

Examining the hemispheric distribution of semantic information using lateralised priming of familiar faces

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ABSTRACT

The way in which the semantic information associated with people is organised in the brain is still unclear. Most evidence suggests either bilateral or left hemisphere lateralisation. In this paper we use a lateralised semantic priming paradigm to further examine this neuropsychological organisation. A clear semantic priming effect was found with greater priming occurring when semantically related prime faces were presented to the left visual field than when presented to the right visual field. Possible explanations for this finding are discussed in terms of the bilateral distribution of different classes of semantic information, a possible role of associative processes within semantic priming and interhemispheric transfer.

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1. Introduction

When we see a familiar face we are very quickly able to access and retrieve semantic information that we associate with that person. Through the use of semantic priming paradigms we have been able to gain greater insights into the psychological processes underlying the storage and retrieval of semantic information; however it is still unclear how this information may be organised in the brain.

In the last 20 years a plethora of studies have focused on the phenomena of semantic (associative) face priming¹ (see Barry, Johnston, & Scanlan, 1998; Bruce & Valentine, 1986; McNeill & Burton, 2002). One strand of this research has taken a more biologically based approach to face priming (Schweinberger, 1996; Schweinberger, Pfütze, & Sommer, 1995). In these studies within-domain (face–face) and cross-domain (name–face) associative priming were examined, recording both reaction times and event-related brain potentials (ERPs). The ERP modulations due to priming for faces and names were found to be topographically equivalent, so Schweinberger concluded that associative priming effects are independent of the nature of the primes (names or faces).

Two models have been proposed which consider how the various aspects of face processing might be differently lateralised (Ellis, 1983; Rhodes, 1985). While a great deal of research has examined the lateralisation of face processing since these models were proposed, no updated models that explicitly consider hemispheric

asymmetries have been suggested (although see Haxby, Hoffman, & Gobbini, 2000). Both the Ellis and Rhodes models propose different patterns of lateralisation for the perceptual and semantic aspects of face processing with the perceptual aspects lateralised to the right hemisphere and the semantic aspects showing either bilateral or more left hemisphere distribution. A considerable amount of evidence is consistent with the perceptual aspects of face processing being lateralised to the right hemisphere. For example, prosopagnosia most typically occurs following right hemisphere lesions (e.g., De Renzi, Faglioni, & Scotti, 1968; Marotta, McKeef, & Behrmann, 2002). Selective right hemisphere activation has also been found using a variety of functional neuroimaging techniques (e.g., Bentin & Deouell, 2000; Dubois et al., 1999; McCarthy, Puce, Gore, & Allison, 1997) and behavioural divided visual field techniques (e.g., Bourne & Hole, 2006; Hillger & Koenig, 1991).

Research regarding the lateralisation of semantic information is rather more contradictory. Evidence taken from clinical patients tends to support the suggestion of left hemisphere superiority. For example, patients who suffer from unilateral left hemisphere lesions have been found to be impaired at accessing semantic information, whereas those suffering from comparable right hemisphere lesions are able to accurately retrieve such information (e.g., Warrington & Taylor, 1978). Further, Sergent and Villemure (1989) report the case of a right hemisphere hemidecorticate whose face processing abilities were disrupted, but who was still able to access semantic information about people and their names. This evidence from clinical case studies suggests that semantic information is lateralised to the left hemisphere; however evidence from non-clinical participants has provided somewhat contradictory evidence. Two studies have considered patterns of lateralisation using a behavioural divided visual field task in which

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¹ Although the terms 'associative' and 'semantic' are often used to describe the same phenomenon the mechanism underlining the formation of associations is still under debate (see discussion).

familiar faces are presented to either visual field and participants have to make a semantic decision regarding the persons' occupation (Kampf, Nachson, & Babkoff, 2002; Sergent, Ohta, & Macdonald, 1992). Sergent et al. (1992) found a right visual field advantage for both speed and accuracy of responding, indicating a left hemisphere advantage that is in line with the clinical evidence. In contrast, Kampf et al. (2002) found no visual field effects, suggesting that semantic information is distributed bilaterally. This bilateral distribution is supported by a study using event related potentials (Huddy, Schweinberger, Jentzsch, & Burton, 2003). However, two positron emission tomography studies have found a different pattern of distribution, with activation asymmetrically spread across both hemispheres with slightly more activation in the right hemisphere (Sergent & Signoret, 1992; Sergent et al., 1992). It therefore seems that the lateralisation organisation of semantic information associated with faces is unclear.

Studies attempting to understand the lateralisation of semantic information within the linguistic domain have utilised lateralised priming paradigms (e.g., Abernethy & Coney, 1996; Collins, 1999; Koivisto & Hämäläinen, 2002). In these studies semantic prime words are presented either to the left visual field, which is initially received and processed by the right hemisphere, or to the right visual field, which is initially received and processed by the left hemisphere. Such studies have shown that greater semantic priming occurs when primes are presented to the right visual field (left hemisphere) than when primes are presented to the left visual field (right hemisphere). This asymmetric effect is interpreted in terms of the left hemispheric specialisation for processing linguistic stimuli and has been supported by ERP studies using lateralised semantic word priming (Atchley & Kwasny, 2003; Bouaffre & Faita-Ainseba, 2007). More recently the research in this area has examined two issues: first whether each hemisphere is specialized for processing different types of semantic information (Beeman & Bowden, 2000; Beeman, Bowden, & Gernsbacher, 2000; Bowden & Beeman, 1998; Drews, 1987; Koivisto, 1998; Koivisto & Laine, 2000) and second, asymmetric effects of stimulus onset asynchronies (SOAs; Bouaffre & Faita-Ainseba, 2007; Chiarello, Liu, Shears, Quan, & Kacinik, 2003).

Only two studies have used a lateralised priming paradigm with face stimuli, both of which have used repetition priming (Bourne & Hole, 2006; Cooper, Harvey, Lavidor, & Schweinberger, 2007). In each of these studies prime faces presented to the left visual field (right hemisphere) produced a greater priming effect than prime faces presented to the right visual field (left hemisphere). This is consistent with the suggestion that the perceptual aspects of face processing are lateralised to the right hemisphere. However, as it is less clear how semantic information associated with faces is lateralised; the use of a lateralised semantic priming paradigm might provide some insights. In this paper we present an experiment which uses a divided visual field lateralised semantic priming paradigm with faces in an attempt to further understand and clarify the way in which semantic information is organised in the brain. Two possible outcomes are predicted. If semantic information is symmetrically distributed then a semantic priming effect should occur for primes presented to either hemisphere. If semantic information is more lateralised to the left hemisphere then a greater semantic priming effect should be found for right visual field primes than left visual field primes.

2. Methods

2.1. Participants

Thirty participants (12 males) completed the experiment. All were right handed by self report and this was confirmed with a

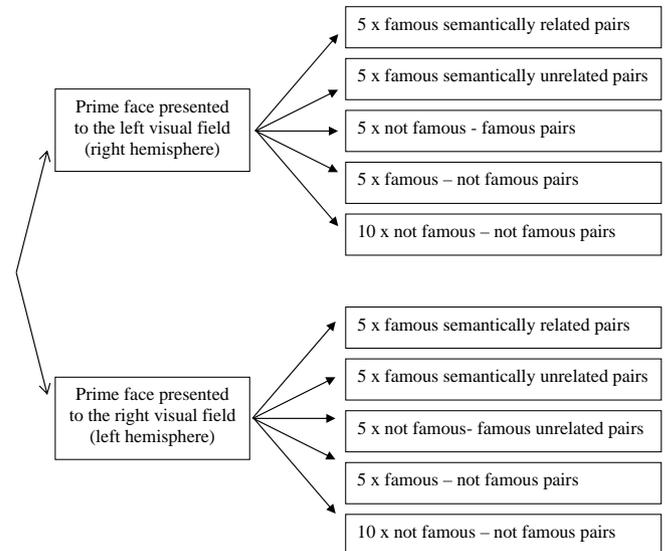


Fig. 1. Summary of the experimental design.

handedness questionnaire (adapted from Dorthé, Blumenthal, Jason, & Lantz, 1995). Mean age was 21 years ($SD = 4.8$).

2.2. Stimuli and procedure

Stimuli comprised sixty famous and sixty unfamiliar faces. Faces were of white males and females, presented in greyscale against a white background and subtended about 6.5° horizontally and 8° vertically. Face pairs² were presented in five priming conditions (see the Appendix for details of famous face pairs): famous–famous semantically related primes (FFr); famous–famous semantically unrelated pairs (FFu); not famous–famous pairs (NF); famous–not famous pairs (FN); not famous–not famous pairs (NN). Hence, we have one experimental condition in which semantic priming is expected to occur (FFr) and two control conditions where no semantic priming should occur (FFu and NF). The FN and NN conditions were included to enable a familiarity decision to be made. Within each prime condition half of the prime faces were presented to the left visual field and half to the right visual field (see Fig. 1). Five trials were presented in each condition, other than in the NN condition where ten trials were presented to balance the number of famous and not famous target faces. While we acknowledge that this is a rather limited number of trials per condition, this decision was based on our previous experience with running such experiments. It is important to ensure that the majority of the familiar faces will be recognised by all participants. If the number of familiar faces included were raised the number of ‘missed’ due to the inclusion of unknown famous faces would also rise substantially. Therefore it is unlikely that an increased number of trials would increase the number of data points. Further, this would increase the number of ‘unfamiliar’ responses and potentially risk a response bias.

Participants were seated centrally at a computer with their head placed in a chin rest to minimise head movements. Each trial included six events (see Fig. 2) based on the divided visual field paradigm (see Bourne, 2006). First participants were presented with a ‘Get ready...’ prompt for 1500 ms. A single uppercase consonant was then presented centrally for 750 ms. Participants had

² The faces pairs that we used were related both in terms of associative and categorical relatedness. A detailed consideration of the distinction between these types of relations is given in the discussion.

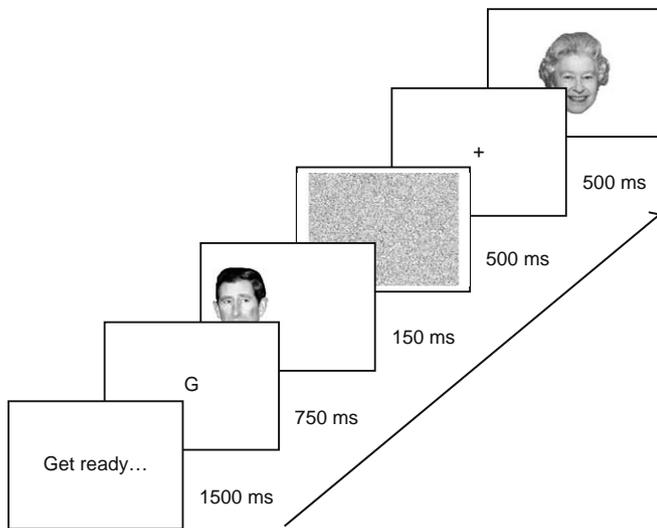


Fig. 2. Trial summary representing a left visual field semantically related prime trial.

to verbally report this uppercase consonant in order to ensure that they were fixating centrally when the lateralised prime was presented. If the digit was incorrectly reported or reporting was delayed the trial was excluded from the analyses ($n = 3$). The prime face was then presented for 150 ms, with the inside edge 4° from the central fixation point. Participants were instructed to take notice of this rapidly presented face, but not to respond to it. A backwards random noise mask was then presented for 500 ms, followed by a central fixation cross for a further 500 ms. The target face was then presented centrally until the participant responded. Participants were asked to respond, as quickly but as accurately as possible, whether the face was familiar to them (i.e., famous) or not. Six practice trials were completed. Responses were made on a Cedrus RB-380 response pad. For half of the participants pressing any of the leftward buttons indicated that the face was familiar and pressing any of the rightward buttons indicated that the face was unfamiliar. The rest of the participants used the opposite pattern of responding. Stimuli presentation was controlled and randomised using Superlab 4. Stimuli were fully counterbalanced across conditions.

Following the semantic priming experiment participants completed two further short experiments. First they were presented with all of the faces used in the experiment and asked to classify them as either famous or not famous. Any errors made, either false alarms ($M = 1.1$, $SD = 1.4$) or misses ($M = 2.3$, $SD = 2.7$), were recorded. Second they were presented with the famous–famous pairs and asked to rate on a visual analogue scale how semantically related the pairs were. The scale ran from -250 indicating ‘not at all’ to $+250$ indicating ‘very much’. There was a significant difference between the relatedness ratings for the related and unrelated pairs ($t(29) = 24.2$, $p < .001$; see the Appendix for ratings for each famous face pair). Ratings were significantly higher for related pairs ($M = 190.1$, $SD = 46.6$) than unrelated pairs ($M = -203.1$, $SD = 58.4$). Further to this, ratings were significantly different from 0 for both related pairs ($t(29) = 22.4$, $p < .001$) and unrelated pairs ($t(29) = -19.0$, $p < .001$). These analyses suggest that our semantic relatedness manipulation was successful.

2.3. Statistical analyses

Accuracy (percentage correct) and mean reaction time data were analysed using 3 (condition: FFr, FFu, NF) \times 2 (visual field:

Table 1

Mean (SD) accuracy as a percentage correct and mean (SD) reaction times in ms across all five conditions as a function of visual field of prime presentation

	Accuracy		Reaction times	
	LVF/RH	RVF/LH	LVF/RH	RVF/LH
Famous–famous related	95.3 (10.1)	97.3 (8.9)	744.0 (259.8)	795.0 (260.1)
Famous–famous unrelated	96.0 (9.7)	92.7 (12.3)	842.8 (320.7)	812.9 (241.8)
Not famous–famous	92.7 (9.8)	92.0 (14.5)	850.7 (297.6)	863.6 (275.1)
Famous–not famous	95.3 (11.4)	93.3 (9.6)	968.3 (442.6)	891.6 (362.1)
Not famous–not famous	96.3 (7.2)	97.0 (5.3)	928.5 (443.4)	904.4 (399.9)

LVF, RVF) repeated measures ANOVAs. Accuracy and reaction times across all five conditions are presented in Table 1. Conditions were only analysed for which participants were responding to famous faces. Reaction times were removed from the analyses if the response was incorrect, if they were faster than 300 ms or longer than 3000 ms. Analyses were also conducted after removing the familiarity and relatedness post test errors. Removal of either type of error or simultaneously removing both types did not influence the analyses, therefore these data were included to maximise the number of data points analysed. All main effects and interactions were analysed using planned pairwise comparisons.

3. Results

Accuracy differed significantly across the three different priming conditions ($F(2,28) = 4.1$, $p = .014$, partial $\eta^2 = .226$). Mean accuracy in the FFr condition was 96.3% ($SD = 1.3$). This was not significantly different from accuracy in the FFu condition ($M = 94.3$, $SD = 1.6$; $p = .149$) but significantly higher than accuracy in the NF condition ($M = 92.3$, $SD = 1.6$; $p = .004$). There was no significant difference in accuracy between the FFu and NF conditions ($p = .182$). The main effect of visual field was not significant ($F(1,29) = .2$, $p = .344$, partial $\eta^2 = .006$) nor was the condition \times visual field interaction ($F(2,28) = 1.5$, $p = .125$, partial $\eta^2 = .094$).

There was a significant main effect of condition on reaction times ($F(2,28) = 14.2$, $p < .001$, partial $\eta^2 = .504$). Participants responded significantly faster to stimuli in the FFr condition than in both the FFu condition ($p = .009$) and the NF condition ($p < .001$). There was no significant difference between the FFu and NF conditions ($p = .105$). The main effect of visual field was not significant ($F(1,29) = .4$, $p = .277$, partial $\eta^2 = .012$). The condi-

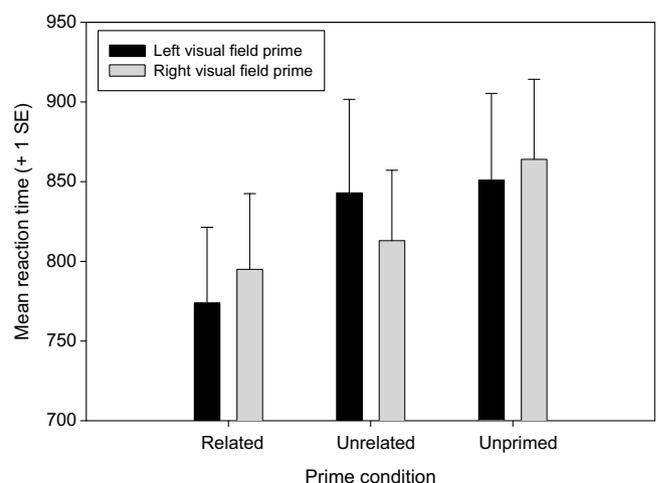


Fig. 3. Mean reaction times (+1SE) to familiar target faces as a function of semantic priming condition and visual field of prime presentation.

tion \times visual field interaction was approaching significance ($F(2, 28) = 1.9, p = .084$, partial $\eta^2 = .120$). Inspection of the means (see Fig. 3) suggests that this may result from visual field differences between the FFr and FFu conditions. This 2 (visual field: LVF, RVF) \times 2 (condition: FFr, FFu) interaction is significant ($F(2, 28) = 3.9, p = .029$, partial $\eta^2 = .120$). Participants responded significantly faster ($p = .004$) to target faces in the FFr condition than in the FFu condition when the prime faces was presented to the left visual field (right hemisphere). When the prime face was presented to the right visual field (left hemisphere) there was no significant difference between the conditions ($p = .254$).

4. Discussion

The aim of this experiment was to examine the lateralisation of semantic information using a lateralised priming paradigm. We predicted that we would either find a left hemisphere superiority priming effect, or priming from both hemispheres reflecting bilateral distribution. Instead, we found more evidence of semantic priming from left visual field (right hemisphere) primes than from right visual field (left hemisphere) primes. This suggests that the semantic information associated with faces may be stored within the right hemisphere. Given that this finding is in contrast to our original predictions, it is interesting to consider how this result might have occurred.

It has been shown that the semantic information associated with faces is distributed bilaterally across the brain (Huddy et al., 2003; Kampf et al., 2002; Sergent & Signoret, 1992; Sergent et al., 1992). One possibility is that different aspects of semantic information are differentially lateralised and that our semantic priming task required the types that are more lateralised to the right hemisphere. Contrasting two case studies, Thompson et al. (2004) showed a double dissociation between person specific and general semantic knowledge. Person specific semantic information was selectively impaired following right temporal atrophy and general semantic knowledge was selectively impaired following left temporal atrophy. These findings are in line with our own suggesting right hemisphere dominance for the semantic information associated with people. This raises the interesting possibility of different types of semantic information being asymmetrically organised. The exact manner in which this reflects person specific semantic information requires further examination.

An alternative explanation is that the right hemisphere priming found here does not reflect a purely semantic effect. The right hemisphere priming effect found in this study may somehow reflect perceptual components of semantic priming. While some have argued that perceptual processes may be involved in semantic priming (Carson & Burton, 2001; Vladeanu, Lewis, & Ellis, 2006), others maintain that there is no perceptual component (Barry et al., 1998; Schweinberger, 1996). While it is unclear whether, or to what extent, perceptual and semantic components of processing may interact, it seems unlikely that a purely perceptual account could explain our findings.

It is also possible that the results may be explained in terms of interhemispheric transfer. Within the divided visual field paradigm, stimuli presented to one visual field are *initially* received and processed by the contralateral hemisphere, but it is likely that information is subsequently passed between the hemispheres. The SOA in this experiment was relatively long at 1000 ms, however such SOAs have been frequently used and have been shown to induce larger semantic priming effects than shorter SOAs of 250 and 750 ms (Bruce & Valentine, 1986). Chiarello et al. (2003) found that longer SOAs reduced the hemispheric asymmetries found through lateralised semantic word priming. It is possible that a more strongly lateralised effect may be found with reduced SOAs. One

implication of a long SOA is that information may be passed between the hemispheres via the corpus callosum. Bourne and Hole (2006) used lateralised repetition priming with familiar faces and found evidence for interhemispheric transfer occurring. It would be interesting to replicate the present experiment using semantic priming between visual fields to consider whether interhemispheric transfer may contribute to the effects found. Further, if semantic information is distributed bilaterally it is predicted that any interhemispheric effect would be symmetrical, whereas if semantic information is lateralised (to either hemisphere) then an asymmetric priming effect might be predicted.

An interesting explanation of the lateralised priming effect presented in this paper is offered by the transcortical cell assemblies (TCA) hypothesis (Pulvermuller & Mohr, 1996). This theory proposes that cell assemblies are distributed across the two hemispheres, possibly asymmetrically, with interhemispheric links between them. Evidence seems to suggest that the highly specialised populations of neurons are dedicated to face processing (e.g., Bentin & Deouell, 2000; Dubois et al., 1999; McCarthy et al., 1997). These are organised in clusters of interconnected neural cells, located across both hemispheres, although asymmetrically with more cells located in the right hemisphere than in the left hemisphere. Our finding that semantic priming showed right hemisphere superiority may be explained in terms of spreading activation across this network to the more dominant right hemisphere cell assemblies.

One possible limitation of this study is the way in which the semantically related familiar faces were paired. Although the face pairs used in this study were all semantically related, it is possible that there were different types of semantic relations between faces, primarily in terms of distinguishing between category membership and co-occurrence. It is very difficult to control the type of relatedness (i.e., a purely semantic relation vs. co-occurrence-based association) in real familiar people, simply because there is often overlap between these two types of relatedness. The pairs of faces used in this study are semantically related, but some are associated (to differing degrees), some are categorically related (they belong to the same group) and some are both associatively and categorically related. Within our data set it is impossible to statistically consider this. However it is interesting to consider how such a distinction might influence the hemispheric asymmetries found. Beeman and colleagues (Beeman & Bowden, 2000; Beeman et al., 2000; Bowden & Beeman, 1998) proposed that the left hemisphere is specialised for fine semantic coding and the right hemisphere is specialised for coarse semantic coding. Further, it has been suggested that the left hemisphere is specialised for processing categorical relationships and the right hemisphere is specialised for processing associative relationships (Drews, 1987). However, Bouaffre and Faita-Ainseba (2007) found bilateral patterns for associatively related word pairs but right hemisphere superiority for processing categorically related word pairs. It is possible that different patterns of lateralisation might be found if the present experiment were replicated with associatively related faces pairs and categorically associated face pairs distinguished between. The combination of associative and categorical relations in our face pairs may further explain why priming effects were found for primes presented to both visual fields.

From inspection of Fig. 3, it can be seen that reaction times to unrelated target faces are faster than unprimed target faces when the prime face was presented to the right visual field (left hemisphere), but comparable when prime faces are presented to the left visual field (right hemisphere). This is an unexpected finding as it would have been predicted that there should be no difference in reaction times to unrelated and unprimed target faces. It is particularly interesting that this is only evident in one visual field condition. A possible explanation of this finding is that a small

categorical priming effect for the category of “famousness” occurred for unrelated prime faces presented to the right visual field (left hemisphere) only. This suggestion fits well with our earlier proposal that different types of semantic information may be differently lateralised and requires further examination.

It is also interesting to consider the implications of the target faces being presented centrally. We have assumed that centrally presented faces will be processed bilaterally; however this may not be the case. According to the split fovea theory any part of a stimulus presented left of centre is initially presented to and processed by the right hemisphere and any part of a stimulus presented to the right of centre is initially presented to and processed by the left hemisphere (e.g., Ellis, Brooks, & Lavidor, 2005; Martin, Thierry, Demonet, Roberts, & Nazir, 2007). The divided visual field paradigm that we used here is based on a similar assumption, however stimuli are typically presented some distance from centre to maximize unilateral presentation (see Bourne,

To some extent the findings of this experiment have raised more questions than they have answered. However, it does show that a lateralised semantic priming paradigm provides an interesting way in which we can further examine the lateralisation of semantic information.

Acknowledgment

Many thanks to Dawn Gray who collected the data.

Appendix A

Stimuli face pairs and mean (*SD*) relatedness ratings. Positive values indicate that the two people are semantically related and negative values indicate that the two people are not semantically related. For all of the semantically related pairs the ratings are sig-

Semantically related face pairs	Semantically unrelated face pairs
Jennifer Aniston–Courtney Cox 200 (51)	Pierce Brosnan–Justin Timberlake –216 (47)
David Beckham–Victoria Beckham 233 (33)	George Clooney–Britney Spears –172 (126)
Tony Blair–Gordon Brown 138 (139)	Tom Cruise–Kate Moss –174 (128)
Leonardo diCaprio–Kate Winslet 91 (140)	Cameron Diaz–Cherie Blair –221 (61)
Geri Halliwell–Emma Bunton 168 (95)	Harrison Ford–Graham Norton –230 (33)
Ozzy Osbourne–Sharon Osbourne 207 (121)	Nicole Kidman–Elvis Presley –220 (60)
Matthew Perry–Matt LeBlanc 185 (90)	Madonna–Anthony Hopkins –197 (107)
Brad Pitt–Angelina Jolie 214 (63)	Julia Roberts–Princess Diana –204 (95)
Prince Charles–The Queen 228 (64)	Jonathon Ross–Jennifer Lopez –189 (91)
Prince William–Prince Harry 238 (32)	John Travolta–George W Bush –208 (62)

2006). Our centrally presented target faces may have been processed by the right hemisphere, rather than bilaterally. Consequently processing following left visual field (right hemisphere) primes would have resulted from within hemisphere priming and processing following right visual field (left hemisphere) primes would have resulted from across hemisphere priming. Previous work has shown that left visual field targets were primed more by within than across hemisphere primes (Bourne & Hole, 2006). The left visual field semantic priming effect reported in this paper may be explained in a similar way. This may be addressed by using within and across hemispheric semantic priming.

The results of this experiment suggest that, at least to some extent, semantic information is lateralised to the right hemisphere. However, both prime and target stimuli were faces. It would be interesting to repeat this experiment with a prime stimulus that might lead to less reliance on the visual processing and perception of the prime face, such as names. Both models of the lateralisation of face processing proposed that names are processed using left hemisphere mechanisms (Ellis, 1983; Rhodes, 1985). More recent evidence, including evidence using functional neuroimaging, provides evidence for the processing of names being lateralised to the left hemisphere (e.g., Huddy et al., 2003; Miceli et al., 2000; Pickering & Schweinberger, 2003; Schweinberger, Pickering, Burton, & Kaufmann, 2002; Seidenberg et al., 2002). If the experiment were to be replicated, but with lateralised name stimuli priming semantically related face stimuli, a left hemispheric advantage may be found.

This experiment was designed in an attempt to further understand the way in which semantic information may be organised in the brain. While we initially predicted either left hemisphere dominance or bilateral distribution, we actually found greater semantic priming from the right hemisphere. From the data presented here it is not possible to discern the reasons for this finding, however a number of possible explanations have been considered.

nificantly greater than 0 (all $p \leq .001$) and all ratings for unrelated pairs are significantly less than 0 (all $p < .001$).

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