again. In this phase all faces were presented centrally and without manipulation. Stimuli were fully counterbalanced across conditions.

Stimuli

All faces were of white males, presented in greyscale against a white background. At the viewing distance used (30 cm) faces were about 4.4° wide. The blurred faces were created by using the Adobe Photoshop Gaussian Blur tool set to a blur level of 4 pixels (see Figure 1). The low-pass spatial frequency cut-off for blurred faces was around 15 cycles per face width (3.4 cycles per degree). The displaced features stimuli were created by selecting the eye, nose, and mouth areas of the face, removing the remainder of the face, and unsystematically moving each eye and the mouth by approximately 0.5°. Following the experiment participants completed a questionnaire, which contained all of the famous faces used in the experiment and 10 unfamiliar distractor faces. For each face participants had to indicate whether or not it was familiar to them (i.e., famous). Data for any faces that were not successfully classified as famous were excluded from subsequent analyses.

Procedure

This experiment used the divided visual field paradigm (see Bourne, 2006). It also follows the same procedure as experiment 1 of Bourne and Hole (2006), but with the addition of the manipulated prime faces. Participants sat in

Figure 1. Example stimuli showing an unmanipulated face (left), a blurred face (centre), and displaced features (right).

front of a computer with their head positioned on a chin rest to maintain a viewing distance of 30 cm. Each trial comprised four events (see Figure 2). First participants were presented with a "get ready" prompt for 2000 ms. They then saw a single uppercase consonant for 750 ms. This letter had to be verbally reported, to ensure that participants were fixating centrally when the stimulus face was presented. Any trials in which the letter was incorrectly reported, or in which reporting was delayed, were excluded from the analyses. Next the face was presented for 120 ms. In the prime phase of the experiment faces were unilaterally presented with the inside edge of the face presented 4° from the central fixation point. The duration and placement of stimuli presentation were chosen to maximise unilateral presentation of the stimuli (see Bourne, 2006). In the target phase of the experiment faces were presented at the central fixation point. Following stimulus presentation a backwards mask of greyscale overlapping circles was presented until participants had responded. Responses were made using a computer mouse. Half of the participants clicked the left button if they thought the face was famous and the right button if they thought it was not famous. The other half of the participants used the opposite pattern of responding. Between

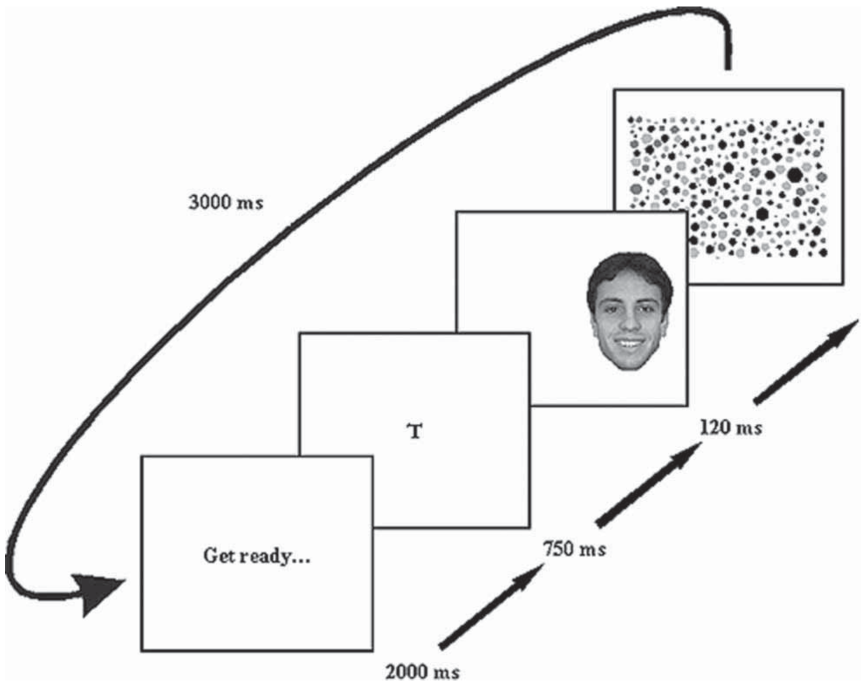

Figure 2. Trial summary representing a prime trial in which an unmanipulated face is presented to the right visual field (left hemisphere).

trials there was a 3000 ms interval. Before completing each phase of the experiment participants completed 10 practice trials. Stimuli were presented and randomised using Superlab 2.0. The randomisation varied for each phase of the experiment. Reaction times and accuracy were recorded.

RESULTS

Difference scores were analysed using 2 (visual field: left visual field vs right visual field) $\times$ 2 (condition: unmanipulated vs manipulated) $\times$ 2 (manipulation: blurring vs displaced features) mixed-design ANOVAs. Reaction times to famous and unfamiliar faces were analysed separately and difference scores were used in line with the analyses conducted by Bourne and Hole (2006). For the difference scores, a negative value represents a priming effect, or facilitation. Accuracy measured using d′ was also analysed. For full results of the ANOVAs see Table 1.

The main effect of visual field was significant, with greater priming from faces presented to the left visual field, $F(1, 68) = 10.0$, $p = .002$, partial $\eta^2 = .128$. The main effect of condition was significant, with greater priming from unmanipulated faces than manipulated faces, $F(1, 68) = 12.3$, $p = .001$, partial $\eta^2 = .153$. The main effect of manipulation, the interaction between condition and type of manipulation, and the interaction between visual field and condition were all non-significant (all Fs < 1). The interaction between visual field and type of manipulation was significant, $F(1, 68) = 9.3$, $p = .003$, partial $\eta^2 = .120$. Importantly, the three-way interaction (see Figure 3) between visual field, condition, and type of manipulation was also significant, $F(1, 68) = 9.9$, $p = .002$, partial $\eta^2 = .127$. For unmanipulated prime faces a significantly larger priming effect was found for participants in both manipulation conditions (blurred: $p = .006$; displaced features: $p = .005$). One-sample t-tests showed that significant priming occurred following unmanipulated prime faces presented to the left visual field, $t(69) = 5.4$, $p < .001$, but not following unmanipulated prime faces presented to the right visual field, $t(69) = 0.7$, $p = .510$.

For the participants who were presented with blurred prime faces there was a significant difference between prime faces presented to each visual field ($p = .001$). One-sample t-tests showed a significant priming effect when blurred primes were presented to the left visual field, $t(34) = 3.1$, $p = .002$, but a significant negative priming effect when presented to the right visual field, $t(34) = 2.51$, $p = .009$. For the participants who were presented with displaced feature prime faces there was a marginally significant difference between prime faces presented to each hemisphere ($p = .054$). One-sample t-tests showed a significant negative priming effect when displaced feature

TABLE 1
Summary of F values for all analyses conducted

	Visual field analyses			Hemispheric specialisation analyses		
	Famous face reaction time analyses	*Not-famous face reaction time analyses*	*d′ accuracy analyses*	*Famous face reaction time analyses*	*Not-famous face reaction time analyses*	*d′ accuracy analyses*
VF/hemisphere	***10.0***	0.1	0.5	***23.6***	0.8	1.1
Condition	***12.3***	1.5	1.0	***12.3***	1.5	1.0
Manipulation	0.1	***4.2***	0.6	0.1	***4.2***	0.6
VF/hemisphere * condition	2.3	1.4	3.2	0.8	0.2	1.7
VF/hemisphere * manipulation	***9.3***	0.1	0.2	0.5	0.8	0.1
Condition * manipulation	0.2	0.6	1.4	0.3	0.6	1.4
Three way interaction	***9.9***	0.8	0.5	1.0	0.1	0.9

VF = visual field; condition = whether a manipulation was applied or not; manipulation = type of manipulation applied. Significant effects are italicised and bold. Degrees of freedom = 1, 68 for all.

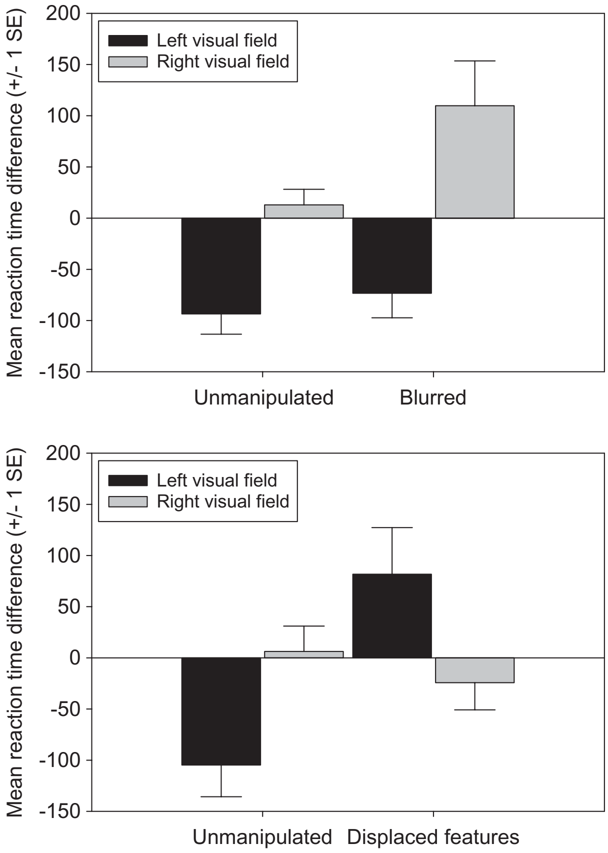

Figure 3. Mean reaction time differences (± 1 *SE*) for famous face stimuli as a function of visual field of presentation. Top: data for participants shown blurred prime faces; bottom: data for participants shown displaced feature primes.

primes were presented to the left visual field, $t(34) = 1.79$, $p = .042$, but not when presented to the right visual field, $t(34) = 0.92$, $p = .182$.

Comparable analyses were run on the reaction time differences to not-famous faces. No main effects and interactions were significant, other than the main effect of type of manipulation, $F(1, 68) = 4.2$, $p = .044$, partial $\eta^2 = .058$, showing more priming from blurred than displaced feature primes. This is consistent with configural information being more important than featural information when processing faces (Collishaw & Hole, 2000). No effects were significant for the accuracy analyses.

An alternative method of analysis is also possible in terms of whether the prime face is presented to the hemisphere that is specialised for processing that particular type of face or not. For unmanipulated and blurred prime faces, primes presented to the left visual field will be presented to the specialised right hemisphere. For displaced feature prime faces, primes presented to the right visual field will be presented to the specialised left hemisphere. A second set of analyses were conducted using 2 (hemisphere: specialised vs not specialised) $\times$ 2 (condition: unmanipulated vs manipulated) $\times$ 2 (manipulation: blurring vs displaced features) mixed design ANOVAs (see Table 1).

For reaction times to famous faces there was a significant main effect of hemisphere, with greater priming from primes presented to the specialised hemisphere, $F(1, 68) = 23.7$, $p < .001$, partial $\eta^2 = .258$. The main effect of whether a manipulation was applied or not was also significant, with more priming from unmanipulated faces, $F(1, 68) = 12.3$, $p = .001$, partial $\eta^2 = .153$. No other main effects and interactions were significant. Importantly, the interaction between hemisphere and the type of manipulation applied was not significant. This suggests that the magnitude of the negative priming effect in the non-specialised hemisphere is comparable to that in the specialised hemisphere, even though each type of manipulation affects a different hemisphere. All effects were not significant for the not famous reaction time analyses and the d′ analyses, other than a significant main effect of type of manipulation in the not-famous analyses, again showing more priming from blurred than displaced feature primes.

DISCUSSION

A clear left visual field (right hemisphere) priming effect was found for the unmanipulated faces, whereas no priming was found for unmanipulated prime faces presented to the right visual field (left hemisphere). This finding replicates Bourne and Hole (2006, exp. 1). In terms of the manipulated prime faces, similar results were found for each manipulation. When the prime face was presented to the hemisphere specialised for processing the relatively intact form of facial information (e.g., a blurred face prime to the right hemisphere), the priming effect was only slightly reduced. In contrast, when a manipulated prime face was presented to the hemisphere specialised for processing the degraded form of information (e.g., a blurred face prime to the left hemisphere) negative priming was found: participants were slower to respond to manipulated target faces than to unmanipulated primes.

Overall, the findings of this study support those of previous research on hemispheric specialisations in face processing, from clinical populations (Marotta et al., 1999; Uttner et al., 2002, Yin, 1970), behavioural divided visual field studies (Fairweather et al., 1982; Hillger & Koenig, 1991; Leehey et al., 1978; Rhodes, 1993; Sergent, 1982), and neuroimaging studies

(McCarthy et al., 1999; Rossion et al., 1999, 2000; Scott & Nelson, 2006). However, a rather unexpected finding for both manipulations was that negative priming occurred when a manipulated prime face was presented to the hemisphere that is specialised for processing the degraded information. It is therefore important to consider how this effect might have occurred.

One of the most influential models of person recognition is the interactive activation and competition model (IAC; Burton, 1994; Burton & Bruce, 1993; Burton, Bruce, & Hancock, 1999; Burton, Bruce, & Johnston, 1990). The model comprises units arranged in pools: face recognition units (FRUs), personal identity nodes (PINs), and semantic information units (SIUs) connected by excitatory (positive) links (for a detailed description of the IAC, see Burton et al., 1999). The IAC simulates repetition priming by strengthening the links between the FRU and its corresponding PIN, using a simple Hebbian learning mechanism. The model shows a significant decrease in the recognition latency for a familiar face when it is primed by the same image of the familiar face or by a different image of the same face, in comparison to unprimed faces. This pattern of responses is consistent with our results in the unmanipulated condition, when the primes were presented to the left visual field (right hemisphere) and reaction times to target faces were reduced. However, it is difficult to account for our finding of negative priming within the IAC model, since this would imply that the strength of the links between the FRU and PIN is decreased to below the level of the unprimed ones. This seems like an unlikely explanation.

The negative priming effect might be explained in terms of interhemispheric transfer. An interhemispheric repetition priming effect for familiar faces has been shown in previous research. Bourne and Hole (2006) found asymmetric interhemispheric transfer, with more transfer occurring from the right hemisphere to the left hemisphere. This was interpreted as the more-specialised hemisphere aiding the processing of faces by the less-specialised hemisphere. It is possible that the negative priming found in this experiment reflects interhemispheric transfer between the hemispheres in an attempt to aid processing. However, given that all target faces were presented bilaterally it is not possible to draw any firm conclusions with regard to the possible role of interhemispheric priming.

It is also important to consider whether methodological factors may have influenced the results. One issue that it is very important to acknowledge is the way in which we manipulated the faces. It is probably impossible to manipulate a face so that one form of facial information is completely removed while leaving the other form of facial information entirely intact. For example, blurring a face also slightly reduces the configural information within it, for example making the distance between features less precise. However, this issue is a rather general one and can probably be applied to almost any research using facial manipulations (see review in Rakover, 2002). While we accept this limitation, it is fair to claim that each manipulation disproportionately impairs one form of information compared to the other. This is supported by our finding that each manipulation showed different patterns of lateralised priming that were consistent with our predictions.

Another methodological issue is that the same image of the face was used as a prime and target, albeit in a manipulated form as the target face. This raises the possibility that we examined picture priming rather than face priming per se. However, this is unlikely to account for our findings for a number of reasons. First, no priming effect was found for the unfamiliar faces. This is a vitally important finding within this experiment. If the identified effects were purely picture priming then the effect should have been the same for both familiar and unfamiliar faces. Therefore the lack of priming for unfamiliar faces provides strong support for our results reflecting hemispheric specialisations in *face* processing. Second, for both the manipulated and the unmanipulated faces the priming effects were as predicted on the basis of our existing understanding of hemispheric specialisations in face processing. Therefore the effects are more congruent with the predicted effects of face priming than of picture priming, which would predict more symmetrical priming effects. Finally, Cooper et al. (2007) contrasted lateralised repetition priming with familiar face stimuli, using either the same image or different images of the person as prime and target stimuli. They found that using different images of the same person further enhanced the priming effect. It is therefore possible that our findings are actually an underestimation of the underlying hemispheric specialisations.

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