Behavioural and Neuroimaging Evidence for Hemispheric Asymmetries in Face Processing Using Divided Visual Field Presentations

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Preface

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration, except were specifically indicated in the text. This work has not been previously submitted in part or in whole to any university for degrees or other qualifications. The dissertation meets the doctoral dissertation requirements in accordance with all regulations of the Biology Degree Committee and the University of Cambridge and does not exceed the word limit specifications of the Biology Degree Committee.

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Abstract

The present thesis combined behavioural and functional neuroimaging techniques to investigate hemispheric asymmetries in human face processing. More specifically, it combined the divided visual field (DVF) and repetition priming paradigms, together with functional magnetic resonance imaging (fMRI) and magneto- electro-encephalography (M/EEG), to reveal a right hemisphere advantage in an early stage of structural encoding of faces.

The initial hypothesis tested was that the right hemisphere (RH) has an advantage in view-dependent processing, whereas the left hemisphere (LH) has an advantage in view-invariant processing (Marsolek, 1999). The central primes and lateralised probes of Experiments 1-4 did not support this hypothesis, particularly for unfamiliar faces. Nonetheless, a consistent pattern emerged in which faces presented to the left visual field (LVF) showed faster reaction times and/or higher accuracy in male/female decisions than did faces presented to the RVF (supporting a basic RH advantage in face-processing), yet the effect of priming on these decisions was greater for RVF than LVF probes (and did not seem to reflect a simple baseline artefact). This led to formulation of a "RH Structural Processing Advantage" (RH-SPA) hypothesis, which states that structural encoding of faces in the RH, but not LH, is close to optimal, so improvement from repetition priming should only be observed when a prime is processed by the RH and a probe is processed by the LH. This hypothesis was tested using lateralised presentations of both primes and probes in Experiments 5 and 6, which confirmed that reliable priming was only found when primes were presented to the LVF and probes to the RVF.

Given that a behavioural effect of hemifield does not necessarily entail hemispheric differences in neural activity, more direct evidence for the RH-SPA hypothesis was sought using fMRI and M/EEG. Unfortunately no clear repetition effects were found with these measures, so the neural loci of the hemifield differences in behavioural priming remain unclear. However, these neuroimaging data identified, for the first time, the likely cerebral basis of the RH face-processing advantage – the right occipital face area (OFA) – and showed that this advantage occurs as early as the face-specific M/N170 component, consistent with an early stage of structural encoding. A simple, computational framework was developed to relate the neuroimaging data to the behavioural data, in which several toy models were explored. Though none was fully satisfactory, this modelling yielded several insights and suggestions for future experiments concerning the neural basis of the RH advantage in face-processing.

Chapter 1: Introduction

1.1 Hemispheric asymmetries in face processing

One of the long-standing issues in cognitive neuroscience is the nature of hemispheric asymmetries in human cognition. Several theories have been proposed concerning such functional lateralisation, which normally view the left hemisphere (LH) and right hemisphere (RH) as having different relative proficiencies along a single cognitive dimension, rather than supporting qualitatively different cognitive processes. The three main such ”global theories” that still maintain some validity and influence are: (i) the LH-verbal/RH-visuospatial theory, which suggests that the LH is relatively more proficient in lexical processing, while the RH is more proficient in visuospatial processing; (ii) the LH-analytic/RH-configural theory (Bradshaw & Nettleton, 1981), which suggests that the LH is more proficient in serial analysis of individual stimulus features, while the RH is more proficient in parallel, holistic processing of stimuli; (iii) the LH-high frequency/RH-low frequency theory (Sergent, 1982b, 1983), which suggests that the LH is more proficient in processing high frequency information, while the RH is more proficient in processing low frequency information (for a recent comprehensive review, see Dien, 2008, 2009)

The present thesis is concerned with face processing, one of the areas of cognition that shows some of the most pronounced effects of hemispheric lateralisation. There is an extensive amount of behavioural, clinical and neuroimaging literature, as reviewed in the following sections, that suggests a RH advantage in the visual processes of face perception and face recognition. It should be noted that the aim of the thesis is not to resolve the debate between the above global theories of lateralisation (although these theories are used as guidelines to help explain certain effects). Rather, the main aim was to combine brief, lateralised presentation of faces with recent neuroimaging methods (specifically, functional magnetic resonance imaging, fMRI, and magneto/electro-encephalography, M/EEG) to find more direct and systematic evidence for the neural bases of this RH face-processing advantage. As Dien (2009) argues, although there is a wealth of neuroimaging studies that show differences between face-related neural activity in left and right hemispheres, these differences are rarely tested explicitly, and even more rarely has the processing been explicitly biased towards one or other hemisphere by using lateralised presentation of stimuli.

Two "direct" types of evidence for the lateralisation of face-processing come from (i) neuropsychological study of patients with lateralised brain lesions and (ii) functional neuroimaging of healthy individuals performing various tasks on faces. This evidence is briefly reviewed below, before considering the slightly more "indirect" behavioural evidence for lateralisation, which is based on the "Divided Visual Fields" (DVF) methodology that utilises the hemispheric processing advantage for stimuli presented (briefly) in the contralateral relative to ipsilateral visual hemifield.

1.1.1 Neuropsychological evidence

Some of the most compelling evidence for the specialisation of the RH in face processing comes from prosopagnosic patients. A distinction was originally made between a visual impairment that hinders the construct of a perceptual representation of a face (i.e., apperceptive prosopagnosia), and an inability to access face-specific semantic information (i.e., associative prosopagnosia; De Renzi et al, 1991). However, this distinction between impairments in face perception and in face recognition is rarely clear-cut, with most prosopagnosic patients have deficits in both. Typically, lesions associated with prosopagnosia occur bilaterally in the occipo-temporal cortex (for reviews see Damasio, Damasio, & van Hoessen, 1982; Meadows, 1974). However, a relatively large number of cases have been found following a unilateral RH lesion (Assal, 1969; Hecaen, de Ajuriaguerra, Magis & Angelergues, 1952; Lhermitte & Pillion, 1975; Michel, Perenin & Sierhoff, 1986; Whiteley & Warrington, 1977).

One limitation of the above early studies is that the lesions were based on post-mortem investigations. More recent studies have used in-vivo neuroimaging methods - i.e. computerized tomography (CT), structural magnetic resonance imaging (MRI), and in some cases, functional MRI (fMRI).). Landis et al. (1986) presented six patients that had confirmed unilateral right posterior lesions and were prosopagnosic using CT. They also identified in literature a further seven patients who had prosopagnosic symptoms after operations in the RH and, thus, suggested that RH lesions alone could induce prosopagnosia. MRI and fMRI studies also provided further evidence for acquired prosopagnosia being caused by unilateral RH lesions (Joubert et al., 2003; Takahashi, Kawamura, Hirayama, Shiota, & Isono, 1995; Wada & Yamamoto, 2001;Wilkinson et al., 2009), with a certain degree of specificity to the ventral occipo-temporal cortex, usually the inferior occipital and/or fusiform gyri (Barton et al., 2002; Wada & Yamamoto, 2001; Rossion, Schiltz & Crommelinck, 2003). Typically, patients with RH fusiform lesions show deficits in the perception of facial structural configuration (Barton, 2008b), especially in the eyes and mouth regions, which are thought to provide critical cues for face recognition.

Right-handed patients with unilateral LH lesions, on the other hand, seem to have problems associated more with retrieving semantic information about faces. For example, Verstichel and Chia (1999) describe a patient that could discriminate familiar and unfamiliar faces, but had a problem recalling semantic information about faces, unless he was given their name, while Damasio, Tranel and Damasio (1988) describe two patients who again could discriminate familiar from unfamiliar faces, but showed a disproportionate incidence of retrieving the name of a different, but semantically-related, individual. Nonetheless, there are at least four cases with more traditional apperceptive/associative prosopagnosia following unilateral LH lesions (Barton, 2008a; Mattson, Levin, & Grafman, 2000; Tzavares, Merriene & Measure, 1973; Wright, Wardlaw, Young, & Zeman, 2006). It is noteworthy however that all four were left-handed, raising the possibility that hemispheric specialisation of face-processing in their brains (as can happen sometimes with language) was the opposite of that found in right-handed people. Thus, there seems to be a general consensus that damage in the RH (at least in right-handed people) disturbs perceptual processing of faces to a greater extent than does damage in the LH (with the LH being more important for semantic than perceptual processing of faces).

An interesting study by Le Grand et al. (2003) found that deficiencies in visual input from the left eye during early development disrupts normal face processing, even if there is no detectable cortical damage to either hemisphere. More specifically, they tested individuals who were treated for a unilateral congenital cataract, but only after six months of age. During the first six months of life, visual input from one eye projects only to the contralateral hemisphere (i.e., unlike the adult nervous system, visual information is not transferred through the corpus callosum). The participants were tested as adults and were required to make same/different judgments about pairs of faces. The group that had had a left eye cataract showed a much larger impairment than did those that had had a right eye cataract (or controls) when the two faces differed in the spacing of their internal features (eyes, nose, mouth), but not when the faces differed in terms of contour or shape of internal features. Hence, this study highlights the importance of the RH in perceptual processing of faces.

Finally, the use of newer techniques such as repetitive transcranial magnetic stimulation (rTMS) has allowed researchers to “simulate” lesions in otherwise healthy participants. Some compelling evidence comes from Pitcher and colleagues. Over two studies (Pitcher, Walsh, Yovel & Duchaine, 2007; Pitcher, Charles, Devlin, Walsh & Duchaine, 2009), they reported the specialisation of the right Occipital Face Area (OFA) within the inferior occipital gyrus (Halgren et al., 1999). These studies show that the right OFA: (i) shows specialisation for face perception, (ii) is responsible for processing early in the face processing stream (~ 100 ms) and (iii) is highly face selective and functionally distinct to adjacent areas in the inferior occipital gyrus (e.g., the lateral occipital complex).

1.1.2 Neuroimaging evidence

Neuroimaging data that use fMRI corroborate neuropsychological studies in showing a RH preference for face-processing, particularly in the ventral temporal/occipital lobes. The two main areas in the ventral temporal/occipital that often show greater fMRI activity to faces than various non-face stimuli (e.g., scrambled faces, houses, objects) are: (1) the OFA (see section 1.1.1) and (2) the Fusiform Face Area (FFA), within the mid fusiform gyrus (Kanwisher, McDermott, & Chun, 1997). Influential models of face processing (Calder & Young, 2005; Haxby, Hoffman & Gobbini, 2000) have suggested that the OFA is responsible for the early structural encoding of facial features whereas the FFA is thought to be involved in later stages of face processing, including recognition. Indeed, a relatively recent study (Rotshtein, Henson, Treves, Driver & Dolan, 2005) showed that the right OFA is sensitive when the physical appearance of a face is varied, even when that change does not lead observers to perceive a different identity. In contrast the FFA showed increased sensitivity only when the face changes caused viewers to perceive a different identity.

Although fMRI studies usually show bilateral FFA activation (e.g., Haxby et al., 1991; Ishai, Haxby, & Ungerleider, 2002), this activation is often of greater magnitude, greater significance, or more spatially extensive in the RH than LH (e.g., Haxby et al., 1999; Ishai, Schmidt, & Boesiger, 2005; Rhodes, Byatt, Michie, & Puce, 2004; Gilaie-Dotan & Malach, 2007). However, very few of these studies reported a direct statistical comparison of face-related activity across the two hemispheres, which is necessary to make strong conclusions about hemispheric lateralization. More specifically, in a review Dien (2009) found four that reported RH lateralization (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Haxby et al., 1999; Ishai, Schmidt, &Boesiger, 2005; Rhodes, Byatt, Michie, & Puce, 2004), two that reported a non-significant trend towards RH lateralization (Gilaie-Dotan &Malach, 2007; Puce, Allison, Gore, & McCarthy, 1995), and two that reported bilateral activity (Haxby et al., 1991; Ishai, Haxby & Ungerleider, 2002). Dien (2009) addressed this issue directly in a meta-analysis of 116 neuroimaging studies reporting face-related FFA activity. After excluding 57 that did not meet the author's criteria for inclusion, 51 reported greater activations in the RH and 8 reported greater activations in the LH; a difference that was significantly greater than chance according to a chi-squared test. In the present thesis, all face-related neuroimaging effects were explicitly tested across hemispheres.

Further evidence for a RH face-processing advantage comes from event related potential (ERP) studies. More specifically, there is an early component between 150-200 ms (the "N170") that is greater for faces than various other non-face stimuli, and which is believed to reflect an early structural encoding phase (Bentin, Allison, Puce, Perez &McCarthy, 1996; Bentin & Deouell, 2000; Eimer, 2000a,b; Herzmann, Schweinberger, Sommer, & Jentzsch, 2004). This component is generally stronger over RH than LH temporo/parieto/occipital electrode sites (Henson et al., 2003; Rossion et al., 2003). Furthermore, there is a later component – the "N250r" – which reflects a modulation of face-processing by repetition priming, particularly for familiar faces, (e.g., Itier & Taylor, 2004; Martin-Loeches, Sommer & Hinojosa, 2005; Pfutze, Sommer & Schweinberger, 2002; Schweinberger, Kaufmann, Moratti, Keil & Burton, 2007; Schweinberger, Pickering, Burton, & Kaufmann, 2002) which also tends to be stronger in the RH.

1.1.3 Behavioural evidence from healthy individuals

One methodology for testing hemispheric differences in face processing behaviourally is the use of tachistoscopic presentations to the left visual field (LVF) or right visual field (RVF); commonly called the Divided Visual Fields (DVF) methodology. The DVF methodology takes advantage of an important property of the visual system: the nasal part of the retina projects directly to the opposite hemisphere. This means that visual information is processed earlier in the contralateral hemisphere relative to the ipsilateral hemisphere. Because this paradigm is used throughout this thesis, it is described in detail below, before considering its previous application to the question of lateralisation of face-processing.

1.2 The Divided Visual Fields (DVF) methodology

1.2.1 Conditions for successful DVF presentations

The DVF methodology has been used for many years to try to tease apart processing differences in the left and right hemispheres. It relies on the anatomical fact that the temporal hemiretinae of each eye project to the visual cortex ipsilaterally, whereas the nasal hemiretinae project contralaterally (Figure 1-1). Two main variables are critical for successful DVF presentations:

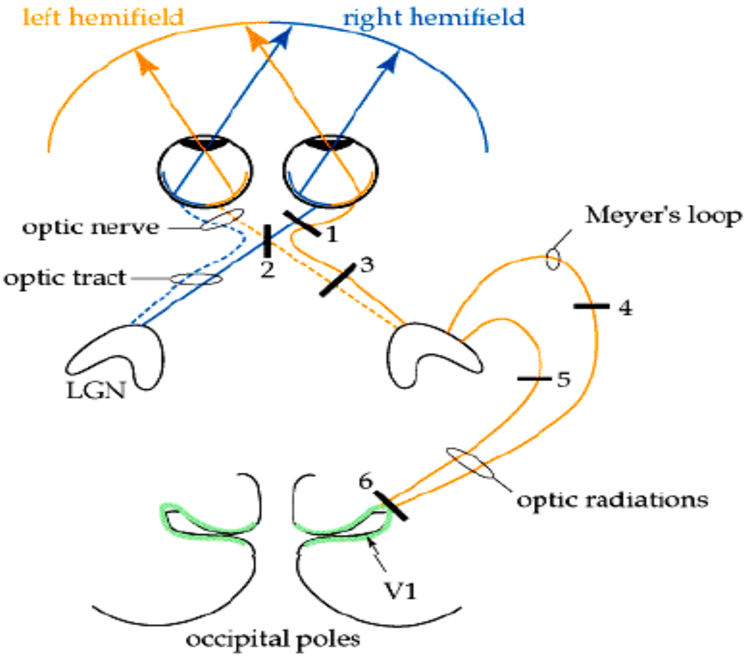

Figure 1-1: Schematic representation of the organization of the visual system. For example, in the left hemifield, the nasal part of the retina projects contralateraly (orange) while the temporal part ipsilateraly (blue). Adapted from www.davidjparnell.com

(i) Stimulus eccentricity: it is generally accepted that when a person fixates on a central point, the nasotemporal overlap of the two visual hemifields along the vertical meridian is in the region of 0.5° to 3°. Although there some controversy over the extent and bilateral or unilateral nature of this overlap, the consensus is that stimuli presented with horizontal eccentricities larger than 1.5° will result in preferential processing by the contralateral hemisphere. This is based on physiological data such as hemianopia patients

(Huber, 1962), animal studies (Leventhal et al., 1988; Stone et al., 1973), and behavioural data (Lavidor & Ellis, 2003; for review see Ellis & Brysbaert, 2010).

(ii) Stimulus duration: since saccades to unexpected stimuli occur within approximately 200 ms (e.g., Gilchrist, Brown & Findlay, 1997), in order to ensure that saccades do not alter the hemifield of stimulation, stimuli should be presented for less than this time. Hence, in the present thesis, the face stimuli were presented for between 80-120ms (except in the fMRI experiment in Chapter 4), with their inner edge always at least 2° from fixation.

In addition, further practical details are important in order to interpret any behavioural differences found as a function of hemifield of stimulation. Firstly, care should be taken to ensure that the distance between the eyes of the participant and the screen (and hence the visual angle) remains constant. This was achieved in the present experiments by using a chinrest (except when in the MEG or MRI scanner, in which case participants' heads were fixed in position anyway).

A second issue that is important to address is the Simon effect (Simon, 1969). This refers to the finding that, when stimuli are presented to the left or right visual fields, responses using the ipsilateral hand are faster than responses using the contralateral hand. In order to control for this effect, bimanual responses were used in the present thesis. For example, in a familiarity judgment task, participants might be required to press simultaneously with the index finger of both hands for famous faces, and the middle fingers of both hands for nonfamous faces. Finally, it is important to note that the projection of a stimulus directly to one hemisphere does not mean that the other hemisphere does not process the stimulus at all, since information is soon relayed through the corpus callosum to the opposite hemisphere. Rather, the general consensus is that the contralateral hemisphere gets a "head start" in processing the lateralised stimulus, though more precise theories are considered in the next section.

1.2.2 Models of how hemispheric asymmetry effects arise in DVF studies

The precise nature of information processing that allows hemispheric asymmetries to arise using the DVF methodology is unclear. There are two main models:

(i) The "callosal relay" model, which suggests that laterality effects reflect an inability of one hemisphere to perform a task, such that when stimuli are presented to it, there is a need to relay information to the other, competent hemisphere, resulting in increased reaction time and/or degrading effects of the stimulus (Rizzolatti, Umilta &

Berlucchi, 1971). In addition, there may be both reaction time delays and decreased accuracy if the relayed percept is degraded in the process. Example fMRI evidence for the callosal relay model would come from the Visual Word Form Area (VWFA), a mid-fusiform region responsive to orthographic stimuli: Activity in the VWFA is left-lateralized regardless of the visual field in which the stimulus appears (Cohen et al., 2002).

(ii) The direct access model (Geffen et al., 1971), which suggests that the initial hemisphere takes control of the information processing, and that differences in performance reflect differential proficiencies of the two hemispheres. Example fMRI evidence for the direct access model would come from a study of face/object-processing by Hemond, Kanwisher & Op de Beeck (2007). These authors found that contralateral presentations of faces produced greater activity (relative to non-face stimuli) in OFA and FFA than did ipsilateral presentations (despite the larger OFA and FFA clusters in the RH for all subjects).

Regardless of the exact nature of the information processing that allows visual field effects to arise, the DVF methodology has been used extensively in studies on hemispheric asymmetries in face processing, and like the neuropsychological and neuroimaging evidence reviewed above, the results seem to converge on a RH advantage in face processing, as reviewed below.

1.2.3 DVF evidence for a RH advantage in face processing

There are a number of behavioural studies that have used DVF to investigate hemispheric asymmetries in face-processing. Faces presented in the LVF are identified more rapidly and more accurately than when they are presented in the RVF, using in a variety of tasks. For example, Young, Hay, McWeeny, Ellis & Barry (1985) reported a LVF advantage for familiarity judgements on familiar and unfamiliar faces, while Hillger & Koenig, (1991) reported a LVF advantage for intact, unfamiliar faces using a match-to-sample task. Interestingly, the latter study did find a tendency for a RVF advantage when faces were matched purely on the basis of their parts, suggesting that the RH (LVF) advantage relates specifically to holistic processing. Levine, Banich, & Koch-Weser (1988) used a face/house discrimination task and found a LVF advantage specific to faces. Nonetheless, it must be noted that DVF research on face processing is sensitive to a variety of other factors, such as stimulus duration, contrast, luminance and spatial frequency. Manipulation of these factors can remove the LVF advantage, or even produce a RVF advantage (for reviews see Christman, 1989; Sergent, 1986; Sergent & Hellige, 1986).

1.2.4 DVF methodology and neuroimaging evidence

However, the RH advantage in face-processing has not been studied extensively by combining the DVF methodology with neuroimaging. To the author's knowledge, only one fMRI study has used lateralised presentations within a scanning session (the Hemond et al. 2007 study mentioned in Section 1.2.2). The main finding was a reported contralateral advantage for face stimuli both in the OFA and FFA. In this study however, presentation times were 300 ms, which is much higher than advised for the DVF methodology and the locus of the stimulus coincided with the locus of spatial attention. DVF experiments usually tend to control for contributions for spatial attention, which likely modulates hemispheric effects. Furthermore, the authors did not explicitly test (or at least do not report) hemispheric asymmetries by statistical comparisons across hemispheres for an interaction between hemisphere, hemifield and stimulus type (see Chapter 4 for a more extended presentation of the study and discussion). One also relevant study by Yovel, Tambini & Brandman (2008) showed a significant correlation between a LVF superiority in the recognition of chimeric faces (different identities for each half of a face) in a behavioural session and the size of participants' activations in right FFA from a separate fMRI session. Although this is an interesting finding (see also Yovel, Levy, Grabowecky & Paller, 2003, for a related ERP study below), it does not provide complete evidence for the LVF-RH face-processing advantage, as the face stimuli in the behavioural session were not contrasted with any other type of stimuli. Furthermore, this study does not provide direct neural evidence for a LVF superiority, as the participants were only scanned in a localising session, which was afterwards correlated to the behavioural session (see further discussion in Chapter 4).

In regards to EEG/ERP studies there is more extensive yet still limited literature. The Yovel et al.(2003) study was the precursor of the fMRI study presented above. The same behavioural task was used while ERPs were recorded. Neural correlates of the LVF superiority, were manifested in a shorter latency of the face-specific N170 component to LVF than RVF faces and in a larger amplitude to LVF than RVF faces at 220–280 and 400–600 ms over both hemispheres. These ERP amplitude differences between LVF and RVF faces covaried across subjects with the extent to which the face-specific N170 component. A second study by de Gelder et al. (2005) used monocular DVF, and reported a larger N170 in the RH occipital-temporal EEG channels for LVF than RVF presentations, while the LH did not show such a contralateral preference. An earlier study by Sobotka, Pizlo & Budohoska (1984) showed that hemifield effects specific to faces rise as early as 100 ms post-stimulus presentation. Finally, a study by Cooper et al. (2007) found a larger N250r to central probe faces in RH electrodes, following face primes that were presented in the LVF and RVF. This effect of hemisphere did not interact with hemifield though, i.e. the RH repetition effect was found collapsing across hemifields (for foveal targets). One important consideration is that none of the above studies had control stimuli that are necessary to show that this advantage is face-specific (e.g., rather than just a RH advantage in processing any briefly-flashed visual stimulus). Although ERP components like the N170 are generally thought to be face-specific, it seems appropriate that such interactions between hemifield and hemisphere need to be tested against non-face stimuli. This issue was explicitly addressed in the present thesis from Chapter 4 and onwards.

1.3 Models of face processing

As noted above, although there is substantial evidence for a certain degree of lateralisation in face processing, few cognitive/neurophysiological models of face-processing explicitly address the question of hemispheric asymmetries. Early cognitive models of face processing did not address lateralisation at all (e.g., Bruce & Young, 1986), or if they did (e.g., Ellis, 1983; Rhodes, 1985), they do not seem to have been updated in light of recent neuroimaging data. Likewise, explicit neurophysiological models of face recognition (e.g., Haxby et al., 2000) do not explicitly postulate differences between the LH and RH. Below is a brief review of the most important models and their contributions (or lack of) to understanding lateralisation effects in face processing.

1.3.1 Ellis (1983)

This is one of the earliest models of lateralisation of face-processing. It maintains that the RH is responsible for the categorisation of a stimulus as a face, perception of facial expressions and the formation of engrams (perceptual representations) for unfamiliar faces. The only aspect that is explicitly LH lateralised is the naming of faces, while the physical analysis of faces, assessing the familiarity with a face and the access of

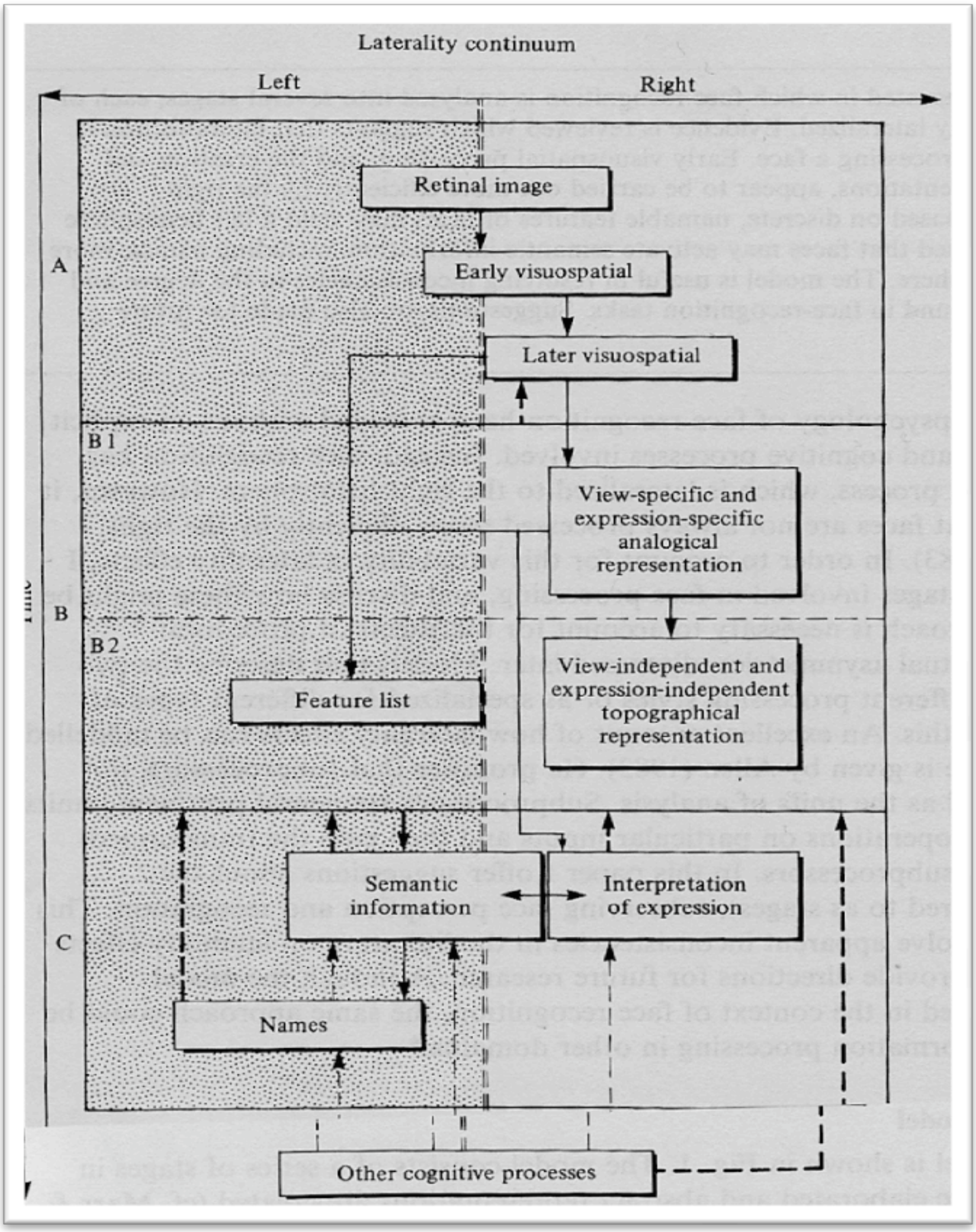

Figure 1-2 *: the Rhodes (1985) model proposing three stages (as seen on the left side of the figure): (A): visuospatial processing, (B) creation and comparison of representations and (C) accessing semantic information. Adapted from Rhodes, 1985* semantic information are bilateral. However, newer neuroimaging and neuropsychological evidence would seem to question some of these assumptions. For example, lateralisation effects (especially in the RH) seem extend further than simple stimulus categorisation, with the RH showing an advantage in the processing of perceptual features and identity (e.g., Rotshtein et al., 2005), and the LH likely showing an advantage in retrieving semantic aspects of faces besides of naming (see Section 1.1.1).

1.3.2 Rhodes (1985)

The model proposed by Rhodes (1985) makes the most explicit claims about hemispheric asymmetries along different stages in a face-processing pathway. Rhodes proposed three different stages of processing: (A) visuospatial processing, (B) creation and comparison of representations and (C) accessing semantic information (see Figure 1-2). During the initial stage of visuospatial processing, the RH plays a prominent role in the perceptual encoding of faces, especially in later stages of visual perception such as the efficiency of extracting visual information from stimuli (for review see Sergent, 1983). In the second stage of creation and comparison of face-representations, the two hemispheres have different functions: the RH is involved in creating view-specific and view-independent representations, as well as representations of facial expressions, while the LH is involved in feature extraction and representation. A more recent, related view is that the RH is specialised for holistic processing of faces, while the LH is specialised for feature-based processing of faces (Rossion et al., 2000). Finally, in the third stage of accessing semantic information, the RH has an advantage in interpreting emotional expressions, while the LH has an advantage in accessing semantic information and names. The model also makes an explicit distinction between the processing of familiar and unfamiliar faces, and how familiarity might affect lateralisation patterns. More specifically, for unfamiliar faces, since there are few semantic associations, and processing is mainly visual, the RH should be more heavily involved. For familiar faces, on the other hand, if semantic information is accessed early, this information can provide top-down facilitation for visual processing, hence lateralisation patterns could be less clear cut.

1.3.3 Bruce & Young (1986) and Haxby et al. (2000)

The Bruce and Young (1986) model gives a comprehensive account for how perceptual and semantic information can be related and accessed, while the Haxby et al. (2000) model essentially maps the Bruce and Young model onto the brain, on the basis of subsequent neuroimaging data. The first stage specifically related to faces is the “structural encoding” stage, which includes the formation of view-centred representations. After structural encoding, several routes diverge, one related to face recognition, and others related to processing of expression, eye-gaze, etc. We will focus on the recognition route, in which the next stage is the activation of Face Recognition Units (FRUs), which are view-independent template representations of faces that we know.

Activation of FRUs can in turn trigger activation of Person Identity Nodes (PINs), which in turn can trigger activation of semantic information and names (details of which are beyond the present interest). The main advantage of this model is that it has subsequently been implemented as a neural network model, in which processes like priming (see section 1.4) are given a concrete instantiation (Burton , Bruce & Johnston, 1990).

Haxby et al. (2000) proposed a box-and-arrow model very similar to the Bruce and Young model, and mapped this onto brain regions on the basis of functional neuroimaging studies. This model is comprised of a core system and an extended system: the core system includes the inferior occipital gyri (and OFA), which appears to correspond to the structural encoding stage of Bruce and Young, and the mid-fusiform gyrus (and FFA), which appears to correspond to the FRUs of Bruce and Young (more specifically, the route from OFA to FFA is assumed to process invariant aspects of faces that are important for identification, i.e., regardless of view and expression, while a different route from OFA to the superior temporal sulcus (STS) is assumed to process the changeable aspects of faces that are important for processing expression, social-attention, etc). The extended system includes, among other regions, anterior temporal cortex (for retrieving semantic information and names) and amygdala/insula/limbic cortices (for processing emotions conveyed by faces). However, although the Bruce and Young and Haxby models have been very influential, neither explicitly addresses any hemispheric lateralisation.

1.4 Repetition priming

The final ingredient to this thesis is the use of the repetition priming paradigm. Priming refers to an increase in accuracy, or decrease in reaction times (RTs), for stimuli that have been perceived recently (primed stimuli) relative to those that have not (unprimed stimuli). The initial presentation of a stimulus (here in a “study phase”) is called the prime, while its repeated presentation (here in a “test phase”), or the presentation of a stimulus that was not presented in the study phase, are called the probes. Priming has long been used to investigate the manner in which stimuli are represented in the brain: for example, if the amount of priming is unaffected by a change in view between the prime and probe, then it is often inferred that the (prime) stimulus has been represented in a view-independent manner. The initial reason for using priming in this thesis was to test a model of hemispheric lateralisation called the Dissociable Neural Subsystems model (DNS; Marsolek, 1999). The majority of evidence for this model is based on differences in the degree to which priming generalises across the visual format of stimuli as a function of the visual field (i.e., by combining the DVF methodology with the priming paradigm). In brief, Marsolek generally finds a greater degree of generalisation over format changes for RVF relative to LVF stimuli, which he uses to support his theory that the LH employs more abstract representations than does the RH (which obviously has parallels to some of the general theories of hemispheric lateralisation outlined in Section 1.1, and also with some claims from the face-processing perspective in Section 1.3). Further details of the model and its evidence are discussed in Chapter 2. Our initial aim was to see whether Marsolek’s previous patterns of interaction between visual field, priming and view, which have been found mainly for words and nameable objects, extended to faces. Though we were unsuccessful in reproducing this interaction with view when using faces, we did find reproducible interactions between hemifield and priming, which is why repetition priming was maintained as a factor in the subsequent chapters.

1.4.1 Repetition priming with central stimuli

Although there is a wealth of priming studies involving faces (e.g., Bruce, Dench & Burton, 1993; Brunas-Wagstaff , Young & Ellis, 1992; Ellis, Young, Flude & Hay, 1987; Ellis,Young,& Flude., 1990; Ellis, Flude, Young & Burton., 1996; Ganel & Goshen-Gottstein, 2002; Goshen-Gottstein & Ganel, 2000; Hay, 2000), they are mainly concerned with the nature of face representations rather than hemispheric asymmetries (i.e., used central primes and probes). Early work by Ellis et al. (1990) argued that repetition priming of faces is not simply mediated by episodic traces of previously encoded faces, but that it is a consequence of changes within the system that responds to the familiarity of facial information. This was based on their findings that repetition priming occurred only when a familiarity task was used at test, while other tasks (expression decision and sex judgement) did not elicit priming, and was only found for familiar faces. These results were used to simulate priming by strengthening of the connections from FRUs to PINs in the Bruce and Young model (see section 1.3.4); no priming is found for unfamiliar faces because they do not have FRUs, nor for tasks that do not require identification because they do not use this FRU-PIN route (though the route may be used spontaneously; see Ellis et al., 1996, for further discussion).

However, one problem with interpreting priming of unfamiliar faces, when using a familiarity-judgment task, is that the repetition of unfamiliar faces may cause them to (temporarily) seem familiar, which may increase RTs / decrease accuracy, counter-acting any tendency for decreased RT / increased accuracy owing to facilitated perceptual processing. A fairer test of priming unfamiliar faces therefore requires a task that is orthogonal to familiarity, such as a sex-judgment task. While Ellis and colleagues repeatedly failed to find priming when using a sex-judgment task, Goshen-Gottstein and Ganel (2000; also Ganel & Goshen-Gottstein, 2002) did find priming of sex judgements, for both familiar and unfamiliar faces, provided that obvious sex-predictive features, like hair-style, make-up, facial hair, etc, are removed. They argued that this forced participants to attend to the internal features of faces, processing of which could be facilitated by prior exposure. Though these authors argued against the Bruce and Young model, one possibility is that their priming results reflect facilitated processing at the level of structural encoding, which is common to both familiar and unfamiliar faces. Nonetheless, the size of the priming effect in a sex-judgment task is much less than the size of priming in a familiarity-judgment task (Henson, 2003), and given concerns about finding modulations of priming by both visual field and view, we employed both tasks at test in the present thesis (see Chapter 2).

1.4.2 Repetition priming and DVF

To the author's best knowledge, only two behavioural studies have combined DVF and repetition priming of faces (and none have combined DVF and priming with view-changes, as in Chapter 2). These are by Bourne and Hole (2006) and Bourne, Vladeanu and Hole (2009). These studies generally only found priming effects when primes or probes were presented to the LVF, supporting a RH advantage in face-processing. Importantly, these priming effects were only found for familiar faces using a familiarity-judgment task (see previous section). These studies are considered in more detail in Chapter 3. There is also one ERP study by Cooper et al., (2007), which used a similar paradigm as Bourne & Hole (2006) (i.e., lateralised primes and central probes) and is discussed more in the next section. One main finding though was that modulation of the N250r was greater over lateral inferior-temporal sites in the RH, supporting a RH basis of the behavioural priming effects, though this effect did not interact with the hemifield of the prime.

1.4.3 Repetition Priming as a function of viewpoint

A number of studies have investigated the degree to which priming of faces changes as a function of various manipulations of those faces, such as rotation in depth about a horizontal axis, changes in spatial frequency content, etc (all using central presentations). These are reviewed in more detail in Chapter 2, but in brief, there is generally greater generalisation of priming across such changes for familiar than unfamiliar faces, suggesting that a relatively abstract, pre-existing representation is necessary to generalise across view changes. There have also been some neuroimaging studies that have suggested that face repetition effects (which are normally manifest as a reduction in the fMRI response, or so-called “repetition suppression” (Grill-Spector, Henson & Martin, 2006) show greater generalisation over view changes in the LH (normally the left FFA or more anterior fusiform regions) than in the RH (though more so for familiar faces, e.g., Eger, Schweinberger, Dolan & Henson, 2005), though others have not found such evidence (Ewbank, Smith, Hancock & Andrews, 2008), or even found the opposite pattern, with greater generalisation across view in the RH (Caharel, d’Arripe, Ramon, Jacques & Rossion, 2009; Caharel, Jiang, Banz & Rossion, 2009). We hoped that the additional employment of the DVF methodology would help clarify such hemispheric differences in repetition effects across viewpoints. Indeed, the only study that combined DVF, priming and view changes is the aforementioned ERP study of Cooper et al. (2007). This study showed an effect in the behavioural data for famous faces, with LVF showing more image-specific priming than abstract priming, whereas presentation to the RVF showed similar image-specific and abstract priming. This pattern was partially replicated in the ERP data on the N250r component. More specifically, visual inspection of their data suggested larger image-specific than abstractive priming for targets following LVF primes, but not for targets following RVF primes, though this was not supported by the statistical analysis.

1.5 Overview of Thesis

Chapter 2 examined whether the degree of generalisation of behavioural priming across different views of familiar or unfamiliar faces differed when probe faces were presented to left versus right hemifields. If Marsolek's DNS theory applies to faces, then there should be evidence of greater priming across views for stimuli preferentially processed by the LH (i.e., presented to RVF). However, four experiments using central primes and lateralised probes (as used by Marsolek) failed to find convincing evidence for this prediction (or even the opposite prediction that one might make from a RH advantage in face-processing, i.e., greater priming across views for LVF stimuli). Nonetheless, overall priming effects were much more consistent for probes presented to the RVF, for both familiarity judgments to familiar faces and sex judgments to unfamiliar faces. While there was also a baseline advantage for unprimed LVF probes (consistent with the well-known RH advantage in face-processing), the greater priming for RVF probes did not appear explicable simply in terms of a range effect. This led to a working hypothesis that face processing is already optimal in the RH, but less than optimal encoding for the LH gives room for priming effects to emerge when a face is repeated in the RVF.

In the two experiments described in Chapter 3, the primes as well as the probes were lateralised, to produce a factorial crossing of prime hemifield and probe hemifield, and allowing exploration of hemispheric differences in the acquisition vs. expression (i.e., encoding vs. probing) of priming. Priming was only found consistently when primes were presented in the LVF and probes in the RVF. This is unlike previous findings by Bourne et al (2009), though important reasons related to our use of unfamiliar faces in a sex-judgment task at test (rather than familiarity judgments to famous faces) are discussed. The fact that priming of RVF probes was only found for LVF primes (or CVF primes in Experiments 1-4) led to our extension of our working hypothesis, in which not only is the RH already optimal in its face-processing efficiency (explaining why no priming was found for LVF probes), but the LH is also unable to encode faces sufficiently to lead to subsequent priming (explaining why no priming was found for RVF primes). We call this the “RH Structural Processing Advantage” (RH-SPA) hypothesis.

Chapter 4 describes an fMRI experiment that used lateralised presentations of both primes and probes (and using both faces and houses), to investigate more directly the hemispheric neural correlates of the RH-SPA hypothesis. Although no repetition effects were found (either behaviourally or in the fMRI data), a neural correlate of the LVF advantage for faces was found in the right occipital face area (OFA); a hemispheric difference that has not been established as conclusively before.

In Chapter 5, an M/EEG version of the fMRI experiment is described. It was performed in case one reason for the failure to find repetition effects in the previous chapter reflected the low temporal resolution of fMRI, in which transient changes in neural activity were concealed. Again however, no repetition effects were found (either behaviourally or in the M/EEG data), suggesting that the use of a face-house judgment task in both the fMRI and M/EEG experiments (in order to accommodate the non-face control stimuli that were necessary to identify face-specific processing in the brain) did not engender sufficiently deep processing of faces in order for repetition (priming) effects to emerge. Nonetheless, there was again compelling and novel evidence for a RH advantage in face processing, which occurred relatively early (around the M/N170), consistent with this advantage occurring at an early stage, such as the structural encoding stage of the Bruce and Young model (and consistent with the right OFA fMRI data).

Experiment 8 in Chapter 6 is an M/EEG experiment that more closely followed the design of Experiments 5 and 6, using a sex-judgment on unfamiliar faces only, and including blocks with central primes and lateralised probes, and blocks with lateralised probes and central primes. The behavioural data replicated those of Experiments 5-6, and a small repetition effect was found for the first time in MEG magnetometer data, though its timing and location were not consistent with an early structural encoding stage, and it was not found in EEG or MEG gradiometer data, suggesting that further replication is necessary before it can be interpreted conclusively.

Chapter 7 concludes the thesis by summarising the main findings, and formalising the RH-SPA hypothesis in a number of toy models that try to relate the fMRI/M/EEG data for a basic RH face-processing advantage with the modulations of behavioural priming found in Experiments 3-6. The chapter concludes with possible extensions of the present work, in terms of future behavioural and neuroimaging experiments.

Chapter 2: Behavioural DVF studies of Hemispheric Differences in Face Priming as a Function of View

2.1 Introduction

One interesting issue in face processing is the ability to recognise faces from different views, since we are able identify a face under a number of circumstances (e.g., from different angles, lighting conditions, hairstyles). There is a quite extensive debate on how different viewpoints are represented in the human brain, some of which relates to hemispheric differences. Below, the main theories of viewpoint dependence and invariance and their supporting findings are reviewed, both for objects (where the most research has been directed) and faces.

2.1.1 Viewpoint effects in object processing

The notion of viewpoint-invariance has been systematically studied by Biederman and his colleagues. (Biederman, 1987; Bierderman & Cooper, 1991; Bierderman & Gerhardstein, 1993; for reviews also see Biederman, 2000; Biederman & Cooper, 2009). A common assumption in viewpoint-invariant theories is that object recognition is based on identifying parts of objects and their spatial relationship; object-centred properties that are maintained across views (unless parts are obscured; Biederman & Gerhardstein, 1993). This was first proposed by Marr (Marr & Nishahara, 1978), who suggested that those parts are generalised cones (or cylinders). In a similar vein, Biederman proposed the recognition-by-components model (RBC; Biederman, 1987), in which there are 36 geometric primitives called *geons* (e.g., cones, pyramids, bricks, cylinders). Such part-based (or "structural-description") theories are supported by evidence, for example, that recognition of an object from a picture can be primed by a vertically-split version of that picture (Thoma, Hummel & Davidoff, 2004), a manipulation that would seem to disrupt any view-based representations (see below).

Other theories assume that object recognition is achieved by storing a number of viewer-centred representations of different views of objects. According to such view-based theories, viewpoint-invariance is achieved by interpolating across those stored views. This would seem the simplest explanation for why rotating views of previously learned shapes results in cost of performance as a function of the amount of rotation (e.g., Tarr & Bulthoff, 1995; Tarr & Pinker, 1989). In particular, Hayward and Tarr (1997) explicitly studied the conditions that Biederman postulated should allow view-invariance (Biederman & Gerhardstein, 1993), and still found viewpoint-dependent effects. View-based theories also receive some neurophysiological support: for example, an fMRI study by Gauthier et al. (2002) found view-dependent effects for object recognition, though interestingly, the neural locus of these effects did not precisely match those from a mental rotation task, as might be expected if recognition is achieved by interpolation. A more compelling example comes from Logothetis and colleagues, who recorded from single neurons in the inferior temporal cortex of monkeys, and found a large number of neurons that only responded to specific views of unfamiliar and familiar objects (Logothetis, Pauls & Poggio, 1995; also see Logothetis & Pauls, 1995 for primate behavioural data). Only a very small number of neurons (~1%) responded to both studied and new views of an object, as might be expected if object representations were viewpoint-invariant. Nonetheless, it should be noted that part-based and view-based theories are not mutually-exclusive; for example, view-invariant neurons might have been found if neurons were recorded in other regions of cortex (see Peissig & Tarr, 2007 for a comprehensive review).

2.1.2 Viewpoint Effects in Face Processing

There is less controversy over the nature of face representations, because it is generally accepted (even by people like Biederman; Biederman & Kalocsai, 1997) that faces are processed holistically (e.g., Bruce & Langton, 1994; Goffeaux & Rossion, 2006; Schiltz & Rossion, 2006; Tanaka & Farah, 1993; Young, Hellawell & Hay, 1987). These studies have shown that face recognition does not appear to depend on identification of specific features/parts, hence part-based processing seems unlikely. Nonetheless, faces do appear to be recognised quickly, independent of viewpoint, but only if they are familiar faces (e.g., Benton, Jennings & Chatting, 2006; Eger et al., 2005; Ryu & Chaudhuri, 2006). Thus it is possible that familiar faces are represented in a viewpoint-independent manner, whereas unfamiliar faces are represented in a viewpoint-dependent manner. Face representations (such as the FRUs in the Bruce and Young model described in Chapter 1) may become view-point invariant after many exposures to different views of the same face (though it is also possible that view-invariance is achieved by interpolating across all these views).

However, even familiar faces can show viewpoint-dependent effects, as in priming studies for example. Henson et al. (2008) used a masked priming paradigm and found greater repetition effects (behaviourally, and with EEG) for repetition of same than different view images of both familiar and unfamiliar faces, even if some of these view-dependent effects were less for familiar faces (see Ewbank, Smith, Hancock & Andrews, 2008, for similar results on the M170 component measured with MEG, and Davies-Thompson, Gouws & Andrews, 2009, for similar fMRI results). These data suggest that view-dependent representations of faces do exist. One possibility is that viewpoint-specific representations exist within the structural encoding stage of the Bruce and Young (1986) model (or even the earlier stage of "pictorial codes", common to both faces and objects), in addition to more viewpoint-independent representations (FRUs) for familiar faces later in the face-processing pathway.

2.1.3 Dissociable Neural Subsystems account

Given that there is evidence for both part-based and view-based theories of visual object recognition, hybrid theories have been proposed that incorporate aspects of both structural descriptions and viewpoint-dependent representations, depending on factors such as familiarity or attention (e.g., Bulthoff & Newell, 2006; Hayward & Williams, 2000; Hummel, 2001; Thoma, Hummel & Davidoff, 2007; Vanrie, Willems & Wagemans, 2001). One hybrid theory specific to hemispheric lateralisation was proposed by Marsokek (1999). Marsolek's Dissociable Neural Subsystems (DNS) theory states that the abstract versus specific nature of visual object representations differs across the two hemispheres, with the LH having a preference for abstract representations and the RH having a preference for specific representations (see, e.g., Burgund & Marsolek , 2000; Marsolek,1999; Marsolek & Burgund, 2003, 2008). Taking an upright piano and a concert piano as examples, the LH would tend to store features that are common to these two exemplars (e.g., features of the keyboard, legs etc), possibly in the form of some sort of primitive geometrical structures; a part-based approach that would allow a piano to be recognised not only across views, but also across exemplars. The RH on the other hand would tend to store whole-based representations, which would allow the two exemplars of a piano to be discriminated (or possibly two different views of the same exemplar to be discriminated). The main rationale for having separate abstract and specific systems is thus to achieve these opposing goals of generalisation and discrimination, which Marsolek proposes, requires different neural computations that are therefore most easily implemented in different parts of the visual system (specifically, the ventral visual processing stream in occipitotemporal cortex; see also Beeri, Vakil, Adonsky, & Levenkron, 2004; Vaidya, Gabrieli, Verfaellie, Fleischman, & Askari, 1998).

Behavioural evidence for Marsolek's DNS theory comes almost exclusively from combining the DVF methodology with the priming paradigm (as described in Chapter 1). During a typical study phase, participants perform a simple orienting task on stimuli presented centrally (at fixation). In the subsequent test phase, probe stimuli are presented to either the left or right visual field. These probes are either the same exemplars as the studied ones, different exemplars (e.g., an object viewed from a different angle), or previously unstudied exemplars. These experiments generally show that for probes presented to the RVF, priming (normally naming accuracy, relative to the unstudied exemplars) is approximately the same for same and different exemplars. For presentations to the LVF however, priming effects are generally greater for same than different exemplars. For example, Burgund and Marsolek (2000) used same and different views of objects, and reported accuracies for RVF probes of 70% and 67% for same and different views respectively (which did not differ significantly), compared with accuracies of 71% and 60% respectively for LVF probes (which did differ significantly; see Section 2.1.6 below). This general pattern seems to hold whether the stimuli are words (Burgund & Marsolek, 1997; Marsolek, Kosslyn, & Squire, 1992; though see Koivisto, 1995); everyday objects (Burgund & Marsolek, 2000; Marsolek, 1999; Marsolek & Burgund, 2003), novel objects (Marsolek & Burgund, 2008) and letter-like abstract patterns (Marsolek, 1995). Some neuroimaging support for DNS theory has also been reported, where fMRI repetition suppression for example tends to generalise to a greater extent in the LH (often fusiform) regions for both different object exemplars with the same name (Koutstaal et al., 2001) and different views of the same object (Vuilleumier, Henson, Driver, & Dolan, 2002).

However, Marsolek's approach has not yet been applied to faces. Furthermore, it is interesting to note that the majority of stimuli used by Marsolek (and in the neuroimaging studies) were familiar and nameable. Given the well-known LH advantage in lexico-semantic processing (see Chapter 1), it is possible that Marsolek's results are driven by lexico-semantic contributions to priming, rather than abstract perceptual representations (though see Marsolek & Burgund, 2008 and below). This possibility is considered more in the next section.

2.1.4 Effects of lexico-semantic processing

The importance of semantic contributions to the interactions between viewpoint and hemifield of the type reported by Marsolek and colleagues is provided by Curby, Hayward and Gauthier (2004). Using a DVF methodology and a matching task for novel objects (greebles), they found that only when participants had learned semantic associations with the objects was a view-independent effect found for RVF presentations; when no semantic associations where made, performance in both hemifields was view-dependent. Neurophysiological evidence for the importance of lexical/semantic processing in the LH comes from the Simons et al. (2003). These authors found that repetition suppression across exemplars changes in the left fusiform was modulated by the presence of a concurrent auditory prime, being greater when the prime was the name of the object relative to a pseudoword.

Recently, Marsolek has published a study to try to rule out lexico-semantic contributions, by using two types of novel objects, classified either as "possible" or "impossible" (Marsolek & Burgund, 2008). Contrary to Curby et al. (2004), they found that view-invariance for RVF stimuli and view-dependence for LVF stimuli for both types of stimuli, which remained even when they were rated for their nameability. It should be noted however that this study had some methodological particularities. Firstly, priming is not normally found for impossible objects (2D depictions of objects that could not exist in 3D), which the visual object system is assumed unable to represent (Schacter, Cooper, Delaney, Peterson & Tharan, 1991) Secondly, the priming effects were very small, and only found for 48 male-only, strongly right-handed participants. Thirdly, the result depended on the task. More specifically, they found greater sensitivity in the LVF for a visual working memory task that asked whether the cue and the probe were the same exemplar, but greater RVF sensitivity for a task that asked whether the cue and the probe belonged in the same category. They proposed that each task type "primes" each hemisphere for the type of processing for which it has a relative advantage (i.e., LH for abstract processing and RH for specific processing). Finally, even if the objects were novel, with "impossible" objects having lower nameability, one still cannot exclude the possibility that they resemble real objects (at least based on the examples that Marsolek & Burgund (2008) show in their paper, page 19).

2.1.5 Precise Interaction Patterns

The precise form of the hemifield-by-view interaction pattern on priming is important to consider. Assuming that RVF maps directly to LH, and vice versa, the most common pattern found by Marsolek and colleagues is shown in Figure 2.1A (y-axis represents priming of accuracy, but with arbitrary numbers), in which there was no reliable difference in priming between the two hemispheres in the Same condition (i.e., when the same exemplar or viewpoint was presented at study and test). This "single dissociation" pattern could represent a general advantage of same exemplar/view in priming, plus an additional LH advantage in generalising over exemplars/views, for example coming from the LH advantage in lexical/semantic processing discussed above. An alternative interaction pattern would be the "double dissociation" shown in Figure 2.1B, where RH > LH in the Same condition, but LH > RH in the Different condition. This would actually seem to be the pattern predicted by Marsolek's DNS theory, if the RH has an advantage over the LH in coding specific representations (which would help in the Same condition). Such a pattern has only in fact been reported once, in Marsolek & Burgund (2008), though even then, specific and abstract processing were tested with different tasks.

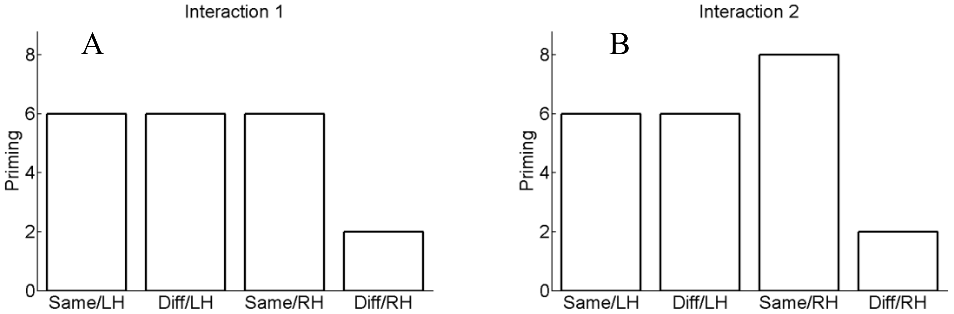

Figure 2-1: Two possible hemisphere-by-view interaction patterns: the common "single dissociation" interaction pattern found in Marsolek studies using objects (panel A) and a "double dissociation" pattern that would seem more powerful support for the dissociable neural systems theory (panel B). Priming scores on the y-axis are arbitrary.

2.1.6 Lateralised view-dependent and -independent systems for faces?

Since the factor of lexical/semantic processing possibly modulates view-dependent priming effects, it seems important to test whether hemisphere-by-view interactions predicted by the DNS theory generalise to other non-verbalisable stimuli apart from novel objects (e.g., unfamiliar faces). Indeed, given the RH advantage for face processing (see Chapter 1), it would seem a particularly powerful test of the DNS hypothesis if the same findings apply to stimuli with the opposite hemispheric preference. Indeed, one might even find a reversal of Marsolek's typical findings for unfamiliar faces: that is, a RH rather than LH advantage in generalising over different views of faces. This would be consistent with some models of face processing that do postulate that view-invariant face representations in the RH (Caharel et al., 2009a,b; Rhodes, 1985).

Furthermore, the effect of lexical/semantic processing can be explicitly tested by using familiar (nameable, e.g., famous) faces as well as unfamiliar (previously unseen) faces. If the critical factor in obtaining results like those of Marsolek is the availability of lexical/semantic information, then one might even see a different pattern of Hemifield-by-View interaction on priming for familiar and unfamiliar faces, viz a RH advantage in view-generalisation for unfamiliar faces, but a LH advantage for familiar faces.

2.1.7 Preview of Experiments

This chapter includes four experiments investigating hemispheric differences in the generalisation of face processing across views as indexed by priming. In this case, "view" refers to a specific photograph of the face of an individual. Note that these views were not always rigidly controlled for viewing-angle or expression, hairstyle, etc (with the exception of Experiments 3 and 4), so "view" is used in a generic sense throughout the thesis.

In some experiments, the faces were either famous (in the "familiar" condition) or novel, i.e., previously unseen (in the "unfamiliar" condition). The "familiarity" of each face was tested in debriefing phases, and only faces that were known or unknown for a given participant were analysed. Experiments 1 and 2 used a "fame" judgment task. Priming was measured by both accuracy and RTs of these judgments. Experiment 1 found partial support by DNS theory, at least for familiar faces. Experiment 2 however failed to replicate this finding, with the only major difference being a shorter lag between study and test trials. Given the difficulty in interpreting priming effects for unfamiliar faces in a "fame" judgment task (see Chapter 1), Experiments 3 and 4 switched to using unfamiliar faces only and a sex judgment task. Despite main effects of priming, of view and of hemisphere, the critical interaction between hemisphere and view on priming was not found. Various reasons for the discrepancy between these findings and DNS theory are discussed at the end of the Chapter.

2.2 Experiment 1: Long-lag Priming in a Fame Judgment Task

The decision to use a fame judgment task was because it typically gives large priming effects (e.g., Ellis et al., 1990), and it was thought that large basic priming effects would be important in order to detect interactions between hemifield and view. However, priming effects are normally restricted to familiar faces in this task. One reason could be that any "fluency" in processing an unfamiliar face owing to prior exposure (i.e., priming) might be erroneously attributed to familiarity with that face (i.e., fame) ("false fame effect"; Jacoby et al., 1989; Buchner et al., 2000). This could increase errors and slow down RTs, potentially counteracting any lower-level perceptual facilitation owing to priming. Thus, while the third factor of familiar vs. unfamiliar faces was of theoretical interest (given the possible LH advantage in lexical/semantic processing of familiar faces, as described above), interactions of this factor with priming are difficult to interpret. Nonetheless, it was reasoned that it would be interesting enough for the first experiment to find lateralisation effects on priming of famous faces alone. Moreover, any additional interactions with hemisphere on priming of unfamiliar faces (even if increased rather than reduced errors or slower, rather than faster RTs) would still be potentially informative.

One problem with using famous faces is that it is difficult in practice to collect two photographs of each famous face that are well-controlled for view, expression, lighting, etc (unlike for unfamiliar faces, for which several large such databases exist). Stimuli were initially limited to a set of 120 famous faces kindly provided by Stefan Schweinberger (and used in Eger et al., 2005). These were approximately, though not perfectly, matched for several variables to another set of 120 unfamiliar faces (see Methods).[1] The number of famous faces was increased to 150, by adding a set of 30 more identities consisting of two photographs of new celebrities from various sources on the internet. Given that unfamiliar faces were of less interest in

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[1] One might ask why we did not take a large set of well-controlled unfamiliar faces, and "familiarise" each subject with a (counterbalanced) half of them. The reason is that it is, in fact, surprisingly difficult for people to learn new faces (e.g., attach semantic information and names, with minimal episodic contribution), particularly in large numbers, as reviewed by Hancock, Bruce & Burton (2000).

this task, and that it was difficult to find new ones that were even approximately matched to the famous faces, no additional unfamiliar faces were added; hence the number of unfamiliar faces remained 120.

Marsolek's hemispheric differences were found mainly in accuracy. Therefore, the duration was of the lateralised probes was piloted, in order to obtain a baseline (unprimed) accuracy of approx 70% correct, in order to give ample room for improvements with priming. With the eccentricity used (see below), this turned out to be 80 ms. Furthermore, unlike Marsolek, priming of reaction times (RTs) was also measured, for those responses that were correct, in case priming resulted in a speed-accuracy trade-off.

An initial pilot study (N=16) was performed using an "immediate priming" paradigm, in which a central prime was followed after ~1s by a lateralised probe. The rationale was that this would allow us to repeat each face a number of times across each condition within participants, maximising power. However, while this study showed strong effects of priming (for famous faces), there were no reliable effects of hemisphere, let alone interaction between hemisphere and priming. If anything, it showed strong view-dependent effects in both hemispheres, for both accuracy and RTs. A “long-lag priming" paradigm was therefore used in Experiment 1, which is most similar to the design used by Marsolek for objects, and in which each face only appeared once in a given condition in the experiment (that condition counterbalanced across participants). In this design, all the primed stimuli are presented centrally in an initial study phase, during which participants perform an incidental task. In this case, it was a sex-judgment, which is orthogonal to the later familiarity-judgment task (thus minimising contributions to priming of response learning, Horner & Henson, 2008; or episodic memory, Henson, 2003). Priming was measured when these faces are presented again (relative to “unprimed” faces not seen at study) during a subsequent test phase in which participants perform a speeded fame judgment to faces presented briefly to left or right hemifield (i.e., the DVF paradigm). Given that the 150 famous faces needed to be divided into six conditions (“same” photograph as at study, “different” photograph as at study, and “unprimed”, for both left and right hemispheres), the downside of this design is that it meant only meant 25 trials per condition for famous faces (and 20 for non-famous faces).

2.3 Methods

2.3.1 Participants

18 right-handed participants, members of the MRC-CBU participant panel and postgraduate Cambridge University students (12 female, 6 male) volunteered for the experiment. The mean age was 26.4 years.

2.3.2 Design

A 2 x 2 x 3 within-participants factorial design was used. Familiarity (famous vs. non-famous), hemifield (LVF vs. RVF) and priming condition (same vs. different vs. unprimed) were the independent variables. "Same"/"Different" priming conditions referred to faces that were seen in the same or different photograph as at study. Reaction times and accuracy were the dependent variables.

2.3.3 Materials

All faces were greyscale images. The 150 famous faces came from photographs of British and North American celebrities (politicians, actors, athletes, singers), 120 collected by Schweinberger and colleagues together with a "matched" set of 120 unfamilar faces, plus 30 new famous faces collected from the internet. There were two images of each face, half male and half female. The images were matched for size, and cropped to show face and hair only. There was no explicit control of the differences across the two images: the two photographs could be taken from different perspectives (though the majority were between frontal and three-quarters views), involve different facial expressions and/or differences in lighting conditions, or hairstyles. There was little difference across the two photographs in the age of the person. Unfamiliar faces were matched to famous counterparts with respect to gender and approximate age. An attempt was also made to homogenise the stimuli with respect to average luminance and contrast. The faces were divided into 6 sets whose assignment to each condition was rotated across participants. Each face was within a 217 x 170 pixel rectangle. A chin-rest was used to keep participants' eyes approximately 57 cm from the monitor. Stimuli were presented using the Cogent software (http://www.vislab.ucl.ac.uk/cogent.php) running in Matlab7 on a 17' CRT monitor running at 85Hz. The lateralised probe faces were presented for 5 screen refreshes (actually 83.33ms).

2.3.4 Procedure

The basic procedure is shown in Figure 2-2. During the initial study phase, each face was presented for 3s in the centre of the screen. There were 180 trials in total, 100 famous-face trials and 80 non-famous face trials. Each trial begun with a presentation of warning signal in the form of a fixation point " + " presented for 500 ms. Participants had to decide whether each face was male or female. During the subsequent test phase, the participants were presented with 270 trials. For the famous faces, 50 were exactly the same view as in the study phase, 50 were the same person but a different view, and 50 faces were not seen (unprimed) in the study phase. Similarly, for the non-famous faces, 40 were exactly the same view, 40 different view and 40 previously unseen. Half of the faces were presented to the LVF and half were presented to the RVF. A test-trial began with a presentation of a circle in the centre of the screen for 2 s, followed by a fixation cross also in the centre of the screen for 500 ms. The onset of the fixation cross functioned as a warning that lateralised stimuli were about to appear, but that participants were told they should keep their fixation on the central cross. Indeed, they were instructed to focus their attention on the centre of the screen throughout the experiment, and not try to guess which side the next face may appear. The inner and outer edges of the probe face subtended horizontal visual angles of 2° and 6° respectively. Participants were instructed to respond as quickly and accurately as possible whether each face was famous. Participants made their judgments via keys on a standard PC keyboard. Importantly, they pressed two outer keys simultaneously with their middle finger of each hand for one decision (e.g., "male" in the study phase or "famous" in the test phase), or two inner keys simultaneously with their index fingers for the other decision. This bimanual task was used to control for a Simon effect (see Chapter 1). Only trials in which both outer or both inner keys were depressed were analysed, in which RTs came from the depression of the first key. The allocation of keys for male/female and famous/non-famous decisions was fully counterbalanced across participants. During a final debriefing phase, all the famous and non-famous faces (both views) were presented randomly in the centre of the screen for 3s each. Participants indicated how familiar they were with each face (with no time pressure this time). They were instructed to press "3" if the thought the face as famous, "2" if they were not sure and "1" is they thought the face was not famous.

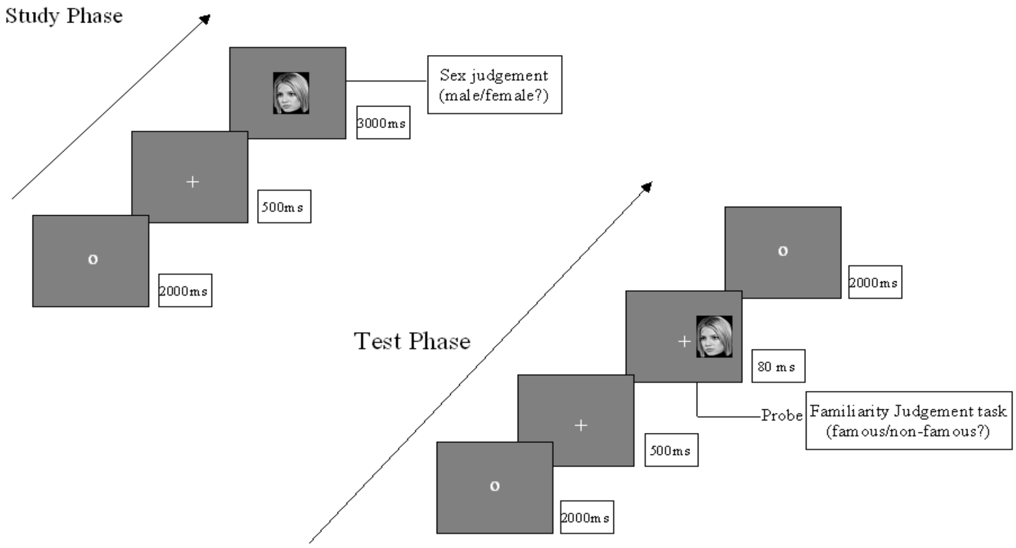
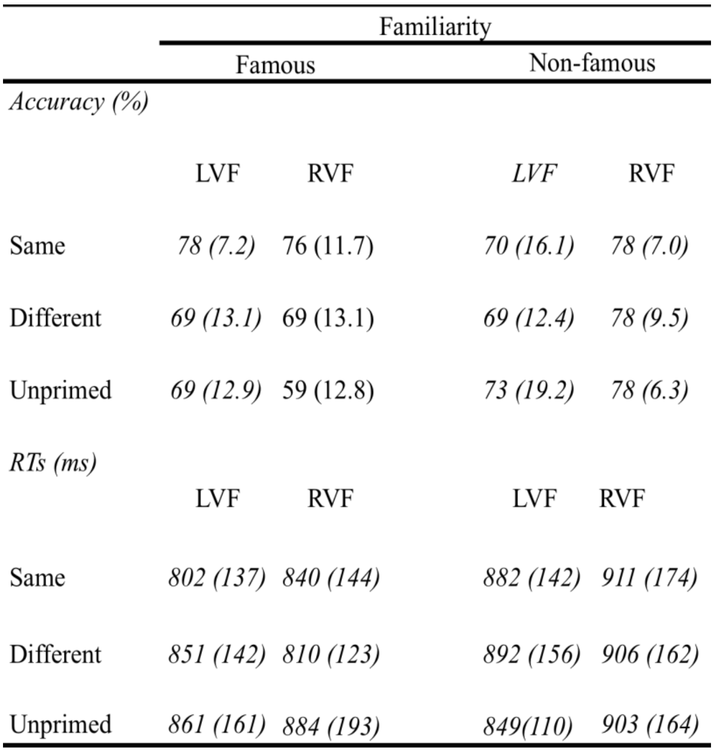


Figure 2-2: Examples of a trial in the Study Phase and in the Test Phase

2.4 Results

A response was scored as “valid” only when the participant classified that face correctly and confidently in the debriefing phase (i.e., pressed “3” or “1” for famous and nonfamous faces respectively*)*. Two participants were removed because they failed to recognise at least half of the famous faces (75/150). For the remaining 16 participants, 88% of the famous face trials and 98% of the non-famous face trials were valid. Accuracy in the study task was close to ceiling, and is not analysed further. Analysis of the test task (lateralised probes) was performed on both accuracy (%) and median RTs for each participant, with trials above 3000 ms and below 250 ms removed. The results are shown in Table 2-1.An omnibus ANOVA was



	Familiarity			
	Famous		Non-famous	
Accuracy (%)				
	LVF	RVF	*LVF*	RVF
Same	*78 (7.2)*	76 (11.7)	*70 (16.1)*	*78 (7.0)*
Different	*69 (13.1)*	69 (13.1)	*69 (12.4)*	*78 (9.5)*
Unprimed	*69 (12.9)*	59 (12.8)	*73 (19.2)*	*78 (6.3)*
RTs (ms)				
	LVF	RVF	LVF	RVF
Same	*802 (137)*	*840 (144)*	*882 (142)*	*911 (174)*
Different	*851 (142)*	*810 (123)*	*892 (156)*	*906 (162)*
Unprimed	*861 (161)*	*884 (193)*	*849(110)*	*903 (164)*

Table 2-1: Mean (N = 16) and standard deviation (SD) of accuracy and RTs as a function of hemifield and priming condition for famous faces and non-famous faces in Experiment 1.

performed using all conditions, followed by an ANOVA on priming scores (unprimed minus same and unprimed minus different), to test the critical interactions with visual field. Corrections for nonsphericity for factors with more than two levels used the Greenhouse-Geisser method ("corrected" df's reported). These ANOVAs were followed by planned t-tests to compare specific effects, e.g., same-view priming across visual field, or differences in the unprimed condition across visual fields. An alpha value of 0.05 was used. Analyses on accuracy used the Signal-Detection d' measure of discriminability, where a hit was a famous face called “famous” and a false alarm was a non-famous face called “famous”, in order to accommodate the possible response bias to say “famous” induced by priming (see section 2.2).

2.4.1 d' Analysis

A 2x3 ANOVA of d' scores with factors hemifield (LVF vs. RVF) and priming condition (same-view vs. different-view vs. unprimed) showed a reliable main effect of priming condition, $F(1,15)=8.66$, $p < 0.01$, and a borderline main effect of visual field, $F(1,15)=4.48$, $p= 0.05$, but any interaction failed to reach significance, $F<1$. The effect of priming condition is further explored below. Across visual fields comparisons of unprimed trials showed a LVF baseline advantage (d' = 1.19) relative to the RVF (d' = 0.78), t(15)=3.89, p<0.001.

2.4.2 d' Priming Effects

Analysis of priming effects using priming scores (primed minus unprimed) showed a main effect of visual field, F(1,15)=7.11, p<0.05, and a main effect of view, F(1,15)=14.1, p<0.01, but no significant interaction, F<1, p>0.20. The same-view condition showed more priming (M=0.33) than did the different-view condition (M=0.006) when collapsing over the factor of visual field, and the RVF showed greater priming effects (M=0.33) than the LVF (M=0.09) when collapsing across view. Indeed, priming was only reliable in the Same-RVF condition (see Figure 2-3, where error bars are 95% confidence intervals).

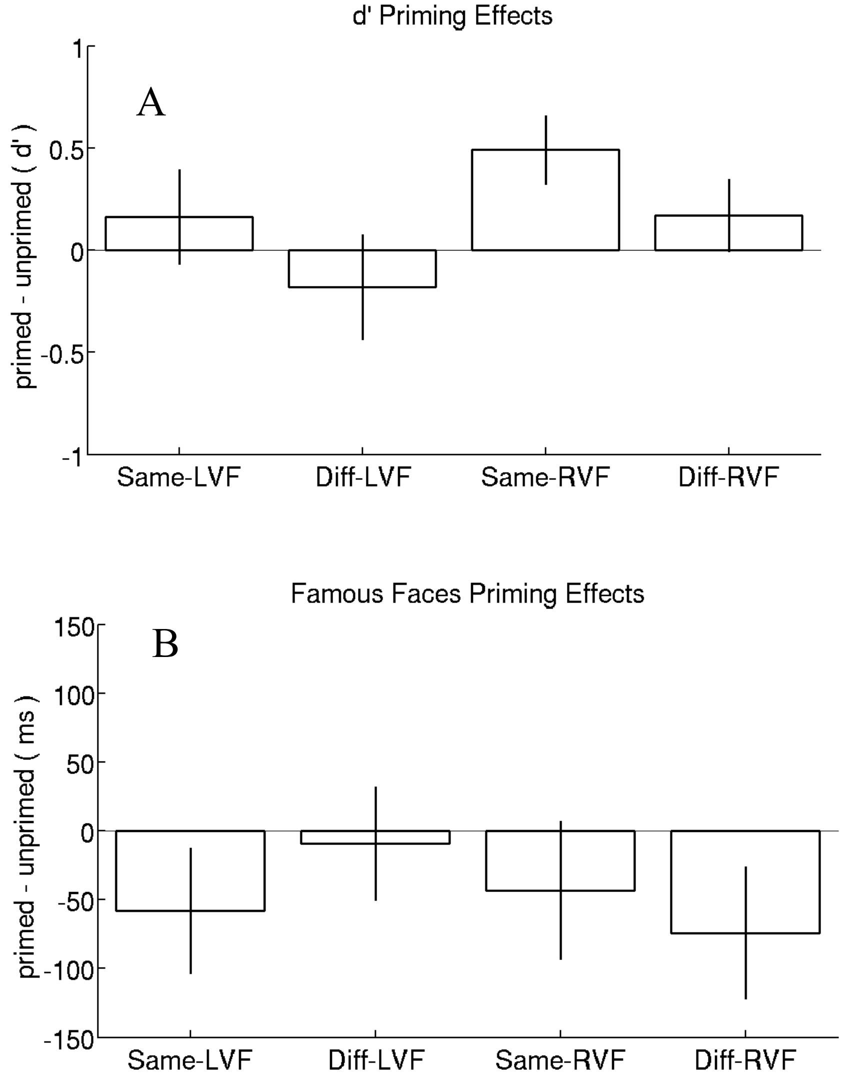


Figure 2-3: Mean (N = 16) and one-tailed 95% confidence intervals (error bars) of priming scores of d'(panel A) and RTs (panel B) as a function of hemifield and view in Experiment 1.

2.4.3 Reaction Times

A three-way ANOVA for RTs with factors familiarity (famous vs. non-famous), hemifield (LVF vs. RVF) and priming condition (same vs. different vs. unprimed) showed a significant two-way interaction between priming condition and familiarity, F(1.90,28.52)=5.72, p<0.01. There was also a trend for a two-way interaction between priming and visual field, F(1.52,22.84)=3.16, p=0.07. These interactions are explored further in the next section. Across visual fields comparisons of unprimed trials showed a trend for a LVF baseline advantage relative to the RVF for non-famous faces, t(15)=2.01, p<0.06, while no difference was found for famous faces, t(15)=0.55, p>0.2.

2.4.4.1 RTs Priming Effects

Since the two-way interaction between priming and familiarity was significant, separate two-way ANOVAs on priming scores (primed minus unprimed) were conducted for famous and non-famous faces, with factors hemifield (LVF vs. RVF) and view (same vs. different). The most important finding in the ANOVA on famous faces was a significant two-way interaction between hemifield and view, F(1,15)=8.91, p<0.01. When famous faces were presented to the LVF, there was more priming for same-view faces (-58 ms) than for different-view faces (-9 ms), t(15) = 2.44, p<0.05. Such an effect was not significant when same-view (-43 ms) and different-view (-74 ms) faces were presented to RVF. Priming was reliable only in the Different-RVF and Same-LVF conditions (Figure 2-3). Unlike d' there was no effect of hemifield, as priming for LVF and RVF probes (collapsing across view) was not significantly different, F<1. Analysis of RT priming effects for non-famous faces showed no reliable main effects or interactions, Fs<1.06, ps>0.20, while no condition approached significance.

2.5 Discussion

Experiment 1 partially replicates Marsolek's findings, at least in the RT measure of priming for famous faces. In this case, there was a significant interaction between hemifield and view on priming, with priming in the RVF but not LVF generalising across views, consistent with the proposal of DNS that the LH uses more abstract representations than the RH (here, for the first time, using faces). Note that this interaction pattern was a single dissociation (see Section 2.1.5), similar to the most typical pattern found by Marsolek (1999), but providing no direct evidence that the RH uses more specific representations than the LH.

As argued in Section 2.1.5, this interaction pattern can also be explained by greater contributions of lexical/semantic processing in the LH than RH. For example, naming the famous face, or retrieving semantic information about it, might facilitate reaction times when it is repeated, even if repeated from a different view (provided it is recognised from both views). This would also explain why no such hemifield-by-view interaction was found for unfamiliar faces (though the lack of overall priming for unfamiliar faces may be a consequence of the "fame judgment" task used here, which makes priming effects for unfamiliar faces difficult to interpret)

When priming was measured by accuracy (fame discrimination), rather than RTs, there were no reliable hemifield-by-view interactions for either d’ or raw scores. If anything, d’ scores show view-dependent processing for both LVF and RVF presentations, as same-view priming was significantly larger than different-view priming when averaging across hemifield Nonetheless, the fact that priming reflected a decrease in RTs accompanied by an increase in accuracy (d’) implies that the results cannot be explained by a speed-accuracy trade-off.

It is also interesting to note that there were significant main effects of hemifield on priming, at least for famous faces, with the RVF showing greater priming for both same and different view conditions than LVF in the d’ measure (and numerically higher priming for RTs). This RVF rather than LVF advantage in priming is somewhat surprising, given that one might expect a RH advantage for face processing. However, this becomes less of a puzzle when one notes the reliable hemifield difference in baseline performance in the unprimed condition. In this case, the expected LVF (RH) advantage for faces was found, with higher accuracy and faster RTs than RVF presentations. The reversal in hemifield effects on priming then has a simple potential explanation: faces repeated in the RVF show priming due to decreased efficiency in encoding, while encoding in the LVF is optimal, hence leaves little room for improvement by priming. In other words, the main effect of hemifield on priming could be artefact of different baseline levels. This "baseline" issue is addressed later in Experiment 4.

Though the precise interpretation of the hemifield-by-view interaction on RT priming for famous faces remains unclear (i.e., whether it reflects more abstract visual representation of faces, or additional lexical/semantic processing, in the LH), the results were deemed sufficiently interesting to pursue further. With a view to ultimately conducting neuroimaging experiments on this question, Experiment 2 was an attempt at replication, but using more trials and a shorter repetition lag.

2.6 Experiment 2: Short-lag priming in a Fame Judgment Task

Experiment 2 was a near-replication of Experiment 1, but given the limited number of stimuli, Experiment 2 attempted to increase the number of experimental trials by using a short-lag paradigm, in which each face was presented once in each priming condition (hence counterbalancing stimuli within participants, rather than across participants as in Experiment 1). While there may be "longer lag" effects of repeating faces across multiple trials, this was minimised by only repeating faces across three separate sessions (i.e., no face was repeated within a session). The expectation was that any such "longer lag" priming effects (across ~400 trials and the intersession break) would be "swamped" by short lag priming effects (across 2-20 trials). Indeed, this was tested by investigating interactions with the session factor. In the absence of an interaction, this design would give a threefold increase in trials compared with Experiment 1, an important consideration whenever attempting to replicate an experimental result (given statistical regression to the mean). In the short-lag design, 8 faces were centrally presented during each study block, on which participants made a male/female judgement. This was followed by a test block of 12 lateralised presentations (8 primed by the previous study block and 4 unprimed) on which participants made a familiarity judgement (as in Experiment 1).

2.7 Methods

2.7.1 Participants, Design and Materials

22 right-handed participants, members of the MRC-CBU participant panel and Cambridge university students volunteered to take part in the study. The mean age was 26.2 years. The 2x2x3 factorial design was the same as Experiment 1**,** with the addition of the factor of session, with three levels (for each session). The same sets were used as in Experiment 1, bar the extra 30 famous faces collected (i.e., the original set of 120 photographs of famous and 120 of non famous faces, 2 views each, from Schweinberger and colleagues). Each face was rotated across the conditions

within each participant, appearing only in one condition in a given session (see Procedure). The assignment of faces to conditions for specific sessions was counterbalanced across participants.

2.7.2 Procedure

The experiment had two main phases: (i) an experimental phase and (ii) a debriefing phase. The experimental phase had 3 separate sessions of 400 trials each. The main difference from Experiment 1 was that instead of using long-lag priming with separate long study and test sessions, we used alternating short study-test blocks. Each session consisted of 20 study-test blocks. In the study blocks, 8 faces were presented in the centre of the screen for 3s, each face preceded by a 500ms fixation cross. Participants had to respond whether the presented face was male or female. Immediately after the 8 study trials, the block of 12 test trials started. In the test blocks, faces were presented left or right of fixation (inner edge 2º, outer 6 º). Each trial started with a 2000 ms circle, followed by a 500 ms cross. Then a face was presented for 80 ms either in the LVF or RVF. Each study and test blocked was preceded by a brief instruction screen (two seconds), reminding participants of the change in task and presentation format. In the subsequent debriefing phase, both views of each face were presented below and above a fixation cross for 4 s. In a slight extension of the debriefing of Experiment 1, participants was asked to indicate whether they had recalled recognising both views as famous during the main experimental phase, or whether they had recalled recognising only one of the views as famous, or whether they had indicated that both views were non-famous. Other procedural details were as in Experiment 1 (i.e., bimanual responses were required; same eccentricity was used).

2.8 Results

As in Experiment 1, a response was scored as “valid” only when the participant recalled during debriefing that at least one view of that face had been correctly classified during the main phase2. Five participants were excluded on this criterion because they did not recognise both views of at least half 60/120) of the famous faces. Of the remaining 17 participants, 72% of the famous faces were scored and 91% of the non-

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[2] If a stricter criterion was used for recognising both views of famous faces during the main experiment, then only 58% of famous face trials would be valid, and we would have to remove 9 subjects in total. Nonetheless, even when this stricter criterion was used, the pattern of significant results was largely unchanged.

A

	Familiarity			
	Famous		Non-Famous	
Accuracy (%)				
	LVF	RVF	*LVF*	RVF
Same	*82 (9)*	79 (7)	*76 (17)*	74 (15)
Different	*74 (11)*	73 (10)	*79 (15)*	73 (15)
Unprimed	*60 (21)*	63 (20)	*72 (11)*	68 (15)
RTs (ms)				
	LVF	RVF	LVF	RVF
Same	*810 (150)*	*804 (167)*	*817 (144)*	*827 (140)*
Different	*815 (152)*	*778 (149)*	*851 (175)*	*817 (149)*
Unprimed	*833 (176)*	*877 (193)*	*813 (150)*	*906 (190)*

B

	Familiarity			
	Famous		Non-Famous	
Accuracy (%)				
	LVF	RVF	*LVF*	RVF
Same	79 (10)	78 (9)	75 (16)	*75 (14)*
Different	68 (12)	69 (16)	76 (15)	*76 (15)*
Unprimed	54 (18)	52 (17)	76 (12)	*73 (15)*
RTs (ms)				
	LVF	RVF	LVF	RVF
Same	*753 (112)*	*757 (112)*	*780 (118)*	*778 (116)*
Different	*773 (127)*	*769 (126)*	*773 (106)*	*782 (125)*
Unprimed	*822 (131)*	*801 (124)*	*796 (107)*	*811 (12)*

Table 2-2: Mean (N = 17) and standard deviation (in brackets) of accuracy and RTs collapsed for Session 1 (panel A) and collapsed across sessions (panel B) as a function of hemisphere and view for famous faces and non-famous faces in Experiment 2.

famous faces. Accuracy in the study task was close to ceiling, and is not analysed further. Since faces were repeated across sessions, in order to exclude any effects of across-session repetition, data were analysed both collapsing across sessions (in the absence of any interactions with other factors) and for the first session only (which would allow a more direct comparison with the single repetition design of Experiment 1). The overall accuracy and RTs are shown in Table 2-2.

2.8.1 d’ Analysis

As in Experiment 1, accuracy data were analysed with d', to minimise potential response biases to famous faces. The omnibus three-way ANOVA with factors session (first vs. second vs. third), hemifield (LVF vs. RVF) and priming condition (same vs. different vs. unprimed) only showed a significant main effect of priming, F(1,16)=27.4, $p < 0.001$, while no other effect or interaction reached significance, Fs<2.41, ps>0.3. For Session 1, the two-way ANOVA with factors hemifield and priming condition showed a reliable main effect of priming condition, F(1,16)=19.6, $p < 0.001$ (Fs<1, ps>0.2 for the effect of hemisphere and the two-way interaction). These priming effects are examined in more detail below. Baseline analysis did not show a significant difference between hemifields neither when collapsing across session,t(16)=0.7, p=0.4, nor for Session 1 only, t(16)=0.03, p=0.9.

2.8.2 d’ Priming Effects Analysis

Two-way ANOVAs with factors hemifield and view were conducted on d’ priming scores, both collapsed across sessions and for first session only. The two-way ANOVA for data collapsed across sessions showed only a main effect of view, F(1,16)=12.6, p<0.01, with same-view priming (M=0.76) being larger than different-view priming (M=0.49). The main effect of hemifield and the interaction did not reach significance, Fs <1, ps>0.2. The corresponding ANOVA for Session 1 likewise showed only a main effect of view, F(1,16)=4.51, p <0.05, with same-view priming (M=0.71) being larger than different-view priming (M=0.49). Contrasts across hemispheres did not show any significant differences. Thus unlike Experiment 1, there were no main effects of hemifield on accuracy in Experiment 2, even when analysing Session 1 only. Priming was reliable in all conditions for both analyses (Figure 2-4).

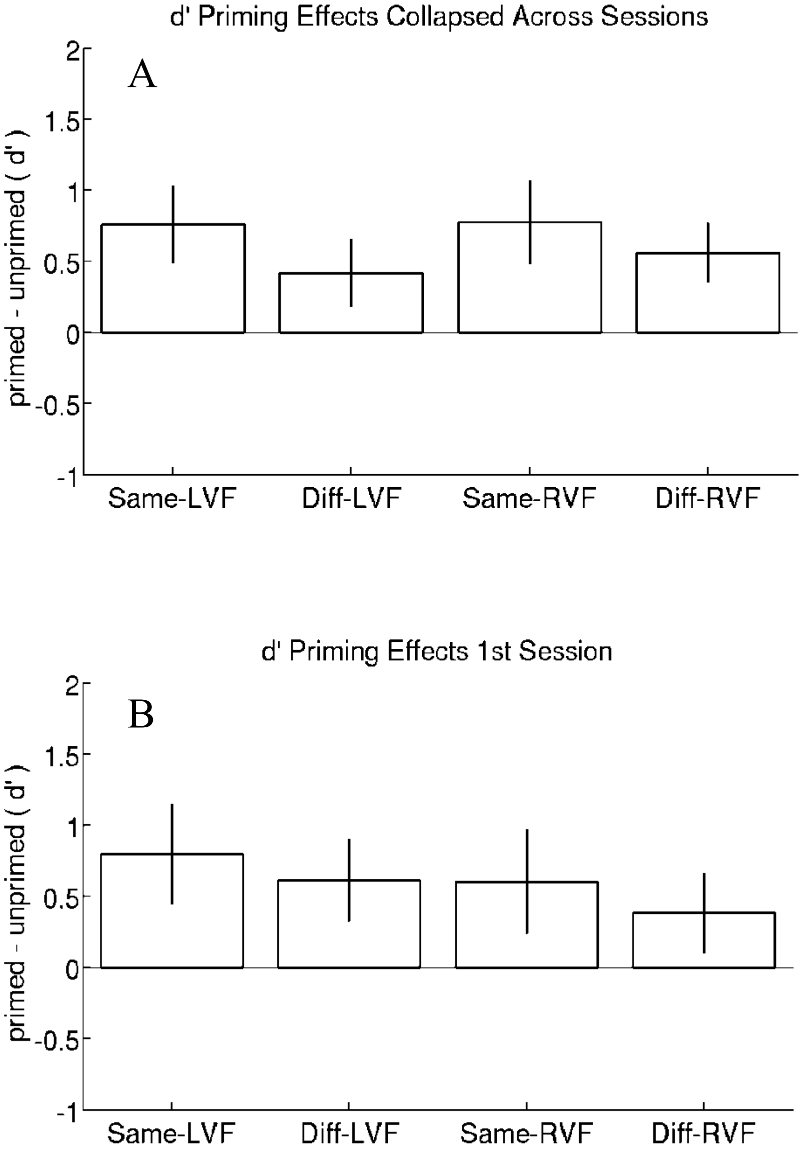


Figure 2-4: Mean (N=17) and one-tailed 95% confidence intervals (error bars) of priming scores on d' for all sessions (panel A) and Session 1 only (panel B), as a function of hemifield and view in Experiment 2

2.8.3 Reaction Times Analysis

The four-way ANOVA with factors session, familiarity, hemifield and priming condition showed a significant three-way interaction between session, hemifield and priming condition, F(2.45,39.2)=5.05, $p<0.01$. Surprisingly, the two-way interaction between familiarity and priming was not significant, F(1.59,25.45)=2.54, p=0.108 (unlike in Experiment 1), and nor did familiarity interact with any other factor, Fs<1, ps>0.2. Nonetheless, to be consistent with Experiment 1, RTs were analysed separately for famous and non-famous faces, using three-way ANOVAs with factors session, hemifield and priming condition (see below).

Analysis of the unprimed conditions with a three-way ANOVA with factors sessions, familiarity and hemifield showed a clear pattern of practice effects, as unprimed RTs decreased from Session 1 to Session 3 (857 ms; 815 ms and 775 ms respectively), F(1,16)=5.11, p<0.05.This session effect also interacted with hemifield (but not with familiarity), as for Session 1, faces presented to the LVF had shorter RTs than those presented to the RVF (823 ms and 891 ms respectively); for Session 2, this was reversed, with the RVF having shorter RTs that the LVF (798 ms and 832 ms); in Session 3, no difference across LVF and RVF was found (772 ms and 778 ms). This baseline pattern seems to also modulate repetition effects (when collapsed across familiarity): For Session 1, the RVF priming was larger than LVF priming.(see section 2.8.4 below) When analysing Session 2, there was a reversal of this effect, with priming for the LVF (-72 ms) being larger than for the RVF (-27), F(1,16)=4.41, p<0.05. Finally in Session 3, there was no difference between LVF and RVF priming, F<1. This pattern explains the significant three-way interaction between session, hemifield and priming condition reported in the omnibus ANOVA.

Thus, further analyses on repetition effects were conducted for (i) Session 1 only (which would represent conditions closer matched to those of Experiment 1) and (ii) by collapsing across sessions (to be consistent with d' analyses above). Baseline analysis on famous and non-famous faces separately in Session 1 showed that RTs for non-famous faces in the LVF were faster than in the RVF, t(16)=2.71, p<0.05. For famous faces, although there was a numerical trend for LVF faces showing faster RTs than RVF faces (see Table 2-2A), this effect did not reach significance, t(16)=0.98, p>0.3. When collapsing across sessions, there were no significant hemifield differences neither for famous faces, t(16)=0.88, p>0.3, nor for non-famous faces, t(16)=1.12, p>0.2.

2.8.4 RTs Priming Effects Analysis

When collapsing across sessions, the two-way ANOVA for famous faces with factors hemifield and view showed no main effects nor interaction, though priming was significant only for the for Same-LVF and Different-LVF conditions (see Figure 2-5A). Analysis for non-famous faces did not show any main effects or interactions either, Fs<1.

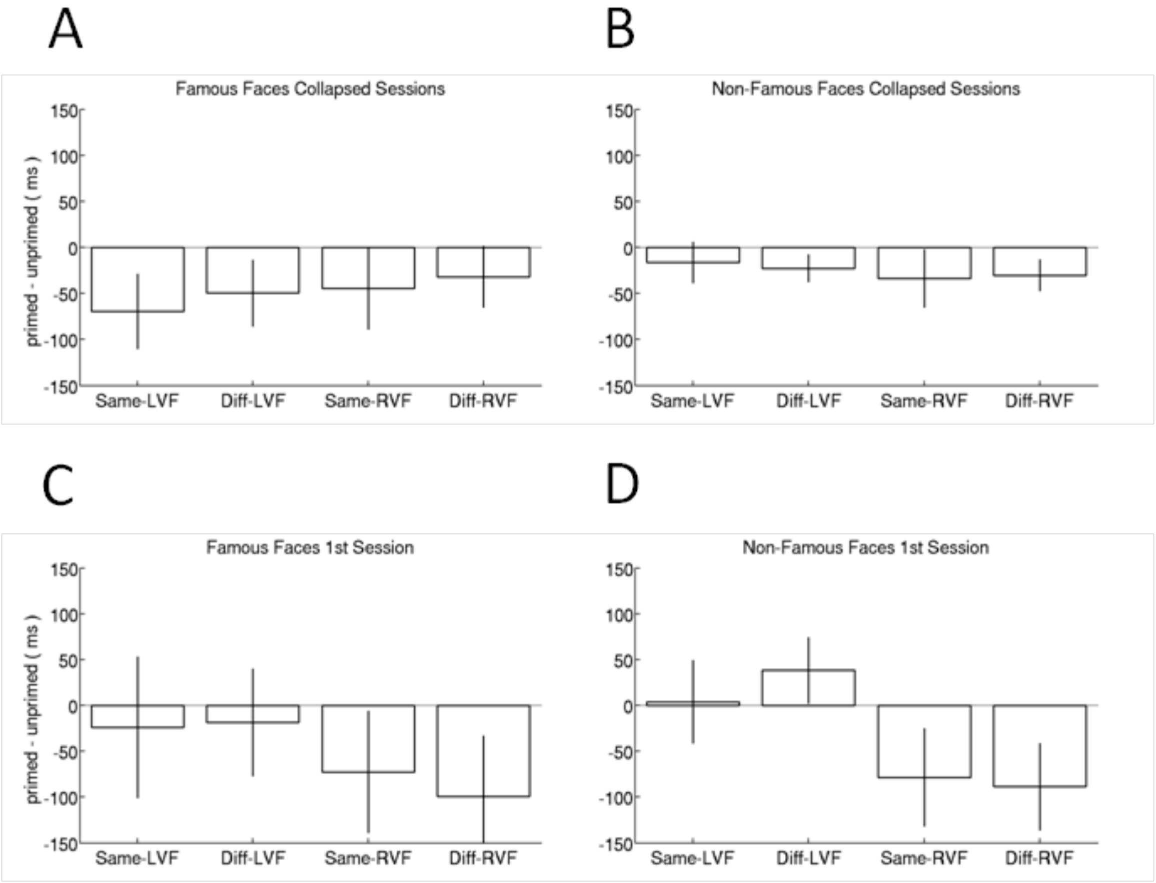


Figure 2-5: Mean (N= 17) and one-tailed 95% confidence intervals (error bars) of RT priming scores for all sessions (panels A and B) and Session 1 only (panels C and D) for famous and non-famous faces, as a function of hemifield and prime condition in Experiment 2.

Priming was found to be significant for the Different-LVF and Different-RVF conditions (see Figure 2-5B). When restricting data to Session 1 only, the two-way ANOVA for famous faces did not show any main effects or interactions, Fs<1.53, p>0.2, though significant priming was only found in the RVF, for both same view and different view conditions (see Figure 2-5C). For non-famous faces, there was a significant main effect of hemifield, F(1,16)=10.3, p<0.01, as collapsing across view, priming in the RVF (M=-84 ms) was greater than priming in the LVF (M=+21 ms). Priming was again significant only in the Same-RVF and Different-RVF conditions (see Figure 2-5D), though there was also a significant negative priming effect (+36 ms) for the Different-LVF condition, t(16) = 1.85, p<0.05.

Note however, that this did not survive a two-tailed test (given that we use one-tailed tests due to our prediction that priming will cause a decrease in RTs), hence may be a Type I error. Note that, unlike with Experiment 1, the hemifield-by-view interaction was not significant.

2.9 Discussion

The main result of Experiment 2 was that it failed to replicate the critical interaction between hemifield and view on priming that was found for RTs to correctly classify famous faces as familiar in Experiment 1. There were main effects of view and hemifield on priming for accuracy and/or RTs, as discussed below, but these do not directly support the DNS theory.

Priming of d' (fame discrimination) in Experiment 2 was reliable in all conditions, unlike in Experiment 1. This probably reflected the shorter lag between prime and probe (rather than greater number of trials), because this priming was found even when analysing the first session only (with trial numbers comparable to Experiment 1). Like Experiment 1, accuracy priming was greater for Same than Different views, though unlike Experiment 1, there was no concurrent evidence of greater priming for RVF than LVF faces. These effects did not interact with session, suggesting that they were not affected by "long-lag" repetition of faces across sessions.

The pattern of priming for RTs was more complex, because it did interact with session. This may be partly due to a main effect of session on unprimed RTs, which decreased across sessions, either due to overall task practice effects, or long-lag repetition effects across sessions. This baseline effect may have modulated priming effects. Indeed, baseline analysis showed that, across sessions, RTs went from a LVF advantage in Session 1 (significant for non-famous faces and numerically so for famous faces), to the opposite pattern of a RVF advantage in Session 2, while there was no hemifield difference in Session 3. This seems to have affected priming (similarly famous and non-famous faces), as in Session 1 there was greater priming for the RVF, in Session 2 there was greater priming for the LVF, and in Session 3 there was no difference in priming. This suggests that multiple repetitions can further modulate hemispheric differences in priming, though this requires further confirmation and exploration (which goes beyond the purposes of the present thesis).

RTs priming for famous faces showed no reliable effect of hemifield, though it is noteworthy that, when analysing the first session only, priming only reached significance in RVF conditions. It remains unclear why this pattern changed across sessions, becoming reliable only for LVF presentations in Session 2 only (data not shown). If this effect does not reflect a Type I error, obviously it requires further investigation in the future, in order to investigate a possible modulation of hemispheric effects for more than a single repetition. For non-famous faces, we obtained reliable priming in RTs, unlike Experiment 1, with the patterns of priming being similar to those for famous faces. Indeed, the RVF advantage in priming was more evident, since the main effect of hemifield on priming was reliable in Session 1. While this may also reflect a baseline difference in unprimed conditions (as above), it is possible that "false fame" effects inhibited priming for non-famous faces in Experiment 1, but these were swamped by the shorter lag in Experiment 2. Nonetheless, the use of a fame judgement task still makes the interpretation of effects on non-famous faces difficult, especially when negative priming was found in some conditions (e.g., the Different-LVF condition in both Experiments 1 and 2).

For these reasons, we decided to restrict the stimuli to non-famous faces in the next experiment. This allows (i) larger stimulus sets containing two views, removing the need for repetition across conditions (sessions), (ii) better control of the two views, and (iii) the ability to address DNS theory without any potential confounds of lexical/semantic processing (see Discussion to Experiment 1). The task at test obviously needed to be changed, and was switched to male/female judgments (in turn requiring a new study task, for which a pleasant/unpleasant task was chosen as approximately orthogonal to the sex of the face, hence again minimising effects of stimulus-response learning; Horner & Henson, 2008). Even though the sex task tends to produce only small priming effects (Goshen-Gottstein & Ganel, 2000) no other tasks were obvious, or had been tested before. We therefore kept the short-lag design, to boost priming effects.

2.10 Experiment 3: Short-lag priming in a Sex Judgment Task for Unfamiliar faces

As explained above, this experiment used the same basic design as Experiment 2, except that only nonfamous faces were used, and the test task was changed to sex judgments. The two views of the non-famous faces were also better controlled than in Experiments 1-2, with the stimuli being taken from a standardised set with two photographs of each face taken under identical conditions, differing only in whether the view was full-frontal or averted by 45°.

2.11 Methods

2.11.1 Participants, Design, Materials

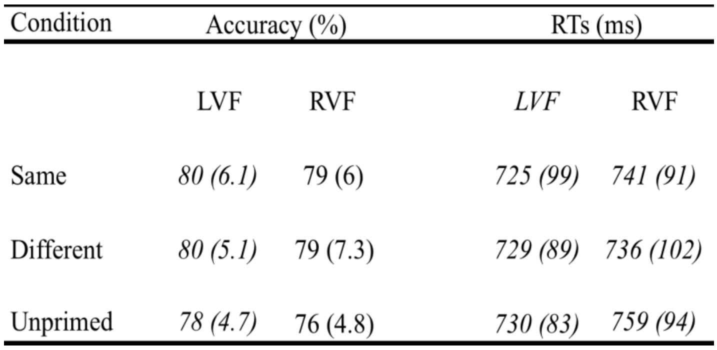
24 right-handed volunteers (15 female, 9 male) were tested. They all were students at the University of Cambridge, with a mean age was of 21 years. The core of the design was a 2 x 3 factorial design, with factors hemifield (LVF vs. RVF) and priming condition (same vs. different vs. unprimed), with an additional factor of session (first vs. second), as two sessions were run for each participant (see Procedure below). Photographs of 240 male and 240 female white Caucasian non-famous faces were taken from the FERET face database (Philips et al., 2000). For each face there were images of 2 views, a frontal view and a right 45° view (i.e., 960 different stimuli in total). Expressions were generally neutral. Each face was additionally cropped in order to remove obvious sex-predictive hair cues. Care was taken not to include in the stimuli set faces with other cues, such as jewellery and make-up, as well as to balance as accurately as possible luminance and contrast across faces. Assignment of stimuli to conditions was counterbalanced across participants.

2.11.2 Procedure

The same short-lag procedure as Experiment 2 was used. The experiment was run in two sessions of 400 trials, to provide a break, but no stimulus was repeated within or across sessions. The main differences from Experiment 2 (other than stimuli) were (i) participants performed a pleasantness task during the study phase (Like/Dislike?) and (ii) they performed a sex judgment task (Male/Female?) in the test phase. Another important difference was that lateralised faces were presented for 120 ms during the test phase (rather than 80 ms, as in Experiments 1 and 2). This was because pilot work had shown that longer durations were necessary to achieve accuracies around 75% correct in this new task. 120 ms should still be too short for saccades. Because there was no obvious bias towards “male” or “female” responses following priming, the d’ measure used in Experiments 1-2 was not deemed necessary for this new task, and accuracy was measured in terms of percentage correct (collapsing male and female faces).

2.12 Results

Accuracy and RTs are summarised in Table 2-3



Condition	Accuracy (%)		RTs (ms)	
	LVF	RVF	*LVF*	RVF
Same	*80 (6.1)*	79 (6)	*725 (99)*	*741 (91)*
Different	*80 (5.1)*	79 (7.3)	*729 (89)*	*736 (102)*
Unprimed	*78 (4.7)*	76 (4.8)	*730 (83)*	*759 (94)*

Table 2-3. Mean (N = 24) and standard deviation (SD) of accuracy and RTs as a function of hemifield and priming condition in Experiment 3.

2.12.1 Accuracy Analysis

The mean accuracy results are shown in Table 2-3. A 2x2x3 ANOVA with factors session (first vs. second), hemifield (LVF vs. RVF) and priming condition (same vs. different vs. unprimed) showed a significant main effect of priming condition, F(1,23)=4.69, $p < 0.05$, and a main effect of visual field, F(1,23)=5.29, $p < 0.05$, with generally higher accuracy for primed trials, and higher accuracy for the LVF than RVF. No other effects (e.g., of session) reached significance, F<1. A pair-wise comparison of the unprimed condition across hemispheres showed a significant advantage of the LVF compared to the RVF, t(23) = 2.55, $p < 0.01$.

2.12.2 Accuracy Priming Effects

Analysis of priming effects did not show any reliable main effects or interactions, F(1,23)’s<1.89, p’s >0.10, though priming was numerically greater in the RVF, as in Experiment 1. Priming was reliable in all conditions (Figure 2-6A).

2.12.3 Reaction Times

The omnibus 2x2x3 ANOVA showed a main effect of visual field, F(1,23)=9.62, $p < 0.05$, as the LVF showed faster RTs (M = 728 ms) compared with the RVF (M = 745 ms), but no other main effects or interactions, F(1,23)'s<1.89, p's>0.10. Direct contrasts of the baseline condition across hemispheres showed faster RTs in the LVF (M = 730ms) than the RVF (M = 759ms), t(23)=2.73, p<0.01.

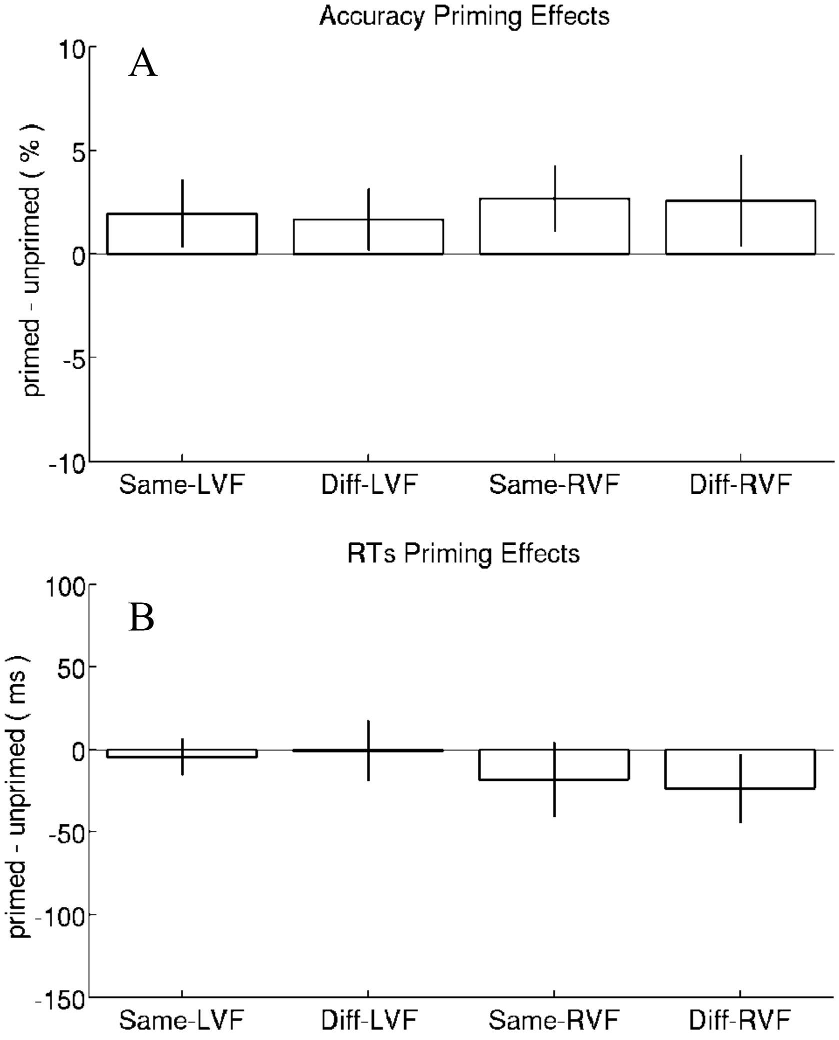


Figure 2-6. Mean (N = 24) and one-tailed 95% confidence intervals (error bars) of priming of (A) accuracy and (B) RTs as a function of hemifield and view in Experiment 3.

2.12.4 Reaction Times Priming Effects

Analysis of RT priming effects did not show any significant effects, Fs<1.89, ps>0.10, though priming was numerically greater in the RVF (-20.9 ms) than the LVF (-2.6 ms) when collapsing across views. Priming only reached significance in the RVF different-view condition (Figure 2-6B), though also approached significance in the RVF same-view condition.

2.13 Discussion

Though the effects of hemifield and of view on priming did not reach significance for either accuracy or RTs in Experiment 3, the numerical pattern of hemifield effects, and pattern of significant effects within each condition, resembled that emerging from Experiments 1 and 2. However, there was not even a trend for the critical hemifield-by-view interaction predicted by the DNS theory.

While there was little indication of effects of view, the numerical pattern of priming of both accuracy and RTs was greater for RVF probes than LVF probes. The fact that this pattern emerged for unfamiliar faces does not seem to concur with the hypothesis, raised in the Discussion of Experiment 1 that a RVF, priming advantage derives from a general advantage of the LH in lexical/semantic processing. However, given the concurrent, significant evidence for higher accuracy and faster RTs for unprimed faces presented to the LVF, the possibility remains that the RVF priming advantage is an artefact of different baseline levels.

One way to check whether greater priming for RVF probes arises because there is more “room” to detect priming, owing to lower accuracy/higher RTs for unprimed RVF probes – i.e., because of a range effect – is to examine the relationship between priming and baseline performance across participants. Figure 2-7 shows a scatter plot of the amount of priming against baseline for each participant for the RVF- Different condition of Experiment 3, where priming was reliable in both accuracy and RTs. If priming were due to a range effect, one might expect a positive correlation. However, there was no hint of any significant correlation for either accuracy or RTs, R’s<0.3, p’s>0.2 (indeed, any linear trend was actually negative).

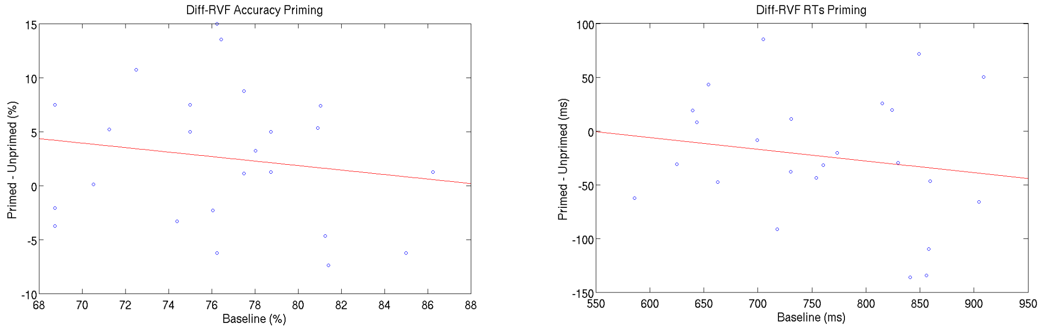


Figure 2-7: Plot of baseline (x-axis) against priming (y-axis) for each participant for the Diff-RVF condition for Accuracy (left panel), and RTs (right panel) for Experiment 3

No reliable correlations were found in any of the other experiments either. Nonetheless, different participants may have different true “baseline” RTs, so the absence of a correlation could simply be due to between-participant differences. A second way to address this potential range effect is to define priming by a proportional rather than additive measure, i.e. (primed - unprimed)/unprimed for RTs. This effectively downscales priming for the RVF, given the longer RTs in its unprimed condition. For accuracy, a proportional priming measure can be defined as (primed - unprimed) / (100% - unprimed), which again downscales priming for the RVF given that its baseline accuracy is numerically lower. When these scaled measures were applied to Experiments 1-3, the results remained almost identical, with the effects reported as significant for analysis of the unscaled (additive) priming scores remaining significant for scaled (proportional) priming scores. More specifically, for accuracy in Experiment 1, the main effect of hemifield remained reliable, $F(1,15) = 5.27$, $p < 0.05$, with the RVF ($M=0.31$) showing more priming than the LVF ($M=0.08$). For RTs for non-famous faces in Session 1 of Experiment 2, the RVF priming advantage also remained, $F(1,16)=8.45$, $p < 0.05$. For RTs of famous faces in Session1 of Experiment 2, as with non-scaled scores, the main effect of hemifield did not reach significance, though priming remained reliable within RVF Same and Different view conditions, $t(16) = 1.76$, $p < 0.05$ and $t(16) = 1.99$, $p < 0.05$ respectively. In Experiment 3, the main effect of hemifield remained nonsignificant (as with the non-scaled scores), but RT priming remained significant in the RVF Different condition, $t(23)=2.01$, $p<0.05$

Nonetheless, one could still argue that the precise scaling metrics are unknown (for example, priming could be non-linearly related to baseline performance), so despite these post hoc attempts to control for baseline differences, Experiment 4 was conducted to try match baseline performance experimentally. We aimed to achieve this by factorially varying the probe stimulus duration (80 ms vs. 120 ms). An absence of interaction between priming and stimulus duration would suggest range effects were not applicable. Furthermore, we planned to compare priming for 80ms LVF probes relative to 120ms RVF probes, in the hope that these conditions would have matched baseline performance. If baseline effects could be ruled out, then the RVF advantage in priming becomes more theoretically interesting, since it suggests that a single presentation of a face (prime) is sufficient to improve LH face-processing efficiency to the level found in the RH.

2.14 Experiment 4: Short-lag priming in a Sex Judgment Task for Unfamiliar faces, with manipulation of baseline.

The main motivation for this experiment was to match baseline performance for RVF (by using 120 ms probe durations) to that of the LVF (by using 80 ms probe durations), so that priming could be compared more safely across hemifields.

2.15 Methods

2.15.1 Participants, Materials, Design, Procedure

Twenty four right-handed participants were tested and paid for participation, (10 female). Mean age was 23 years. Participants were students of Cambridge University and members of the MRC-CBU volunteer panel. The procedure was identical to Experiment 3, except that the two sessions used probe durations of either 120ms or 80ms, the order of which were counterbalanced across participants.

2.16 Results

The mean results are shown in Table 2-4 :

2.16.1 Accuracy

The omnibus ANOVA with factors probe duration (80 ms vs. 120 ms), hemifield (LVF vs. RVF) and priming condition (same vs. different vs. unprimed) showed a borderline main effect of priming $F(1.97,45.4)=2.97$, $p=0.06$, but no other main effects or interactions were significant. The absence of a main effect of probe duration was surprising, since higher accuracy was expected for longer probe durations. This issue will be returned to later. Nonetheless, the planned comparison of 120 ms RVF probes with 80 ms LVF probes was conducted, for which baseline performance did not differ reliably, $t(23) = 0.42$, $p > 0.2$.

	Duration			
	80 ms		120 ms	
Accuracy (%)				
	LVF	RVF	*LVF*	RVF
Same	*77 (8.2)*	76 (9.3)	*80 (8.6)*	*77 (7.2)*
Different	*76 (10.4)*	76 (9.1)	*77 (7.1)*	*78 (10.5)*
Unprimed	*75 (9.1)*	76 (9.3)	*77 (6.8)*	*74 (8.1)*
RTs (ms)				
	LVF	RVF	LVF	RVF
Same	*670 (101)*	*677 (100)*	*705(79)*	*715 (84)*
Different	*667 (92)*	*678 (98)*	*692 (73)*	*694 (73)*
Unprimed	*674 (91)*	*683 (99)*	*704 (81)*	*711 (80)*

Table 2-4. Mean (N = 24) and standard deviation (SD) of accuracy and RTs as a function of hemifield and priming condition in Experiment 4.

2.16.2 Accuracy Priming effects with Matched Baselines

The priming effects from RVF-120 ms and LVF-80 ms were entered into an ANOVA with factors hemifield (LVF vs. RVF) and view (same vs. different). No effects were reliable. However, even though the main effect of hemifield did not reach significance, F(1,23)=1.42, p=0.24, the only individual conditions in which priming reached significance were in the RVF, i.e. Different-RVF, and Same-RVF (see Figure 2-8A).

2.16.3 Reaction Times

The omnibus ANOVA with factors probe duration hemifield and priming condition showed a borderline main effect of stimulus duration, F(1,23)=4.18, p=0.052, with 80 ms probe durations showing faster overall RTs than the 120 ms durations (675 ms and 704 ms respectively). The main effect of priming was also marginally significant, F(1,23)=3.16, p=0.06. Unfortunately, the RVF-120 ms

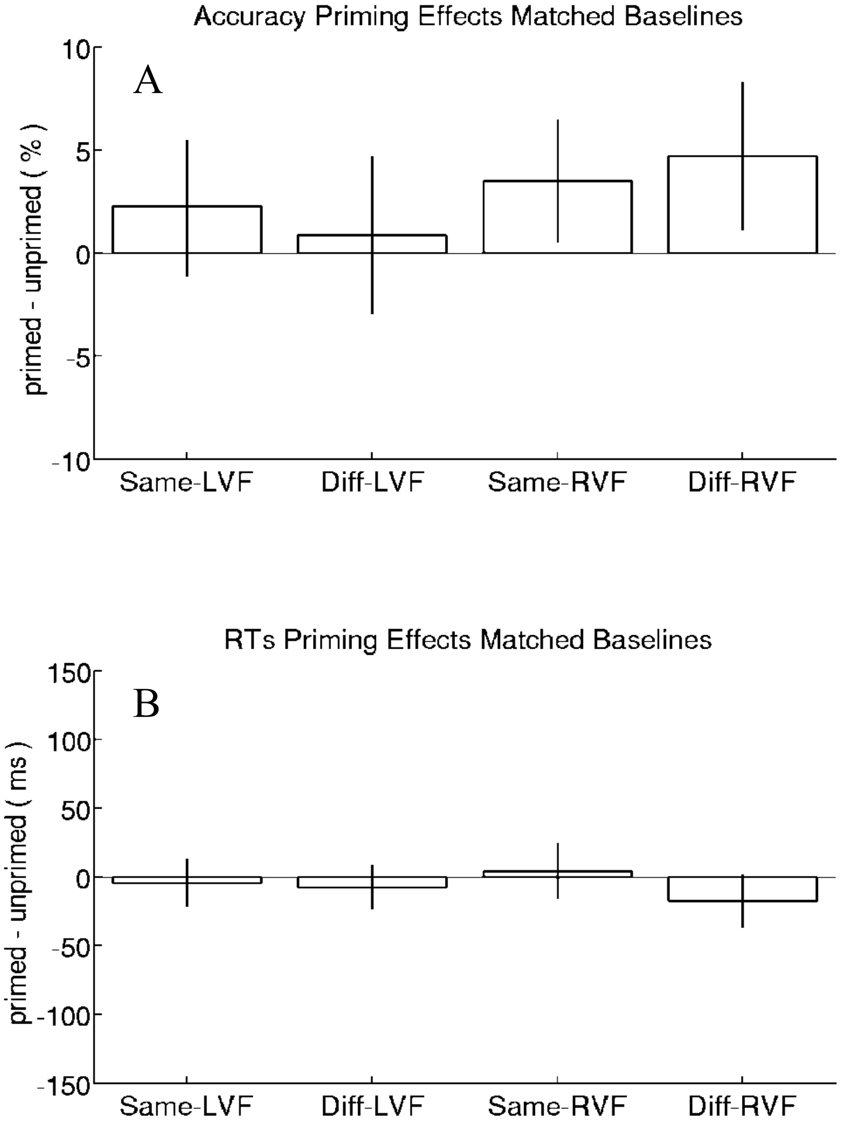


Figure 2-8. Mean (N = 24) and one-tailed 95% confidence intervals (error bars) of priming of accuracy (panel A) and RTs (panel B) as a function of hemifield and view in Experiment 4.

(M=711 ms) and LVF-80 ms (M=674 ms) RT baselines were not as well-matched as for accuracy, with a decrease in RTs for LVF relative to RVF that approached significance, t(23) = 1.80, p = 0.09 (two-tailed) Nonetheless, the planned comparison of LVF-80 ms and RVF-120 ms conditions was conducted

2.16.4 RT Priming Effects with "Matched" Baselines

The RTs priming effects from RVF-120 ms and RH-80 ms were entered into an ANOVA with factors hemifield and view. There were no significant effects, Fs<1.

Note that similarly with Experiment 3, the only condition that approached significance was the Different-RVF condition (see Figure 2-8B).

2.17 Discussion

The purpose of this experiment was to extend the results of Experiment 3 - where priming appeared to be greater for RVF than LVF probes - to a situation in which baseline (unprimed) performance was matched, by comparing across two different probe durations. Unfortunately, the probe duration manipulation did not produce the expected pattern of more accurate and slower RTs for shorter probe durations (80 ms versus the 120 ms used in Experiment 3). The reason for this is unclear, since the same baseline manipulation worked better in Experiments 5-6 of the next chapter. Nonetheless, the numerical pattern of priming in accuracy and RTs (Figures 2-8A and 2-8B) resembled that in Experiment 3 (Figure 2-6A and 2-6B), with greater priming for RVF than LVF probes, while for RTs only consistently reaching significance for RVF probe conditions. Again, there was no support for the DNS prediction of a hemifield-by-view interaction on priming.

2.18 General Discussion

Across four experiments, little support was found for DNS theory. The only supportive evidence came from RT priming effects in Experiment 1 for famous faces, but this was not replicated in Experiment 2. Even if this interaction were real, the fact that it was found for famous faces also means that it could reflect the well-known LH advantage in lexical-semantic processing, rather than anything to do with the abstract/specific nature of visual object representations assumed by DNS theory. Experiments 3 and 4 therefore only used unfamiliar faces (with no lexical/semantic associations), and in neither experiment was there any sign of an interaction between hemifield and view on priming. One possibility is that evidence for DNS theory only comes from long-lag repetition paradigms, since only Experiment 1 used long-lags (Experiments 2-4 used short lags of approximately 8-20 intervening stimuli). However, the theoretical reason for this importance of lag is unclear. Alternatively, some other minor procedural differences between Marsolek's paradigms and those in Experiments 1-4 were important (e.g. longer presentation times), though such boundary conditions arguably make DNS theory less appealing. However, Experiment 1 was conducted after direct communication with

Marsolek, following his directions in methodology and design. Furthermore, it should be noted that Marsolek has recently adopted somewhat extreme procedural requirements. For example, in Marsolek and Burgund (2008), only male, right-handed participants were used, and effects were very small, requiring 48 participants (making neuroimaging investigations less feasible). This severely restricts the generalisation of Marsolek's DNS theory, which is one reason why it was not pursued further in this thesis.Another possibility is that DNS theory does not apply to faces, which may have specialised processing in the brain, such as holistic processing in the RH (see Section 2.1.3), relative to other visual objects. Given the focus of the present thesis on face processing, this is another reason why DNS theory (specifically manipulations of view) were not explored in subsequent chapters.

Although no significant in every experiment, one clear pattern that did emerge across Experiments 1-4 was greater priming for RVF than LVF probes. This was only a numerical pattern in Experiments 3-4, but was reliable in Experiment 1 (for famous face accuracy and d') and in Experiment 2 (for non-famous RTs). Indeed, the only conditions in which priming in accuracy and/or RTs was consistently reliable across experiments involved RVF probes. Another consistent pattern that was found was better performance for unprimed probes in LVF than RVF. This replicates the basic RH advantage in face processing. However, it also raises the possibility that the greater priming for RVF probes is an artefact of different baseline performance rates. This seemed unlikely however because (i) there was no evidence for a positive correlation between the amount of priming and unprimed performance in accuracy or RTs across participants, (ii) essentially the same results remained when priming was scored by a proportional rather than additive measure, and (iii) the same numerical pattern (and pattern of significant single condition priming effects) remained in Experiment 4 when baseline performance was better matched empirically, by comparing longer duration RVF probes (120ms) with shorter duration LVF probes (80ms). Indeed, a similar pattern is found in Experiments 5-6 of Chapter 3, which achieved much closer matching of baseline performance.

Thus the greater priming effects for RVF than LVF probes seem to reflect a real phenomenon. In loose terms, absence of priming in the RH may reflect a "saturation" of face-processing efficiency. In other words, if the RH is already close to "optimal" in face-processing, it may benefit little (or not at all) from priming, so no priming is found from CVF primes (which are processed by both hemispheres) to LVF probes. This working hypothesis is tested more fully in Chapter 3, where both primes and probes were lateralised, with a factorial crossing of prime and probe hemifield.

2.19 Conclusions

In four experiments we aimed to examine whether the degree of generalisation of behavioural priming across different views of familiar or unfamiliar faces differed when probe faces were presented to left versus right hemifields. As predicted by Marsolek's DNS theory, there should be evidence of greater priming across views for stimuli preferentially processed by the LH (i.e., presented to RVF). However, the experiments using central primes and lateralised probes (as used by Marsolek) failed to find convincing evidence for this prediction. Presentations to the RVF showed consistently greater priming, for both familiarity judgments to familiar faces and sex judgments to unfamiliar faces. There was a also baseline advantage for unprimed LVF probes (consistent with the well-known RH advantage in face-processing), however, the greater priming for RVF probes did not appear explicable simply in terms of a range effect. This led to a working hypothesis that face processing is already optimal in the RH, but less than optimal encoding for the LH gives room for priming effects to emerge when a face is repeated in the RVF.

Chapter 3: Behavioural DVF Priming Crossing Prime and Probe Hemifield

3.1 Introduction

In Chapter 2 hemifield differences in priming were explored as a function of view. One consistent finding across almost all experiments was a LVF advantage for unprimed stimuli, for both accuracy and RTs consistent with the well-known RH advantage in face-processing. However, this was not reflected in priming, as in all four experiments, probes in the RVF showed more priming from central primes than did probes in the LVF (mainly for RTs). This was most consistent for non-famous faces. As discussed in Chapter 2, it is possible that lower baseline performance in the LVF suppressed priming effects: Though priming remained using a proportional measure, and did not appear affected by manipulations of baseline performance (in Experiment 4), this issue was not resolved conclusively (which was another aim of the experiments in this chapter).

The priming results from Experiments 1-4 suggest that priming of a face is modulated by an encoding advantage of the RH. We call this the "RH Structural Processing Advantage" (RH-SPA) hypothesis. The "structural" term refers to the "structural encoding" step in the Bruce and Young (1986) model, which assumes an early perceptual stage where encoding of faces occurs, before face recognition. Rhodes (1985) suggested that this component is likely to have an advantage in the RH. Indeed, recent neuroimaging data show that the right OFA is particularly involved in the process (e.g., Pitcher et al., 2007, 2009; Rotshtein et al., 2005), while commonly a larger N170 (also thought to manifest structural encoding) is found over RH occipo-temporal channels (e.g., Rossion et al., 2003). Since we have consistently found a LVF-RH baseline advantage for nonfamous faces, it is likely that this reflects an advantage within this "structural encoding" component. More specifically, if structural encoding by the RH is already close to optimal, then it should show little to no effect of priming, i.e., for LVF probes that follow a central (or RVF) prime. Non-optimal structural encoding of the LH however means that RVF probes benefit from prior encoding in the RH of a central (or LVF) prime. The main goal of the experiments in the present chapter was to test this hypothesis further, by using lateralized presentations of primes as well as probes. If our hypothesis is correct, then priming should be seen only in one of the four factorial combinations of prime and probe hemifields: namely, for LVF primes and RVF probes.

Although there is a wealth of studies reporting hemifield/hemispheric differences in face processing (see Chapter 1), surprisingly there are only three prior studies, published relatively recently, that investigated hemifield asymmetries in face priming (Bourne & Hole, 2006; Bourne, Vladeanu & Hole, 2009; Cooper et al., 2007). All three studies focused on a design that essentially mirrored that of Experiments 1-4, with lateralized primes and central probes (rather than central primes and lateralized probes)[3]. Furthermore, all three studies focused on famous face priming within a familiarity-judgment task at both study and test (a task in which it is difficult to interpret priming for nonfamous faces, and repetition of which raises the possible confound of stimulus-response learning, as discussed in Chapter 2). Because probes were foveal, and the authors used highly famous faces, accuracy was close to ceiling, and so priming was measured in RTs. The two Bourne studies found significant priming only when primes were presented in the LVF. The Cooper et al. study found priming for both hemifields, but larger for LVF (behaviourally), while they also reported a larger in amplitude N250r component over the RH (though not dependent on hemifield).

Prima facie, these findings of priming for LVF rather than RVF probes would appear to contradict findings from the experiments in Chapter 2. Furthermore, because central visual field (CVF) probes are processed by both hemispheres, and the RH is already assumed close to optimal in structural encoding, our RH-SPA hypothesis does not predict such priming from LVF primes to CVF probes. One possibility for these differences is the use of lateralized primes (in these prior studies) versus lateralized probes (in Chapter 2). It is worth emphasizing however that we think a more likely explanation for the difference between these previous experiments and those in Chapter 2 is that the previous studies found priming for famous faces only (no priming was found for non-famous faces). This means that additional face recognition and semantic processing might have contributed to priming. This is an important variable that could possibly modulate priming effects, given that the RH might have a further advantage in processing of famous faces (as well as structural encoding). Our working hypothesis is

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[3] These studies also used different repetition lags, with Bourne & Hole, 2006 and Bourne et al., 2009 using long-lag priming, and Cooper et al., 2007 using immediate priming.

mainly concerned with perceptual effects reflected by the RVF priming effects found for non-famous faces in Experiments 2-4. Hence, the following two experiments used only non-famous faces, with tasks and lags identical to those in Experiments 3-4 of the previous chapter.

3.2 Experiment 5: Priming of Non-famous Faces with Lateralised Primes

If the condition in which primes are presented to the LVF and probes to the RVF is denoted as "LVF-RVF ", etc, then our RH-SPA hypothesis predicts that priming will be maximal for the LVF-RVF condition, but that there should be little priming for the LVF-LVF or RVF-LVF conditions, since the RH is already optimal at structural encoding (of the probe). The precise prediction for the RVF-RVF condition is less clear, because the impact of preferential LH (versus RH) encoding of primes cannot be determined from the central primes used in Chapter 2. Nonetheless, we would expect any priming in the RVF-RVF will be less than for the LVF-RVF condition, if primes are less well encoded by the LH than RH.

As it happens, Bourne and Hole (2006) did factorially cross prime and probe hemifieds in one experiment (their Experiment 2), therefore including a RVF-RVF condition. Consistent with our hypothesis (though with famous faces), they found priming in the LVF-RVF condition. Interestingly, they found no reliable priming in a RVF-RVF condition, suggesting that the LH does not encode faces well enough to produce subsequent priming. Nonetheless, it should be noted that they also found priming when probes were presented to the LVF (i.e., the RVF-LVF and LVF-LVF conditions), contrary to the hypothesis proposed here. In addition to the differences in stimuli, tasks and repetition lag (described above), a somewhat unusual aspect of their data, however, was that there was a difference in baseline (unprimed) RTs that was actually the opposite to what would be expected from the well-known RH face-processing advantage: Namely, mean RT for unprimed LVF faces (M=699ms) was longer than unprimed RVF faces (M=634ms). This slower LVF baseline may have artifactually inflated the amount of priming for LVF probes. One possible explanation for this atypical baseline difference might be contributions from more efficient semantic processing in the LH (see Chapter 2). This may have been further exasperated by the fact that Bourne and Hole only used five stimuli for each famous face condition, which were highly familiar to participants.

The present experiments used a much larger set of stimuli, in order to maximize the number of trials for any neuroimaging experiment (as in Chapter 6), while avoiding repetition of stimuli across blocks/sessions. Furthermore, to re-address such baseline issues, the present experiments had a further factorial manipulation of stimulus duration (of both prime and probe). Two groups of participants were used, either with 80 ms or 120 ms presentations.

3. 3 Methods

3.3.1 Participants, Design, Materials and Procedure

For the 80 ms group, 16 volunteers (10 female, 6 male) were tested (of which 4 were dropped for reasons given in Results). For the 120 ms session 12 participants were tested (8 female, 4 male). They were all right handed students at the University of Cambridge. Mean age was 22. The design was a mixed 2 x 2 x 3 factorial design. The between-participants factor was stimulus duration (80 ms vs. 120 ms). The within-participants factors were: hemifield and repetition condition. The factor hemifield refers to the visual field in which the probe was presented (LVF vs. RVF), while the factor of repetition condition refers to prime-probe location (repetition in same hemifield vs. repetition in different hemifield vs. unprimed probe). During the study blocks, primes were presented either to the RVF or the LVF. During test blocks, a probe in either the RVF or the LVF would be primed by a RVF prime, a LVF prime, or a novel face would be presented, which served as the baseline (unprimed) condition. Hence the six main conditions resulting from this design were: RVF-RVF, LVF-LVF (i.e., same prime-probe location); LVF- RVF, RVF -LVF (i.e., different prime-probe location), unprimed RVF probes; unprimed LVF probes. Note that view was no longer a factor, so the frontal views of the nonfamous faces from Experiments 3 and 4 were used. Otherwise, the procedure was identical to that in Experiments 3-4.

3.4 Results

Four participants were excluded from the 80ms session for the following reasons. One reported after the experiment that he had Attention Deficit Disorder, and analysis confirmed a large number of missed trials (43%). Two more participants had also a large number of missed trials (62% and 58%), possibly due to a technical fault. One participant was removed due to extreme bias to respond “male” (82%). Mean accuracy and RTs are shown in Table 3-1.

3.4.1 Accuracy

The omnibus 2 x 2 x 3 mixed ANOVA with the between-participant factor of stimulus duration (80 ms vs. 120 ms) and the within-participant factors of hemifield (RVF vs. LVF) and repetition condition (repetition in same hemifield vs. repetition in different hemifield vs. unprimed probe) did not show any reliable effects (Fs < 1). Comparison of unprimed conditions did not show any significant hemispheric differences, t(22) = 0.29, p = 0.38. While the lack of any effect of presentation duration on accuracy is surprising, clear effects of presentation duration were found on RTs.

Accuracy (%)	Presentation Duration			
	80ms		120ms	
Probe **Prime**	LVF	RVF	LVF	RVF
RVF	*75 (9.7)*	*78 (7.2)*	*75 (8.6)*	*78 (7.1)*
LVF	*75 (8.5)*	*74 (6.7)*	*76 (8.5)*	*78 (9.5)*
Unprimed	*77 (6.9)*	*76 (8.5)*	*76 (10.6)*	*78 (6.3)*
RTs (ms)				
RVF	853 (153)	864 (149)	653 (100)	663 (93)
LVF	*867 (174)*	*789 (111)*	*673 (182)*	*647 (99)*
Unprimed	*844 (132)*	*862 (163)*	*664 (106)*	*682 (136)*

Table 3-1: Accuracy and RTs for 80 ms and 120 ms presentations as a function of Prime and Probe hemifields in Experiment 5

3.4.2 Reaction Times

The omnibus 2 x 2 x 3 mixed-ANOVA showed a main effect of stimulus duration group, F(1,22) = 14.6, p <0.001. Participants with 120 ms presentations were almost 200 ms faster (M = 664 ms) than participants with 80 ms presentations (M = 860 ms), as expected. Interestingly, duration did not interact with hemifield or repetition condition (Fs < 1). The only other effect that was significant was the hemifield-by-repetition condition interaction, F(1,22) = 2.96, p=0.07, which was deemed reliable given the predicted direction of greater priming for RVF probes (i.e., when one-tailed). This interaction is explored further in the analysis of priming effects below. No reliable difference between hemispheres was found for the baseline contrast collapsed across presentation duration, t(22) = 1.05, p = 0.16 (nor for either for 80 ms durations, t(11) = 0.62, p = 0.27 or 120 ms durations, t(11) = 1.07, p=0.15, separately).

3.4.3 Reaction Time Priming effects

A 2 x 2 x 2 mixed-ANOVA on priming scores (primed minus unprimed) showed only a significant main effect of prime-probe location (same vs. different), F(1,22) = 5.35, p<0.05.This main effect seems to be driven by a significant priming effect for the LVF-RVF condition (see Figure 3-1A) which also showed larger priming that than the RVF-RVF condition, t(11)=3.36, p<0.05. There were no reliable effects of probe hemifield or of stimulus duration on priming. The priming effects for each condition are shown in Figure 3-1, collapsed across stimulus duration

3.4.4 Matched Baseline analysis

Unfortunately, the RTs for the unprimed conditions were not precisely matched. They were approximately 160 ms faster for RVF stimuli presented for 120ms than for LVF stimuli presented for 80ms, t(11)=3.29, p<0.01, i.e., were reversed by the manipulation of stimulus duration. Nonetheless, an ANOVA with factors prime-probe location and hemifield failed to show any significant effects or interactions Fs<2.3, ps>0.15 possibly due to reduced power. Note that the only condition that approached significance was the LVF-RVF, t(11)=1.57, p=0.07 (also see Figure 3-1B). However, the absence of interaction of stimulus duration with priming, and the fact that LVF-RVF condition was significant for both when collapsing across duration t(22)=2.55, p<0.01 as well as for 80 ms probes, t(11)=2.92, p<0.01, provides strong evidence in support of the claim in Chapter 2, that the greater priming for RVF probes following LVF or CVF primes is not an artifact of range effects.

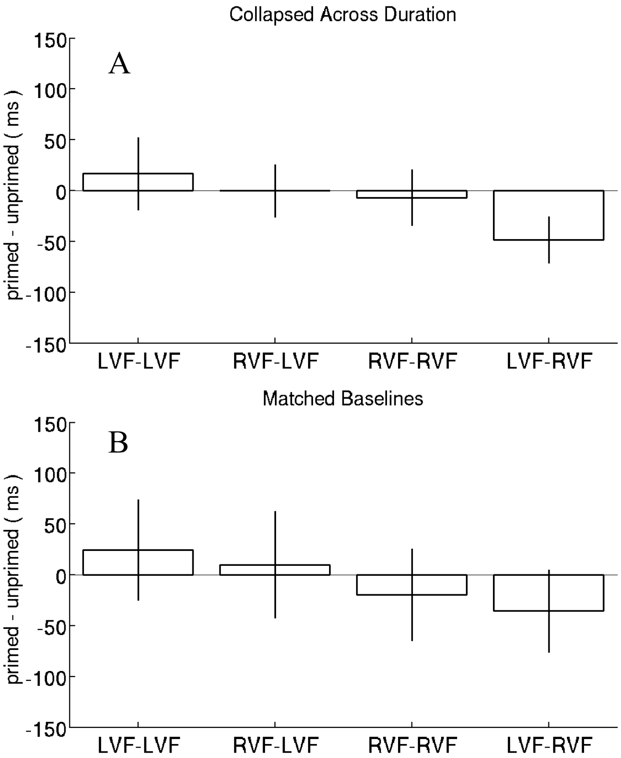


Figure 3-1: Mean (N = 12) and one-tailed 95% confidence intervals (error bars) of priming effects of RTs as a function of prime and probe hemifield for collapsed across stimulus duration (panel A) and for matched baselines (panel B) in Experiment 5.

3.5 Discussion

The results of Experiment 5 are consistent with the RH-SPA hypothesis, in that the LVF-RVF condition showed greatest priming of RTs. Moreover, this pattern did not seem to be affected by the manipulation of stimulus duration (which had a large effect on overall RTs), it was the only condition that showed priming for both 80 ms and 120 ms durations (and when durations were collapsed). Also given the absence of any interaction of priming with stimulus duration suggests that the results are not due to a range effect. It is also interesting that no priming was found for the RVF-RVF condition, suggesting that the LH cannot encode (non-famous) faces sufficiently to produce priming (a situation that could not be tested using the CVF primes in Chapter 2).

The lack of priming in the two LVF probe conditions does not replicate the findings of Bourne and Hole, (2006; Experiment 2). As mentioned in Section 3.2, there are several possible reasons for this, including their use of famous faces in a familiarity-judgment task, and their unusual baselines that actually showed a RVF rather than the typical LVF advantage. These issues will be revisited in Section 3.10. Firstly though, we ran a replication of Experiment 5, but using a within- rather than between-participant manipulation of stimulus duration. This is because the effect of stimulus duration in Experiment 5 was larger than expected, and the opposite of that found with the within-participant manipulation in Experiment 4 (and might therefore be an uninteresting random difference in groups). A second reason was that the claim that reliable priming only occurs in the LVF- RVF condition is a strong and novel claim, which required replication.

3.6 Experiment 6: Within-participants replication of Experiment 5

Experiment 6 was conducted to replicate the priming pattern found in Experiment 5 as well as address surprisingly large between-groups differences in RTs. Hence, Experiment 6 was exactly the same as Experiment 5, but with stimulus duration being a within-participants factor (i.e., each participant had both a 80 ms and a 120 ms session).

3.7 Methods

3.7.1 Participants

13 volunteers (7 female, 6 male) were tested (one was dropped for reasons given in Results). They all were students at the University of Cambridge and members of the CBU volunteer panel. Mean age was 24.2 years.

3.7.2 Design, Materials and Procedure

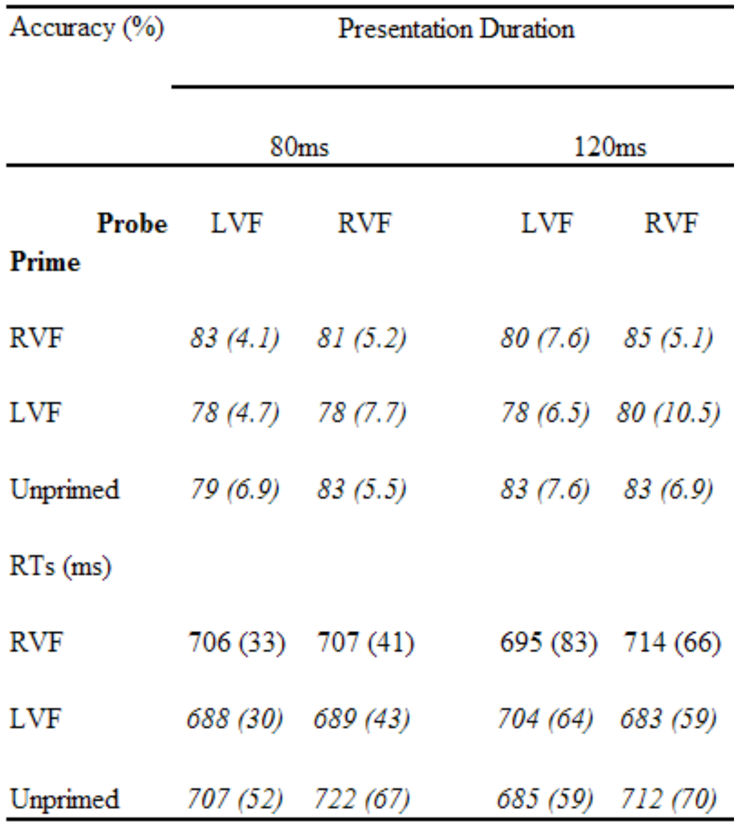
Same as Experiment 5. The only differences were that stimulus duration was a within-participants factor, hence the 80 ms and 120 ms sessions were counterbalanced across the same participants.

3.8 Results

One participant (male) was removed from the analysis because he had a high percentage of missed trials for both sessions (68%). Accuracy and RTs are shown in Table 3-2.

3.8.1 Accuracy

Overall accuracy for 80 ms presentations was 80% and for 120 ms sessions was 81%. Analysis of accuracy with factors stimulus duration (80 ms vs.120 ms), hemifield (RVF vs. LVF) and repetition condition (same vs. different vs. unprimed) showed a reliable three-way interaction, F(1.86,20.44)=4.73, $p<0.05$. This interaction is further explored by analysing priming effects below. T-tests of unprimed conditions did not show any significant hemispheric differences for 120 ms presentations, t(11) = 0.39, p= 0.44, and was borderline significant for 80ms presentations, t(11) = 1.65, p = 0.06, with the RVF showing larger accuracy than the LVF, as expected.



Accuracy (%)	Presentation Duration			
	80ms		120ms	
Probe **Prime**	LVF	RVF	LVF	RVF
RVF	*83 (4.1)*	*81 (5.2)*	*80 (7.6)*	*85 (5.1)*
LVF	*78 (4.7)*	*78 (7.7)*	*78 (6.5)*	*80 (10.5)*
Unprimed	*79 (6.9)*	*83 (5.5)*	*83 (7.6)*	*83 (6.9)*
RTs (ms)				
RVF	706 (33)	707 (41)	695 (83)	714 (66)
LVF	*688 (30)*	*689 (43)*	*704 (64)*	*683 (59)*
Unprimed	*707 (52)*	*722 (67)*	*685 (59)*	*712 (70)*

Table 3-2: Accuracy and RTs for 80 ms and 120 ms presentations as a function of Prime and Probe hemifields in Experiment 6

3.8.2 Accuracy Priming Effects

Repetition effects for each condition are shown in Figure 3-2. Since the three-way interaction on accuracy scores was significant, it was further explored with priming scores (primed minus unprimed), using separate two-way ANOVAs for each duration, with factors probe hemisphere (RVF vs. LVF) and prime-probe location (same vs. different). Analysis for 80ms conditions showed a significant two-way interaction of probe hemisphere and prime-probe location, F(1,11)=6.72, p<0.05. Priming was only reliable in the LVF-RVF condition: However, it was negative priming, i.e., reduced accuracy relative to unprimed baseline. Analysis of priming effects of 120 ms presentations showed a significant main effect of prime-probe location, F(1,11)=6.02, p<.05, with greater negative priming for LVF probes. However, priming did not reach significance in any condition. The quite different patterns of priming across 80 ms and 120 ms conditions (see Figure 3-2) suggest that some of these priming effects may be type I error. Therefore the three-way interaction between stimulus duration, prime-probe location and hemifield were not explored further, especially given clearer effects in the RTs.

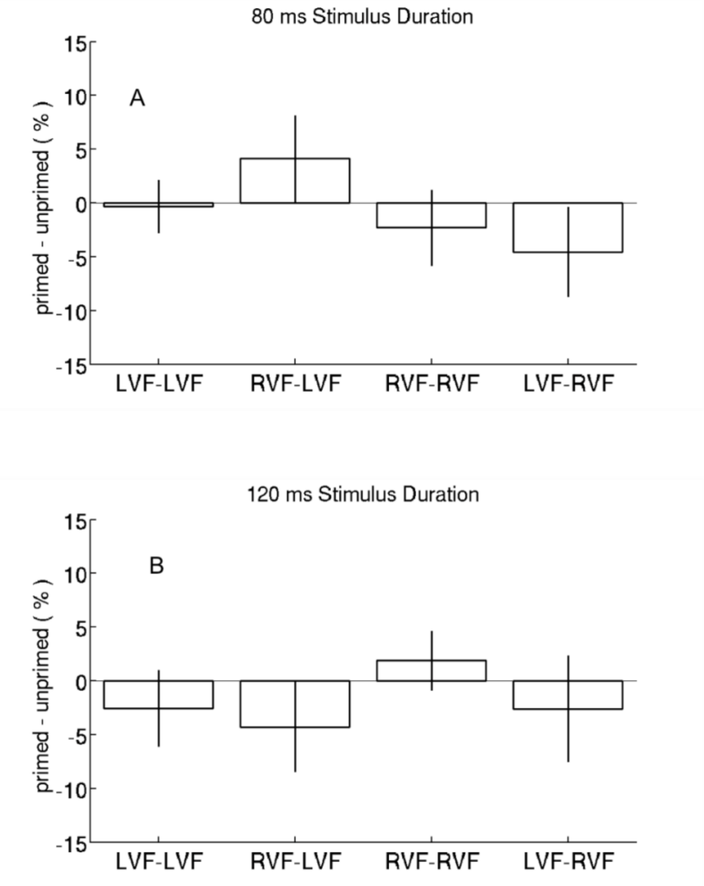


Figure 3-2: Mean (N =12) and one-tailed 95% confidence intervals (error bars) of priming effects of Accuracy as a function of prime and probe hemifield for 80 ms stimulus duration (panel A) and 120 ms stimulus duration (panel B) for Experiment 6

3.8.3 Reaction Times

The omnibus 2 x 2 x 3 ANOVA with factors stimulus duration, hemifield and repetition condition, showed a reliable two-way interaction between hemifield and repetition condition, F(1.40,15.35)=7.15, $p<0.05$. Unlike Experiment 5, results did not show a main effect of stimulus duration, F(1,11)=1.33, p=0.27. The two-way interaction will be further explored below as repetition effects. When collapsing across durations, a paired t-test for the baselines showed that RTs for unprimed probes were borderline faster for the LVF (M=696 ms) than for the RVF (M=717 ms), t(11) = 1.72, p = 0.06.

3.8.4 Reaction Time Priming effects

The repetition effects for each condition are shown in Figure 3-3. Since the omnibus ANOVA did not show any effects of stimulus duration, data from 80 ms and 120 ms durations were collapsed in analysis of priming scores. The two-way interaction with factors hemifield and prime-probe location was significant, F(1,11)=24.1, $p<0.001$. Priming was only reliable in the LVF-RVF condition t(11)=3.05, $p<0.01$, as predicted and replicating Experiment 5.

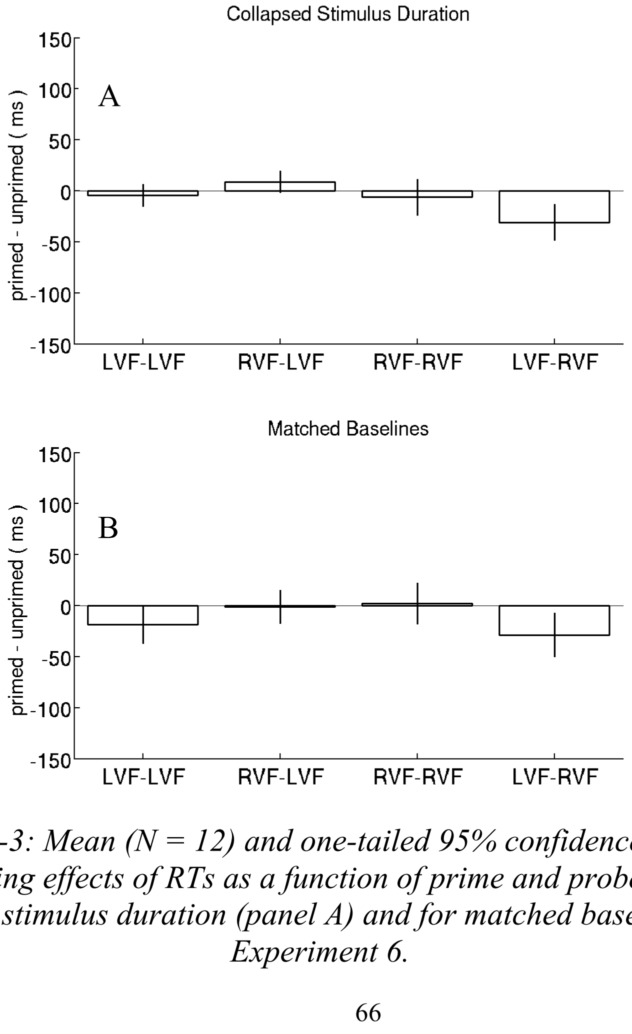


Figure 3-3: Mean (N = 12) and one-tailed 95% confidence intervals (error bars) of priming effects of RTs as a function of prime and probe hemifield for collapsed across stimulus duration (panel A) and for matched baselines (panel B) in Experiment 6.

3.8.5 Matched Baseline analysis

Since the LVF baseline for 80 ms presentations (M = 707 ms) matched the RVF baseline for 120ms presentations (M = 712 ms), t(11)=0.25, p>0.8, the priming effects of RVF probes for 120ms presentations and LVF probes for 80ms presentations were entered in an ANOVA. Analysis with factors hemifield and prime-probe location hemisphere showed a significant two-way interaction, F(1,11)=14.2, p <0 .01. Furthermore, only priming in the LVF-RVF condition was reliable t(11)=2.4, p<0.5. Hence, the predicted pattern of greatest priming for the LVF-RVF condition remains reliable when baselines for RVF and LVF probes are matched.

3.9 Discussion

The within-participant results of Experiment 6 replicate the between-participant results of Experiment 5, at least with regard to RT priming. Thus, while the manipulation of presentation duration did not have such a large effect on RTs in Experiment 6 as it did in Experiment 5 (possibly due to smaller between-participant differences in Experiment 6 compared to Experiment 5), the pattern of priming was essentially the same, with greatest priming in the LVF-RVF condition. Importantly, the interaction between hemifield and prime-probe location remained reliable even when baseline (unprimed) performance was matched. These findings support our RH-SPA hypothesis. It should be noted that accuracy showed negative priming (which was reliable for the RVF-LVF 80 ms condition) for the first time with these stimuli and this task. Thus, it is possible therefore that the positive priming (faster RTs) reflect some form of speed-accuracy tradeoff in this experiment. However, even if this were the case, such a tradeoff could not explain the general RT priming pattern seen in Experiment 5 where no such negative priming effects were found in accuracy. We therefore think that this negative accuracy priming was a type I error (particularly since it was not consistent across stimulus durations).

3.10 General Discussion

Experiments 5 and 6 supported our working hypothesis. More specifically, a robust finding of these experiments was that significant priming only occurred for the LVF-RVF condition, i.e. when the prime was preferentially processed by the RH and the probe preferentially processed by the LH. Furthermore, the lack of priming when the LH preferentially processed both prime and probe (i.e., the RVF-RVF condition) allows our hypothesis can to be elaborated to state not only that no priming is found for LVF probes because the RH is already optimal at structural encoding, but also that no priming is found from RVF primes, because the structural encoding in the LH is unable to support subsequent priming (though see Chapter 7 for more detailed exposition of this hypothesis, e.g., in terms of inter-hemispheric communication).

It should be noted that our findings are not consistent with the only prior studies to investigate priming as a function of hemifield (Bourne & Hole, 2006; Bourne et al., 2009; Cooper et al., 2007). These studies report a priming advantage when primes were presented in the LVF, and significant priming in the LVF-LVF and RVF-LVF condition in Experiment 2 in Bourne & Hole (2006; we did not find reliable priming for these conditions). The main difference is that the studies of Bourne et al and Cooper et al used famous faces in a familiarity judgment task. There were also other methodological differences between our experiments and theirs (i.e., 4 °of eccentricity, long lag priming and backward masking in the Bourne et al. studies or 2 ° eccentricity and immediate priming in the Cooper et al study) it is not clear how they could have affected different patterns of lateralisation between our experiments and theirs. Therefore it seems that the deciding factor is familiarity.

Thus, it has to be made clear, that the priming effects predicted by the RH-SPA hypothesis are mostly relevant to perceptual priming effects (since nonfamous faces, should be associated with very little semantic information). It is possible that for famous faces priming, the top-down contribution of semantic effects could possibly change the pattern of priming. For example, maybe using a task with heavily semantic demands could produce larger priming effects for the LVF-RH (contrary to the RVF-LH found in Chapter 2). If the LH has an advantage in semantic/lexical processing (in the same way that the RH has an advantage in face processing), then opposite effects could be found (e.g., larger priming RVF to LVF). In fact, this is a pattern found for words (e.g., Collins & Coney, 1998; Koivisto & Hämälainen, 2002), and also was reliable in the in the Bourne studies.

Note, however, that intentionally all the effects in Chapter 2 and the present chapter have been defined and "hemifield" effects and not as "hemispheric" effects. Although the relation of hemifield and hemispheric effects is reasonably understood, because of interhemispheric transfer (i.e., information is relayed from one hemisphere to the other after approx. 20 ms), hemifield asymmetries do not exclude possible further interactions with the left or right hemisphere (e.g., in the retention interval between study and test blocks). Thus, behavioural data using hemifield effects cannot directly provide information on the actual hemisphere that repetition effects occur as a result of hemifield prime and probe lateralization. It may be that the effect of LVF priming on a RVF probes occur in the RH (rather than LH). For example, even if the LH receives the information first through RVF presentations, processing of a repeated face might occur in the RH, if the RH is dominant in face processing (consistent with the "callosal relay" model, Rizzolatti et al., 1971). Indeed, fMRI data (though with central presentations) have shown greater perceptual repetition effects in the right OFA, a region early in the face processing stream that is believed to be specialised for perceptual processing of faces (Rotchstein et al., 2005). As it happens, the author is not aware of any study in the literature that investigates the effects of hemifield in repetition of nonfamous faces, using neuroimaging methodologies. Hence, Chapters 4-6 aimed to investigate the spatial (using efMRI) and temporal (using M/EEG) correlates of such possible effects, so as to test how hemifield repetition effects might be related to hemispheric effects. Another advantage of fMRI and M/EEG methods (apart from indicating hemispheric effects) is that they can test whether the present priming effects occur in "early" stages of the face processing stream identified by fMRI, and/or early in peristimulus time identified by M/EEG, and hence likely to reflect perceptual rather than post-perceptual (e.g., decisional) processes. More specifically, one expectation was that neural structures like the IOG/OFA and the face-specific N170 ERP component (both thought to be involved in structural encoding of faces) would show the same repetition effect pattern as the behavioural data in the present chapter, hence providing neural evidence for our RH-SPA hypothesis.

3.11 Conclusions

The experiments in the previous chapter used central primes and lateralized probes and suggested that, for non-famous faces, priming is only found for RVF probes. The experiments in the present chapter explored this further by crossing lateralization of primes and probes. Priming (of RTs) was consistently only found in the LVF-RVF condition, where primes were assumed to be preferentially processed by the RH and probes by the LH. These findings both support and extend our RH-SPA hypothesis, which says that the RH specialization in structural encoding of faces means that LVF probes shows little effect of prior processing (priming), while the relatively poor structural encoding of faces by the LH means that no priming is seen from RVF probes either. Further neural evidence for this hypothesis, and its possible instantiation in left and right hemispheres, are explored in the neuroimaging experiments described in the next three chapters.

Chapter 4: event-related fMRI Investigation of "RH Structural Processing Advantage" hypothesis

4.1 Experiment 7

In previous chapters, it was found that the RH shows an advantage in face processing that modulates repetition priming. More specifically, for lateralised presentation of faces for less than 120 ms, the RH (LVF) shows little benefit for repeated faces, which was interpreted as face processing that is close to optimal (for that duration). The LH (RVF), on the other hand, did show facilitated processing after repetition (high accuracy and/or faster RTs), which was interpreted as sub-optimal face processing in that hemisphere, but which can be optimised by prior processing of that face in the RH (i.e., following prior central or LVF presentation). These findings lead to the formulation of the "RH Structural Processing Advantage" (RH-SPA) hypothesis. It suggests a RH (and possibly a LVF) advantage in the structural encoding of faces, that is reflected from two main findings: (i) baseline advantage for LVF-RH, and (ii) absence of priming for LVF-RH (as efficiency is already optimal), while priming for RVF-LH, but only when faces have been encoded fovealy or in the LVF.

The present chapter describes the first of three experiments that sought neural evidence for this hypothesis. Surprisingly, although there is a wealth of neuroimaging and neurophysiological studies that have shown the right fusiform gyrus to be particularly involved in face processing and priming (Eger et al., 2005; Henson et al., 2002, 2003; Rotshtein et al., 2005), the author is not aware of any research addressing hemispheric asymmetries in face processing per se, using the DVF paradigm. There are two studies, one by Hemond et al. (2007) and one by Yovel et al. (2008) which are relevant, but neither provided direct neuroimaging evidence for the LVF-RH specialization in face processing. More specifically, in the Hemond et al. study, the researchers where mostly concerned on the contralateral preference in face/object selective areas. While they did present faces, objects, and houses in the LVF and RVF, their presentation time was 300 ms, which is longer than a typical DVF paradigm (i.e., less than 200 ms). As they also suggest, in such a design the focus of attention coincides with the locus of the presented stimulus. Usually, stimuli presented in experiments that employ the DVF methodology are considered as unattended, given that an important factor for successful DVF presentations is the focus of attention in a central fixation point. This is important as attention seems to modulate hemispheric (Bryden & Mondor, 1991) as well as repetition effects (e.g., Henson & Mouchlianitis, 2007). Furthermore, they do not report specific interactions between hemifield and stimulus type in each hemisphere (though they do report contralateral preference for both OFA and smaller for the FFA). It is unclear whether they do not present interactions between hemifield, hemisphere and stimulus category due to absence or because it was not part of their specific scientific question. In the present experiment such interaction were explicitly tested.

In the Yovel et al. (2008) paper the evidence for a LVF superiority are indirectly correlated with neural data. More specifically, first they tested behaviouraly participants using chimeric faces (each half of a face consisting of a different identity) and they found an LVF advantage in accuracy over the RVF. Then, they used a localiser scanning session and identified face-specific regions (i.e., the OFA and FFA), which were then analysed in terms of spatial extent of activation in each hemisphere. They reported that participants who showed a larger LVF bias (LVF minus RVF) in the behavioural task had a larger face-selective activation over the right FFA. Although this is an interesting finding it needs to be noted they did not use any control stimuli in the behavioural task. Given their short presentation times (59 ms), this could possibly reflect a LVF superiority to low-frequencies (Sergent, 1985), rather than a face-specific advantage per se. Second, their methodology might not be the most appropriate to assess hemifield differences, as the eccentricity of each half of a face only subtended from fixation 0.2 °, possibly not enough to isolate each hemifield, given that nasotemporal overlap is thought to extent 1-3°(see section 1.1.3). In fact, in their paper the LVF superiority was only marginal, $t(16)=1.95$, $p=0.07$. Also note that neither of the above studies was concerned with repetition effects, hence possible modulations of repetition effects by a LVF bias to face processing was not tested.

Thus, as described below, the present experiment used a methodology that aimed to provide direct neural evidence for and LVF superiority and a possible modulation of priming effects (consistent with the RH-SPA hypothesis), using common DVF parameters and control stimuli. Hence, an event-related fMRI (efMRI) and DVF was used in a "short-term" priming paradigm similar to that in Chapter 3 (though repetition was randomly intermixed, rather than blocked across study and test blocks). However, to provide a control condition with which to define neural activity related to "face processing", non-face stimuli were added, viz pictures of houses. This also entailed a change of task, since a sex-decision task on houses could not be used, and switching tasks between faces and houses tried to be avoided. Before deciding on the task, three pilot studies were conducted using pleasantness (Like/Dislike?), size judgment (Bigger/Smaller than average?) and stimulus identification (Face/House?)

The stimulus identification task was finally used, as it provided an objective control of correct and incorrect responses, which allows for collection and analysis of accuracy data. In fact, the experimental design was identical to a previous efMRI experiment with bilateral presentation that was used to address the role of attention in fMRI repetition effects (Henson & Mouchlianitis, 2007). In the present experiment one of the stimuli on each trial was simply removed from either the left or right hemifields. As with Experiments 5 and 6 both primes and probes were lateralised, a design that would allow us to investigate possible hemispheric differences both during encoding and probing.

4.2 Materials and Methods

4.2.1 Participants

Eighteen right-handed volunteers (8 female) with normal or corrected to normal vision and no history of neurological disease participated in the study after giving written consent. Mean age was 28 years.

4.2.2 Materials

The stimuli were greyscale photos of 288 front views of unfamiliar buildings (henceforth termed houses) and 288 frontal views of unfamiliar faces (half male) cropped to fit inside an oval mask. The faces were taken from the Facial Recognition Technology (FERET) Database (Phillips et al, 2000). The houses came from various sources on the Internet.

4.2.3 Procedure

An example of a trial sequence is shown in Figure 4-1 below:

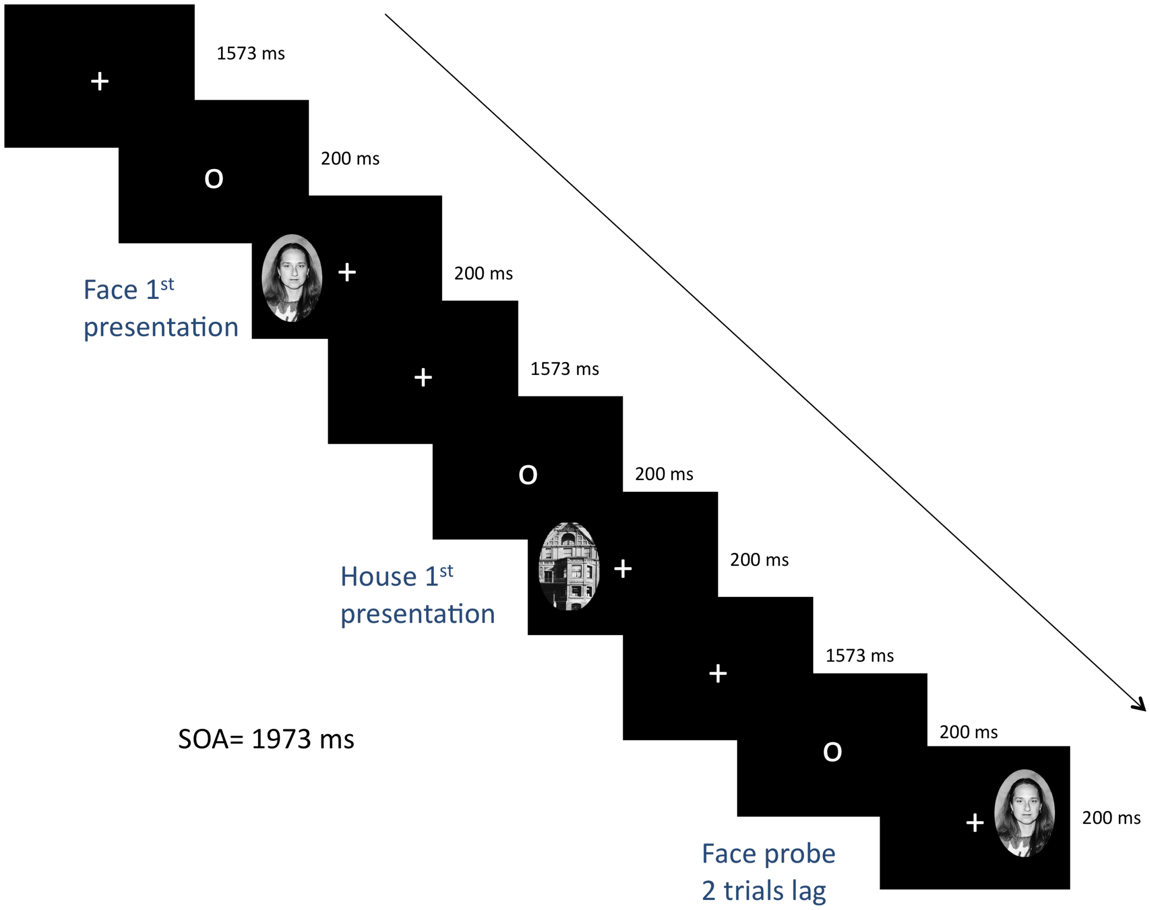


Figure 4-1. Example of a face and house trial. A stimulus (either face or house) would be repeated either in the same hemifield, or in the opposite hemifield. The figure above presents a face repeated on the opposite hemifield, with one intervening stimulus.

On each trial, a stimulus was presented for 200 ms, either to the left or to the right of a central fixation point. The stimulus was either a face or a house. Stimuli were displayed against a black background, projected onto a screen 82.6 cm behind the participant, which they viewed via a mirror placed above their eyes. The inner edge of each stimulus was 2° from fixation, and the outer was 4°. The experiment consisted of 12 experimental blocks of 36 trials, lasting approximately 71 s. Each block started with the warning “READY” presented in the centre of the screen, for approximately 2 s (same duration as SOA). All blocks were run within one single session of 18.5 min. At the beginning of the session and between each block, eight trials of blank grey ovals (baseline) were presented randomly to the left or right side of the screen. Participants had to alternate left and right key presses for each oval. They were instructed to keep their eyes on the fixation point in the centre of the screen, throughout the experiment.

The lag between the first presentation and a repetition was between 2 and 16 trials, hence there was always at least one intervening trial between first and repeat presentation. No stimuli were repeated across blocks. The first 4 trials of each 36 trial block were fillers that were not included in the effects of interest. The rest of the 32 trials consisted of one example of each of the 12 main experimental conditions, presented in a randomly permuted order, which were a combination of the following factors: hemifield (LVF/RVF), stimulus category (faces/houses) and priming condition (first presentation/probe in same hemifield/probe in different hemifield). Participants had to decide whether the presented stimulus they saw was a face or a house. The fixation point momentarily changed from a from a cross (+) to a circle (O) 200 ms prior to the onset of the image, in order to draw their attention to the fixation point and help make sure their eyes were fixated centrally. The SOA was 1973 ms (1.33 TRs; see below). Participants provided responses by pressing a key with the index finger of either the left or right hand, each corresponding to a house or face. The assignment of hand to response alternated across participants. Both accuracy and speed of reaction were emphasised.

This experiment was run as the second session during the scanner; in the first session, the same participants performed the experiment described in Henson & Mouchlianitis (2007), which examined the role of spatial attention in repetition effects from bilateral stimuli.

4.2.4 fMRI acquisition

A 3 T TIM Trio system (Siemens, Erlangen, Germany) was used to acquire 24 T2*-weighted transverse echoplanar (EPI) images (64 x 64 x 3 mm pixels, TE=30 ms, flip-angle=78) per volume with blood oxygenation level dependent (BOLD) contrast. EPIs comprised 3 mm-thick, 1.2 mm-gap near transverse slices, tilted up by approximately 30 at the front to minimise eye-ghosting, and posterior lateral inferior temporal susceptibility artifacts. The slices were acquired in an odd-even interleaved descending direction. 750 volumes respectively were collected continuously with a repetition time (TR) of 1480 ms. The first 10 volumes were discarded to allow for equilibration effects. The ratio of SOA to TR ensured that the impulse response was sampled approximately every 500 ms. An MPRAGE T1-weighted structural image was also acquired for each participant with 1 x 1 x 1 mm voxels using GRAPPA parallel imaging (flip-angle=9; TE=2.99 s; acceleration factor=2).

4.2.5 fMRI analysis

Data were analysed using Statistical Parametric Mapping software (SPM5, http://www.fil.ion.ucl.ac.uk/spm5.html). Preprocessing of the image volumes included spatial realignment to correct for movement followed by spatial normalisation to Talairach space, using the linear and non-linear normalisation parameters estimated from warping each participant's structural image to a T1-weighted template image from the Montreal Neurological Institute (MNI). There re-sampled images (voxel size 3 x 3 x 3 mm) were smoothed spatially by a 8 mm FWHM Gaussian kernel (final smoothness approximately 11 x 11 x 11 mm).

Statistical analysis was performed in a two-stage approximation to a Mixed Effects model. In the first stage, neural activity was modeled by a delta function at stimulus onset. The BOLD response was modeled by a convolution of these delta functions by a canonical Haemodynamic Response Function (HRF). The resulting time-courses were down-sampled at the midpoint of each scan to form regressors in a General Linear Model. Separate regressors were modelled for the 12 conditions of interest (conditional on correct responses) plus three additional regressors for (1) the warning cue at the beginning of each block, (2) the filler trials at the start of each block, (3) trials with erroneous responses.To account for (linear) residual artefacts after realignment, the model also included six further regressors representing the movement parameters estimated during realignment, plus an additional regressor for each scan identified as an outlier (defined as a scan containing a slice in which the mean or variance over voxels was more than 6 standard deviation s of the average mean/variance for that slice across scans). Voxel-wise parameter estimates for these regressors were obtained by Restricted Maximum-Likelihood (ReML) estimation, using a temporal high-pass filter (cut-off 128 s) to remove low-frequency drifts, and modeling temporal autocorrelation across scans with an AR(1) process.

Images of the contrasts of the resulting parameter estimates (collapsed across left/right hand key presses) comprised the data for one of the three second-second stage models (see below), analogous to factorial analysis of variance (ANOVA), which treated participants as a random effect. Within these models, Statistical Parametric Maps (SPMs) were created of the T or F-statistic for the various ANOVA effects of interest. These maps were thresholded after correction for multiple comparisons using Random Field Theory (RFT) (Worsley et al., 1996). Stereotactic coordinates of the maxima within the thresholded SPMs correspond to the MNI template

4.2.6 Second-stage analyses

Repeated measures factorial analyses were conducted with a 2 x 2 x 3 ANOVA with factors “hemifield” (LVF vs. RVF), “stimulus category” (faces vs. houses) and “repetition condition” (first presentation vs. probe in same hemifield vs. probe in different hemifields). These analyses were performed as (i) a “whole-brain” search of every voxel to show a reliable effect after correction for multiple comparisons, and (ii) a functional “regions of interest” (fROI) analysis of the single voxels that showed maximal statistical differences between faces vs. houses and between LVF vs. RVF presentations. In order to control for possible bias, the maxima coordinates for faces vs. houses were taken from a previous session run for Henson & Mouchlianitis (2007) study, but since this study did not have DVF presentations, the LVF vs. RVF maxima were defined from the session run for the present experiment. The whole-brain analyses are advantageous in identifying voxels outside the fROIs and for allowing functional variability within the fROIs (Friston et al., 2006). The fROI analyses are advantageous in allowing further factorial analysis of differential responses *across* regions, where those regions are defined independently of the effects of interest. For the results presented below, the locations of the fROI were defined from the group analysis, i.e. reflect the location of common activation across spatially normalised brains (since this proved more effective than defining fROIs on an individual basis in the very similar design reported in Henson & Mouchlianitis, 2007; see Supplementary Material).

The whole brain ANOVAs used a pooled error, while the fROI analyses (and behavioural analyses) used a partitioned error (Henson & Penny, 2003). The reason for using a pooled error in the whole-brain analyses was to ensure sufficient degrees of freedom that the corrections for multiple comparisons across voxels afforded by RFT were not overly conservative (Nichols & Holmes, 2002).

4.3 Results

4.3.1 Behavioural results

Accuracy was close to ceiling in all conditions (mean = 96%), so only reaction time data were analysed (see Table 4-1 for summary measures of RTs). An omnibus three-way ANOVA with factors, hemifield (LVF vs. RVF), stimulus category (faces vs. houses) and repetition condition (first presentation vs. probe in same hemifield vs. probe in different hemifield), only showed a reliable effect of hemifield, $F(1,17)=6.07$, $p<0.05$, and a main effect of stimulus category, $F(1,17)=6.41$, $p<0.05$. Participants responded faster when stimuli were presented in the left hemifield (M=547 ms) than on the right hemifield (M=559 ms), and faster when the stimulus was a face (M=544 ms) than a house (M=561 ms). As with behavioural analysis in previous chapters, across hemisphere t-tests were conducted for the unprimed (first presentation) stimuli, to investigate baseline effects. A paired t-test for faces was marginally significant, $t(17) = 1.69$, $p=0.054$, and significant for houses, $t(17) = 2.09$, $p<0.05$. RTs for faces presented to the LVF were faster ms than RVF presentations, and the same pattern was found for houses. The analysis of repetition effects (first presentation minus repeated), with factors hemifield (LVF vs. RVF), stimulus category (faces vs. houses) and prime-probe location (same vs. different) did not show any reliable main effects or interactions. The lack of priming effects is not surprising, considering the ease of the task used (stimulus categorisation).

Stimulus	Visual Field					
	LVF			RVF		
	Prime	Same (LVF)	Different (RVF)	Prime	Same (RVF)	Different (LVF)
Faces	542 (62)	532 (83)	538 (64)	551 (57)	547 (64)	557 (65)
Houses	552 (53)	556 (47)	563 (65)	566 (70)	569 (70)	563 (80)

Table 4-1: Mean RTs for faces and house stimuli, as a function of stimulus category and prime/probe hemifield (standard deviations in brackets)

4.3.2 fMRI Whole-brain Analyses

There are seven effects in the 2x2x3 ANOVA . The only effect that showed significance was a two-way interaction between hemisphere and hemifield, for a small cluster (4 voxels) in the left parahipocampus, (-27 -36 -12), Z = 3.55, that survived small volume correction for the Houses>Faces contrast, but not a whole-brain FWE correction (nor for the Face>Houses contrast). This is a region falls within the defined fROIs, Hence, analysis was conducted first on the three main effects across the whole-brain, before re-examining the more subtle interactions in the fROI analysis.

4.3.2.1 Whole brain analysis: LVF vs. RVF

These contrasts were important in order to test whether activations were actually lateralised, i.e., that LVF presentations activated the RH and RVF presentations activated the LH. As with the Faces vs. Houses contrasts above, planned T-contrasts were performed for LVF versus RVF presentations and for RVF versus LVF presentations (collapsing across stimulus category and repetition). SPMs were produced after thresholding for 10 continuous voxels at p < 0.001 uncorrected. The

SPMs for LVF presentations showed a very large cluster in the right hemisphere with a maximum on the right lingual gyrus (i.e., right cuneus, see Table 4-2). SPMs for RVF presentations showed a similarly large cluster in the left hemisphere, with a maximum on the left posterior fusiform gyrus (see Table 4-2 and Figure 4-2) Importantly, results show that LVF presentations activated only RH regions, while RVF presentations only activated LH regions. (see Figure 4-2). These contrasts were used as functional localising contrasts within the same session (Friston et al., 2006) to identify functional regions of interest (fROIs) which defined voxels that preferred either the LVF or the RVF.

Region	Voxels	MNI coordinates			Z
LVF > RVF					
Right Cuneus	1635	+15	-81	-9	7.51*
Right Fusiform		+24	-75	-9	5.33*
Right Calcarine		+12	-90	0	4.13*
RVF > LVF					
Left Fusiform	1513	-24	-78	-9	13.6*
Left Calcarine		-12	-90	-6	12.3*
Left middle occipital		-21	-96	+9	6.08*

*Table 4-2: Main effect of hemifields (functional localising contrast), t-tests, p<0.001, 10 voxels, * = p<0.05 whole-brain FWE correction*

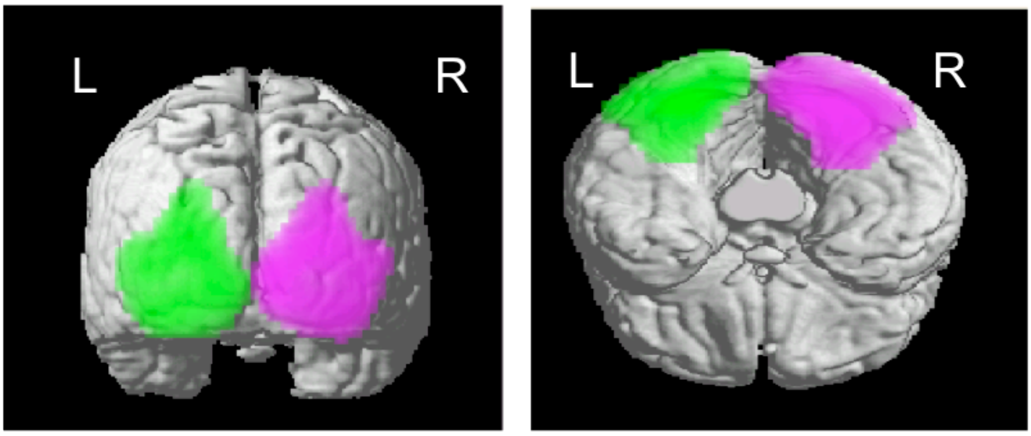


Figure 4-2: Effects of LVF vs. RVF contrasts. Responses are shown in the LH and RH. Suprathreshold voxels for these contrasts are rendered in magenta (LVF > RVF) and green (RVF >LVF) on the occipital temporal surface of a canonical brain (p<0.001 uncorrected, 10 continuous voxels), shown in a posterior coronal plane (left panel) and inferior transverse plane (right panel)

4.3.2 2 Whole brain analysis: Faces vs. Houses

Planned t-contrasts were conducted for faces versus houses and houses versus faces (collapsing across hemifield and repetition). SPMs were produced after thresholding for

Region	Voxels	MNI coordinates			Z
Faces > Houses					
Right Fusiform	176	+42	-45	-21	7.51*
Left Fusiform	92	-42	-45	-18	5.33*
Left Lingual	68	-9	-75	-6	4.13*
Right Lingual	25	+12	-66	-3	3.98*
Right Cuneus	84	+12	-87	+18	3.64*
Houses > Faces					
Right parahippocampus	287	+30	-45	-9	Z>6.08*
Left parahippocampus	309	-27	-45	-6	Z>6.08*
Left middle occipital	125	-33	-87	+15	6.08*
Right middle occipital	141	+39	-78	+24	5.74
Right posterior cingulate	56	+21	-57	+18	5.01
Left posterior cingulate	20	-21	-63	+15	4.25

*Table 4-3: Main effect of stimulus category (functional localising contrast), t-tests, p<0.001, 10 voxels, * = p<0.05 whole-brain FWE correction*

10 continuous voxels at $p < 0.001$ uncorrected (Table 4-3; see also Figure 4-3). The SPMs for faces showed bilateral mid-fusiform activations (which we will call for convenience the Fusiform Face Area, FFA), bilateral lingual gyrus and right cuneus. SPMs for houses showed bilateral parahippocampal regions (which we will call for convenience the Parahippocampal Place Area, PPA), as well as bilateral mid-occipital and posterior cingulate regions.

4.3.2.3 Whole-brain analysis: Repetition Effects

No repetition effects survived correction for $p<0.05$ two-tailed, whole brain correction and with either of the two localiser images for faces and houses .No interactions were found either. Hence, in the following sections analyses are performed for the fROIs.

4.3.3 fROI Analyses

The data for the fROI analyses were obtained from a previous fMRI study (Henson & Mouchlianitis, 2007), which was a variant of the present experiment, run as a separate session previous to the scanning session of the experiment presented in this chapter (with bilateral stimuli presentation instead of unilateral). Hence, the maxima were defined based on the whole-brain main effect of Face vs. House for the right FFA (+42 -45 -21) and left FFA (-42 -45 –18) and right PPA (+30 -45 -9) and left PPA (-27 -45 -6), as well as the right OFA (+48 -75 0) and left OFA (-48 -75 0). Furthermore, the maxima from the right calcarine suclus (+12 -90 0) and left calcarine sulcus (-12 -90 -6) from the LVF vs. RVF contrasts were chosen, since they define a highly retinotopic region (V1) which was of interest of the present study in regards of effects of hemispheric asymmetries and DVF presentations. Since the maxima for faces vs. houses and LVF vs. RVF contrasts were taken from different experiments, they were not entered in the same ANOVA (since they are differentially susceptive to bias) but separate ANOVAs were conducted for face/house-specific areas and retinotopic areas (V1). Furthermore, retinotopic areas were not expected to show any face-house specificity, hence their inclusion in an ANOVA with face/house-specific regions would introduce unnecessary error, which would reduce power.

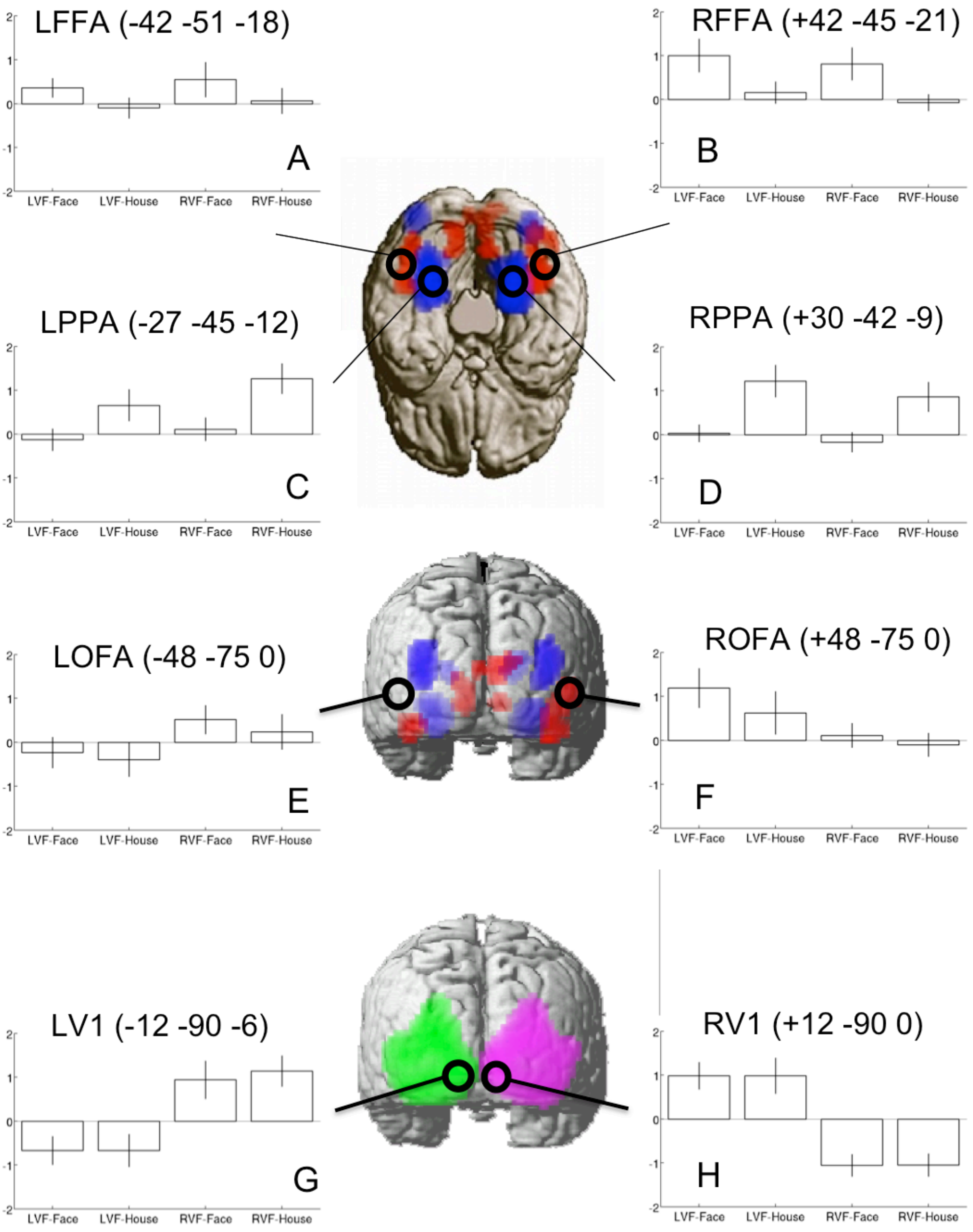


Figure 4-3: Group-defined functional region of interest (fROI) analyses of visual-field effects. Responses are shown in eight brain regions, left/right fusiform face area (FFA, panels A and B), parahippocampal place area (PPA, panels C and D), occipital face area (panels E and F) and V1 (panels G and H). Their coordinates are determined from the maxima of the main effect of faces vs. houses from Henson & Mouchlianitis (2007),and the main effect of LVF vs RVF from for V1. Suprathreshold voxels for the face localising contrast are rendered in red (faces>houses) and blue (houses>faces) and magenta (LVF>RVF) and green (RVF>LVF) for V1 on the ventral temporal surface of a canonical brain (p<0.001 uncorrected, 10 continuous voxels). FFA, PPA, OFA and V1 maxima are circled in black. Plots show % signal change for the main effect across the 8 conditions of interest for each region. Error bars show the 95% confidence interval. The condition labels "LVF-Face" and "RVF-Face" indicate that a face was presented to the LVF or to the RVF, whereas the labels "LVF-House" and "RVF-House" indicate that a house was presented to the LVF or to the RVF

4.3.3.1 fROI Analysis: Repetition Effects

The data from the fROIs were initially submitted to an omnibus five-way ANOVA, by entering them into a 3x2x2x2x2 ANOVA with factors region (FFA vs. PPA vs. OFA), hemisphere (right vs. left), hemifield (LVF vs. RVF), stimulus category (faces vs. house) and repetition condition (first presentation vs. probe in same hemifield vs. probe in different hemifield). The five-way interaction was not significant, $F<1$, $p>0.5$. The next higher significant interaction was the four-way interaction between region, hemisphere, hemifield and stimulus category, $F(1.67,28.36)=18.1$ $p < 0.001$. These interactions are further analysed in the section below.

A four-way ANOVA for V1 with factors hemisphere, hemifield, stimulus category and repetition condition only showed a significant two-way interaction between hemisphere and hemifield, $F(1,17)=113.78$, $p < 0.001$. This reflected the contralateral preference for both faces and houses in each hemisphere (see Figure 4-3, panels G and H).

4.3.3.2 fROI Analysis: Main effects of hemisphere and hemifield

By collapsing across the factor of repetition, first effects of hemisphere and hemifield were then examined for the maxima from the faces vs. houses contrasts. Since the four-way interaction above is difficult to interpret, three-way ANOVAs were therefore conducted for the FFA, PPA, OFA separately, which showed a reliable three-way interaction between hemisphere, stimulus category and hemifield for all three regions (FFA, $F(1,17)=8.29$, $p<0.01$; PPA, $F(1,17)=22.4$, $p<0.001$; OFA, $F(1,17) = 8.01$, $p <0.01$).

Further two-way ANOVAs for the left and right FFA, PPA and OFA were conducted, with factors stimulus category and hemifield. For the LFFA there was as main effect of stimulus category, $F(1,17) =22.3$, $p <0.001$, with faces showing greater activation that houses. There was no significant main effect of hemifield or an interaction, Fs <1. For the RFFA there was a significant main effect of stimulus category, $F(1,17) = 25.81$, with faces showing greater activations than houses, and a main effect of hemifield, $F(1,17) = 6.76$, $p <0.05$, with LVF presentations showing greater activations than RVF presentations, though the two-way interaction was not significant (i.e., the hemifield effect was not face specific). It has to be noted that the RFFA showed evidence for a face-specific advantage over the LFFA. More specifically, the two-way interaction between hemisphere and stimulus category was significant in the three-way ANOVA for

FFA reported above, showing that face-related activity was greater in the RFFA than in the LFFA, F(1,17)=8.34, $p<0.01$ (see Figure 4-3, panels A and B). In the PPA (see Figure 4-3, panels C and D), the two-way ANOVA for the left PPA showed a reliable two-way interaction between stimulus category and hemifield, F(1,17) = 5.89, $p < 0.05$. Activations for house stimuli were greater when they were presented in the RVF (contralateral) than in the LVF (ipsilateral), whereas there were no significant differences in activations for face stimuli across the LVF and RVF. In the right PPA, the two-way interaction was not significant, $F <1$, $p >0.2$. The main effect of stimulus category was significant though, F(1,17) = 83.7, $p <0.001$, with houses showing greater activations that faces. The main effect of hemifield was significant as well, F(1,17) = 14.1, $p < 0.001$, with the contralateral hemifield (LVF) showing greater activation than the ipsilateral hemifield (RVF).

Finally, the two-way ANOVA for the right OFA showed a significant interaction between hemifield and stimulus category, F(1,17)= 4.47, $p<0.05$, as activations were greater when face stimuli were presented in the contralateral hemifield (LVF) than in the ipsilateral hemifield (RVF). Note that this is the only face specific region that shows such an interaction (see Figure 4-3F). This is an important finding, since for the first time we have neural evidence for an advantage of hemifield in face processing. In the left OFA there was only a main effect of hemifield, F(1,17)=62.3, $p <0.001$, which reflected a contralateral advantage (RVF) for both faces and houses (see Figure 4-3E), while the two-way interaction was not significant, $F<1$. Given the contralateral advantage for both the right and left OFA, face-related activity (faces minus houses) was calculated for LVF presentations in the ROFA and RVF presentations for the LOFA. A one-way T-test was not significant t(17)=1.12, $p>0.2$. Note however that the size of face-related activity in the ROFA (0.56) was twice greater than for the LOFA (0.28).

Analysis of the effects for each region helped interpret the significant four-way interaction ANOVA: in the PPA, the RVF in the left PPA showed a RVF specificity to houses, which was not found in the right PPA. In the FFA, there was two-way interaction between hemisphere and stimulus category, with the right FFA showing greater activations to faces compared to the left FFA. Furthermore, the right FFA showed hemifield effects, since contralateral hemifield activations (LVF) were greater than ipsilateral (RVF), an effect not found in the left FFA (note, however, that this effect was not specific to faces). Analysis of the right OFA showed a LVF sensitivity in faces, as activations for contralateral (LVF) presentation of face-stimuli was greater than ipsilateral

(RVF) presentations. This effect was not found in the left OFA. Finally, the V1 areas in both the left and right hemispheres showed greater activation to contralateral stimuli.

4.4 Discussion

4.4.1 Repetition effects

Unfortunately the repetition effects found in the present experiment were minimal, hence any conclusions cannot be made regarding the neural correlates of the RH-SPA hypothesis. We were hoping that repetition effects could occur in face-sensitive areas (i.e., OFA and FFA). The lack of behavioural priming effects probably reflects the ease of the face-house categorisation task, as reflected by the high accuracy and fast RTs (no priming was found in Henson & Mouchlianitis, 2007). This task was chosen because sex-judgments from Chapters 2-3 could not be performed on houses, and pilot studies using tasks that could in principle be performed on both faces and houses (e.g., bigger/smaller than average, pleasant/unpleasant) did not show any priming. Therefore, we chose the face-house task just so that we could be sure that participants did perceive faces and houses accurately despite the short duration (and scanning environment). But this could not explain the lack of neural repetition effects since these were found in Henson & Mouchlianitis (2007), using the same task and very similar design. However, one important difference in that study and the present one (in addition to its bilateral stimulus presentation) is that participants were told in advance which hemifield to attend to, whereas in the present experiment, participants were unable to predict the hemifield of the next trial in advance (as necessary for DVF paradigms). Therefore the stimuli in the present experiment were unlikely to have been attended as much as in Henson & Mouchlianitis (2007). Indeed, they were more likely to correspond to the "unattended" condition of that study. The present lack of repetition effects are therefore consistent with the same lack in Henson & Mouchlianitis (2007) which concluded that fMRI repetition suppression is only found for stimuli attended on both their initial and repeated presentations.

However, the factor of attention by itself cannot completely explain the absence of repetition suppression in the present experiment, since robust priming effects were found over two different experiments with lateralised primes in Chapter 3. Priming effects have also been reported with lateralised primes for famous faces, both behaviourally (Bourne

& Hole, 2006; Bourne et al., 2009, Experiments 5 and 6 in Chapter 3) and using EEG (Cooper et al, 2007). This means that at least behavioural and EEG methods (with high temporal resolution) do show repetition effects for lateralised primes. Hence, one strong possibility for the absence of repetition suppression in the present experiment is the low temporal resolution of fMRI. It is possible that repetition effects when primes are lateralised are transient (compared to bilateral presentations in Henson & Mouchlianitis, 2007) to contribute majorly to the BOLD impulse response, which is dominated instead by later processing. This possibility motivated conducting M/EEG research in the next two chapters, in order to take advantage of their high temporal resolution.

4.4.2 Lateralisation of face processing

The main finding of the present experiment was that for the first time (to the author's knowledge) neural evidence has been found for hemifield and hemisphere sensitivity to different types of stimuli as shown in the ROFA the LVF showed sensitivity to faces. More specifically, a two-way interaction between stimulus category and hemifield was found only in the right OFA, with LVF activations to faces being larger than LVF activations to houses, while there was no difference between the two types of stimuli for the RVF. On the other hand, in the left OFA, no differences between faces or houses were found for neither RVF or LVF presentations. This suggests a certain degree of sensitivity within the LVF-ROFA for the encoding of face stimuli. This finding corroborates with the extended behavioural literature that has shown a LVF advantage and an important role of the RH in face processing (see Chapter 1). It, therefore, seems that the neural locus of this LVF advantage lies in activation of the right OFA. This region has been found to be involved in early stages of the face-processing stream (Pitcher et al., 2007), and seems to be mainly involved in early perception of facial features (Haxby et al., 2000; Rotshtein et al., 2005).

Our data also provide neural evidence for the localization of the LVF face-processing advantage, further extending the findings of Yovel et al. (2008). Note that in that study the LVF bias was correlated with the RFFA rather than ROFA. One possibility (also suggested by the authors) is that the recognition task they used in the behavioural session was better suited for correlation with the FFA, known to show greater sensitivity to identity rather than perceptual processing per se (Rotshtein et al., 2005). In our experiment participants only had to identify whether a stimulus was either a face or a house, which is a rather automatic process. Probably this task engages perceptual information more so than identity, hence the OFA becomes more involved. Indeed, given that the OFA is closer to retinotopic areas than the FFA, it is likely that a task that engages low-level perceptual processes should show greater sensitivity to hemifield. Nevertheless, to the best of our knowledge, this is the first fMRI study that provides evidence for the neural locus of the LVF advantage in face processing, at least for perceptual processing.

In regards to other face specific areas, the right FFA did not show any interaction with stimulus category and hemifield. There was a main effect of hemifield for contralateral presentations, but was not specific to faces. This agrees with Hemond et al. (2007), which also showed contralateral preference for both the OFA and FFA (though reduced in regards to the OFA). Significantly though, face specific activations in the right FFA were greater than in the left FFA, as the two-way interaction between hemisphere and stimulus category was significant, showing a right FFA sensitivity in face processing as well (though not modulated by hemifield as in the ROFA). This finding contributes to the limited fMRI literature that explicitly tests for hemispheric asymmetries in the FFA (see Dien, 2009).

Most importantly though, neural evidence for a LVF-ROFA face-sensitivity also complements the behavioural data in Chapters 2 and 3 that have shown the importance of the LVF in face processing, and how this modulates priming. In Chapter 2, for central primes and lateralised probes, LVF probes showed no priming as efficiency was close to optimal already. In the RVF, less than optimal encoding efficiency allowed priming effects to emerge when a stimulus was repeated. In Chapter 3, in the case when both primes and probes were lateralised, the advantage of the LVF was clear, since priming was found only when primes were presented in the LVF and probes in the RVF, suggesting that the LVF has an increased efficiency in the encoding of faces, which allows the creation of facial representations. On the other hand, no priming was induced when the primes were presented to the RVF, again reflecting decreased efficiency in encoding. Hence, the LFV-ROFA face processing advantage found in the present fMRI experiment partially confirms the hypothesis for a RH advantage for faces modulating priming. Unfortunately, since no repetition suppression effects were found, neural evidence for the behavioural effects cannot be explicitly provided. Thus, this set of data cannot resolve: (i) whether the repetition effects found in Chapters 2 and 3 occur early in the face processing stream (i.e., OFA) or later (i.e., FFA) and (ii) the interactions between hemifield and hemisphere in terms of repetition effect. As argued in the Discussion of

Chapter 3, the behavioural data alone cannot test whether the repetition effects found for RVF probes in both Chapters 2 and 3 reflect the LH showing facilitation after repetition, or whether processing that induces priming occurs within the RH after information has been transferred from the LH to the RH. By using M/EEG methods in the next two chapters, we were hoping that we would see repetition effects that would address those two issues.

4.5 Conclusions

By using efMRI methods we were hoping to find neural correlates of the repetition effects reported in Chapters 2 and 3, viz how a LVF-RH advantage in structural encoding of faces possibly modulates repetition effects. Unfortunately, no repetition effects were found, hence no neural evidence was provided for this modulation. However, there were significant findings regarding an LVF-RH increased efficiency in structural encoding, as reflected by the increased face related activations in for the LVF in the ROFA. This finding supports the core assumption of our RH–SPA hypothesis, that perceptual repetition effects are modulated by increased efficiency in early stages of face processing.

Chapter 5: M/EEG Replication of efMRI Experiment on Lateralised Faces vs. Houses

5.1 Experiment 8

In Chapter 4, the fMRI data suggested a relative lateralisation of the Occipital Face Area (OFA). More specifically, faces produced greater activity in right OFA than did houses when these stimuli were presented to the left visual field (LVF), but not when they were presented to the right (RVF), whereas the left OFA showed no evidence for a face vs. house preference in either hemifield. However, one limitation of the data was that no significant repetition effects were found, with one possible reason being that such repetition effects were too transient for the time-integrating BOLD signal to detect (Furey et al., 2006). Therefore, we decided to repeat the experiment with concurrent acquisition of MEG and EEG data, which offer much higher temporal resolution than fMRI (though worse spatial resolution). Furthermore, by examining the latency of the various effects of faces vs. houses, hemifield, and their interaction, we might better understand the right hemisphere specialisation of face-processing (or at least, the greater sensitivity of face-processing in the right hemisphere to the hemifield), and the effects of this on priming. For example, knowing when the effects of faces vs. houses, and their repetition, occurs relative to the onset of hemifield differences might help determine whether these effects are "bottom-up" (more automatic) effects or "top-down" (re-entrant) effects (Henson, 2003).

The concurrent acquisition of MEG and EEG offers a number of advantages over using each modality alone: although MEG and EEG are sensitive to the same neuronal currents (i.e., predominantly in the apical dendrites of pyramidal cells in the cortex; Nunez & Srinivasan, 2006), magnetic fields are less distorted by the resistive properties of the skull and scalp than are electrical fields, generally making the localisation of these currents easier for MEG than for EEG. On the other hand, EEG and MEG have different sensitivity to the orientation of the currents, with MEG being less sensitive to the radial component (indeed, for a spherical volume conductor, there would be no radial component of the magnetic field at the surface) Therefore EEG will be better able to detect some sources. Indeed, the combination of EEG and MEG offers superior localisation than either modality alone (Henson, Mouchlianitis & Friston, 2009).

Finally, the MEG system used here contains two types of sensor at each of 102 locations: a magnetometer and two orthogonal, planar gradiometers (i.e., leading to a total of 306 information “channels”). While magnetometers measure the total magnetic flux (in the “z” direction), planar gradiometers measure the difference in flux (gradient) along the x and y in-plane directions. Gradiometers are less sensitive to deep brain sources (that produce a smoother field across the sensor locations), but also less sensitive to non-brain (far-field) noise sources (for the same reason, i.e., smoother fields from further sources result in less of difference across the two gradiometer coils). Magnetometers are more sensitive to deeper sources, but also pick up more noise as a consequence. Thus like with EEG versus MEG, the two types of MEG sensor offer complimentary advantages.

Because one does not normally care about the direction of these gradients (unless doing source localisation), here we have taken the Root Mean Square (RMS) of the values recorded in the two orthogonal directions at each gradiometer location (i.e., the length of the planar vector). The largest values of this scalar gradiometer RMS tend to be directly over the underlying, superficial currents (i.e., where the gradients change fastest), thus allowing informal topographic localisation of the gradiometer RMS maps. For the magnetometers however, the largest values tend to be either side of an underlying current (depending on the orientation and depth of that current). The polarity of these “lobes” is determined by the “right-hand” rule of electromagnetic fields. This means that the locations with the maximal magnetometer values do not correspond to the approximate topographic location of the current source. These issues are important when interpreting the statistical maps of magnetometer, gradiometer and EEG topographies (over time) reported later.

5.2 Methods

5.2.1 Participants, Materials, Procedure and Design

Eighteen right-handed participants (eleven female) were tested, aged mean age 26 years. Due to technical fault one participant's data were not used. The materials, procedure and design used were almost identical with the fMRI experiment described in the previous chapter. There were two main differences: (i) stimulus presentation time was reduced from 200 ms to 120ms to match the presentation time of previous behavioural chapters (also more consistent with DVF methodology, see Chapter 1) and (ii) participants gave bi-manual responses rather than pressing a single key for either a house or face (to control for Simon effects, see Chapter 1)

5.2.2 M/EEG Data Acquisition

The MEG data were collected with a VectorView system (Elekta-Neuromag,Helsinki, Finland), containing a magnetometer and two orthogonal, planargradiometers located at each of 102 positions within a hemispherical array situated in a magnetically-shielded room. The position of the head relative to the sensor array was monitored continuously by feeding sinusoidal currents (293-321Hz) into four Head-Position Indicator (HPI) coils attached to the scalp. The EEG was recorded from 70 Ag-AgCl electrodes placed within an elastic cap (EASYCAP GmbH, Herrsching-Breitbrunn, Germany) according to the extended 10% system and using a nose electrode as the recording reference. Vertical and horizontal EOG were also recorded. All data were sampled at 1 kHz with a band-pass filter from 0.03-330 Hz.A 3D digitizer (Fastrak Polhemus Inc, Colchester, VA) was used to record the locations of the EEG electrodes, the HPI coils and approximately 50-100 'headpoints' along the scalp, relative to three anatomical fiducials (the nasion and left and right pre-auricular points).

5.2.3 M/EEG Data Pre-processing

External noise was removed from the MEG data using the temporal extension of Signal-Space Separation (SSS; Taulu, Kajola & Simola, 2004) as implemented with the MaxFilter software (Elekta-Neuromag). The MEG data were also compensated for movement every 200ms. Manual inspection identified some bad channels (numbers ranged across participants from 0-7 in the case of MEG, and 0-12 in the case of EEG). These were recreated by MaxFilter in the case of MEG, but rejected in the case of EEG.

The EEG data were re-referenced to the average over remaining channels. After uploading to SPM5 (http://www.fil.ion.ucl.ac.uk/spm), the continuous data were down-sampled to 100 Hz, low pass filtered to 40 Hz in both forward and reverse directions using a 5th order Butterworth digital filter, and epoched from -100 ms to 400 ms post-stimulus onset (removing the mean baseline from -100ms to 0ms). Epochs in which the EEG or EOG exceeded 80 μV were rejected from both EEG and MEG datasets (number of rejected epochs ranged from 1 to 144 across participants, median = 14). These epochs were averaged to form a single mean evoked response to each of the 12 main conditions, conditionalised on correct responses. Mean numbers of trials per condition were: Faces-LVF (primes; M=55); Faces-LVF (same VF probes; M=21) Faces-RVF (different VF probes; M=20); Houses-LVF(primes; M=54); Houses-LVF (same VF probes; M=19); Houses-RVF (different VF probes; M=18); Faces-RVF (primes; M=52); Faces-RVF (same VF probes; M=20) Faces-LVF (different VF probes; M=17); Houses-RVF(primes; M=54); Houses-RVF (same VF probes; M=20); Houses-LVF (different VF probes; M=18)

5.2.4 Behavioural Analysis

An omnibus, repeated-measures Analyses of Variance (ANOVA) was conducted on mean RTs, with factors hemifield (LVF vs. RVF), stimulus category (faces vs. houses) and repetition condition (primes vs. primes/probes in same hemifield vs. primes/probes in different hemifield). Significance was defined as a p-value below 0.05. Significant effects were only reported in the absence of significant higher order interactions.

5.2.5 M/EEG Analysis

5.2.5.1 Space x Time analysis

Given that there were limited a priori predictions for when (within the epoch) or where (over sensors and channels) face repetition, stimulus category or hemifield effects might arise, a mass univariate approach was first adopted in which *F*-tests were performed at every point in a 3D image of channel space × time. The 2D channel space was created by a spherical projection of the 102 MEG sensor locations and the 70 standardised Easycap channel locations onto a plane, followed by a linear interpolation to a 32 × 32 pixel grid; the time dimension consisted of the 50 (-100 to 400) 10ms samples in the epoch. For the gradiometer data, the signals for the two orthogonal, in-plane directions at each location were combined into a scalar magnitude by taking their Root-

Mean-Square (RMS). The RMS was taken before averaging across trials because the uneven number of trials across conditions (with fewer trials for repeated versus initial presentations) would mean that otherwise, noise would constitute a greater proportion of the RMS for conditions with fewer trials (for an extended explanation see http://imaging.mrc-cbu.cam.ac.uk/meg/SensorSpm). *F*-tests corresponding to the main effects of repetition condition, stimulus category and hemifield and their interactions, were performed within a GLM using a pooled error over the 12 conditions. The nonsphericity across conditions (owing to repeated measures from the same subject) was estimated using Restricted Maximal Likelihood, and used to pre-whiten the model and data (Friston et al., 2002). *F*-values were subsequently converted to *Z*-values. The p-values for the maxima within the resulting statistical parametric maps (SPMs) were corrected for multiple comparisons at a family-wise error (FWE) of .05 using Random Field Theory (Worsley et al., 1996; Kiebel & Friston, 2004a,b), with the estimated Gaussian FWHM smoothness being approximately 6 pixels in space and 5 samples in time.

5.2.5.2 Time Window Analysis

Having identified time windows of interest from the SPM analyses, additional ANOVAs were performed on the mean amplitude (with respect to mean pre-stimulus baseline) during these time windows, with the factors of hemifield, stimulus category and repetition condition being supplemented by further channel factors (see results for further information).These factors were entered in an omnibus ANOVA, which was then, depending on significant interactions, was followed by lower-level ANOVAs. For ANOVA effects involving more than 1 *df*, a Greenhouse–Geisser correction for nonsphericity was used.

5.3 Results

5.3.1 Behavioural Results

As with the fMRI data, overall accuracy was high (M = 95%), so not analysed further. In the RT data, for the three-way ANOVA with factors hemifield, stimulus category and repetition condition, none of the main effect or interactions reached significance, apart from a trend for a main effect of stimulus category, F(1,16)=3.628, p=0.075, as faces showed faster responses than houses (M = 565ms and M= 579ms respectively), similarly to the fMRI data in Chapter 4. Baseline analysis for LVF and RVF primes (first presentation) did not show any significant effects for either faces or houses, in either accuracy or RTs, ts < 1, ps>0.2. Mean RTs are summarised in Table 5-1.

Stimulus	Visual Field					
	LVF			RVF		
	Prime	Same (LVF)	Different (RVF)	Prime	Same (RVF)	Different (LVF)
Faces	567 (73)	565 (83)	571 (79)	564 (76)	565 (71)	561 (64)
Houses	578 (82)	586 (83)	575 (80)	569 (77)	581 (85)	582 (96)

Table 5-1: Mean RTs and standard deviations (in brackets) for face and house stimuli as a function of stimulus category and prime-probe hemifield

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5.3.2 Space x Time SPM Results

The omnibus three-way interaction with factors hemifield, stimulus category and repetition condition did not reveal any reliable effects neither for the EEG nor for either type of MEG sensor. Hence further analysis focused on the remaining main effects and their interactions, which are summarised in Table 5-2.

5.3.2.1 EEG data

For the EEG data, the main effect of stimulus category showed bilateral temporal-occipital clusters with negative potential differences (for Faces – Houses; Figure 5-1A), which were maximal at approximately 190 ms (and suprathreshold from 150 to 210 ms), most likely associated with the face-specific “N170” component (Bentin et al., 1996). The third anterior cluster in the same time range most likely reflects the positive component of the same effect, relative to the average reference. Later on, there were further clusters, maximal at 270 ms (and suprathreshold from 240 to 290 ms). For the main effect of hemifield, there were bilateral occipito-parietal clusters that were maximal at 90 ms (and suprathreshold from 80 to 100 ms), negative on the left and positive on the right (for LVF – RVF; Figure 5-1B). There were also later clusters maximal at 270ms (and suprathreshold from 220 to 290 ms). Most importantly, the two-way interaction between hemifield and stimulus category showed bilateral occipito-parietal clusters at 170 ms (and suprathreshold from 140 to 190 ms), located similarly to those showing the main effect of hemifield above, but approximately 80ms later in time (Figure 5-1C).

There were also later clusters maximal at 240ms (and suprathreshold from 220 to 270 ms)

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	N	x	y	t/ms	Z
EEG					
ANOVA effect					
Stimulus category (faces vs. houses)	308	-27	-30	190	7.99
	280	-21	-21	270	7.37
	89	+36	-30	190	5.75
	198	+6	+45	200	5.71
Visual Field (LVF vs. RVF)	1144	+39	+15	270	6.95
	1451	-33	+27	320	6.49
	75	-18	-24	90	5.99
	81	+30	-18	90	5.69
Stimulus category x Visual Field	176	-27	-24	170	6.39 *
	44	+39	-27	170	5.39 *
	30	+39	+21	240	4.89
	26	-21	-15	240	4.78
Magnetometers					
ANOVA effect					
Stimulus category (faces vs. houses)	165	+45	-3	180	6.33
	289	+42	+21	280	6.05
	307	-39	-18	290	5.77
	23	-39	_21	360	5.02
	26	-36	-15	180	4.71
Visual Field (LVF vs. RVF)	494	0	-24	150	7.12
	216	+6	-42	100	6.56
	216	-9	+45	260	5.47
	32	+45	-12	150	4.88
Stimulus category x Visual Field	62	-3	-36	160	5.38

Table 5-2. Maxima within Space-Time SPMs for EEG and Magnetometers that survived correction for multiple comparisons (no effects survived correction in the Gradiometer RMS). The origin of SPM coordinates is midpoint of a square image, with x ranging from -48 (left) to +48 (right) and y ranging from -39 (posterior) to +45 (anterior);" t" refers to the peristimulus times; Z= Z-score; N = number of voxels;

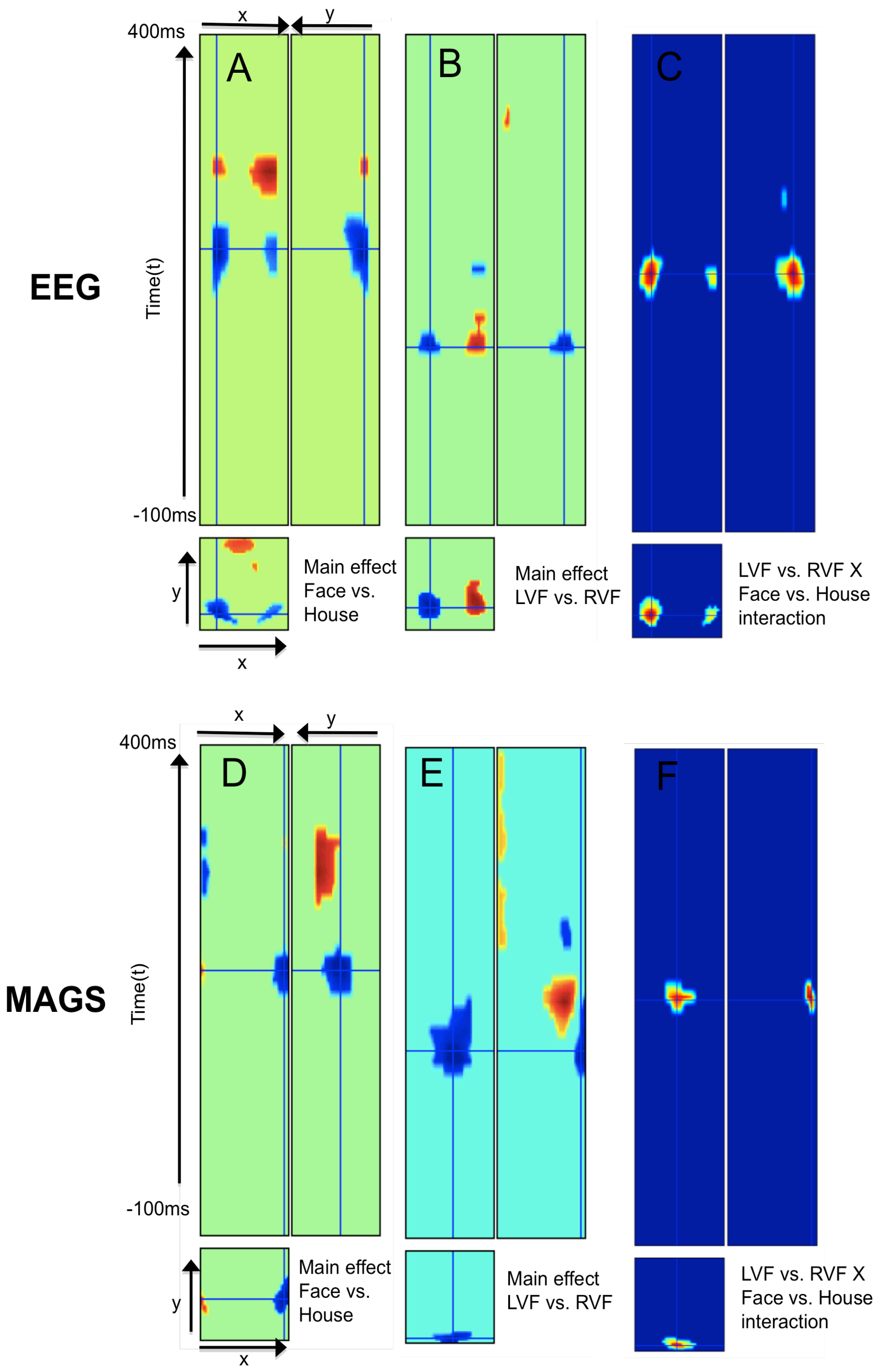


Figure 5-1. Two-tailed SPMs of maxima thresholded at p<.05 FWE-corrected for EEG (panels A, B and C) and Magnetometer (panels D, E and F) data for the main effects of stimulus category (A and D), hemifield (B and E) and their interaction (D and F). The main effects are directional (red=positive, blue=negative; see text), whereas the interaction is unsigned. The crosshair is located at the maxima of each effect (see Table 5-2). The three images in each panel represent orthogonal planes (x-t, y-t, and x-y) through the 3D image at the location of the crosshair.

5.3.2.2 Magnetometer data

Magnetometer data revealed clusters within essentially the same timewindows as the EEG data above. Their maximal location across the scalp differed, as expected from the nature of the in- and out-going magnetic flux to which they are sensitive. More specifically, the main effect of faces vs. houses that suprathreshold from 150 to 200 ms (the "M170") was maximal at 180ms over lateral temporal sensors (Figure 5-1D), with opposite flux directions on the left and right (consistent with bilateral posterior temporal dipoles, whose fields cancel over midline occipital regions). The earlier main effect of hemifield (suprathreshold from 80 to 120 ms) was maximal of occipital pole (Figure 5-1E), as was the later interaction between hemifield and stimulus category (suprathreshold from 140 to 180 ms; Figure 5-1F), again suggesting similar generators for these two effects.

5.3.2.3 Gradiometer data

No effects survived correction for the RMS of gradiometers. This probably reflects the sensitivity of the RMS measure to noise (though see ANOVA RMS results later).

5.3.2.4 Summary

There seem to be at least three temporally-distinct effects in the EEG and MEG (Magnetometer) data: an "early" effect of hemifield from 80-120ms, coincident with the typical visually-evoked P100/M100 component; a "second" effect from 140-190 in which stimulus category interacts with hemifield, coincident with the typical face-specific N170/M170 component; and a "late" effect from 200-300 ms onwards. However, analysis of the HEOG and VEOG channels in the next section suggest that the late effect at least may be confounded by differential eye-movements.

5.3.3 HEOG and VEOG Results

The same ANOVA with factors hemifield (LVF vs. RVF), stimulus category (faces vs. houses) and repetition condition was conducted separately on the HEOG and VEOG channels, for the mean potential difference across each of the three timewindows identified above as showing experimental effects in the EEG/MEG, viz 80-120 ms, 140-190 ms and 200-300 ms. Analysis of the HEOG for the 80-120 ms window showed a significant main effect of stimulus category, $F(1,16)=6.03$, $p<0.05$, with amplitude being larger for faces than houses (Figure 5-2A). For the 140-190 ms window, a reliable interaction between stimulus category and hemifield was found, F(1,16)=12.01, p<0.01, while the same interaction was also significant for the 200-300 ms window, F(1,16)=13.8, p<0.01. Analysis of the VEOG for the 80-120 ms time-window did not show any significant effects, Fs<1.3, p>0.2. For the 140-190 ms time-window, there was a significant main effect of stimulus category, F(1,16)=15.8, p<0.001, with faces showing larger amplitudes than houses (Figure 5-2B). The late 200-300 ms window only showed a main effect of repetition, F(1,16)=4.09, p<0.05. Given the lack of repetition effects elsewhere in the data, this effect is possibly a Type I error, hence not considered further. Some of these condition effects in the HEOG and VEOG channels could reflect differences in brain activity that happened to be picked up by the bipolar EOG electrodes, or they could reflect true differences in eye-movement. It is difficult to tell from scalp data alone, although the large HEOG differences would suggest that the eyes were saccading horizontally, consistent with the lateralised presentations and typical time of

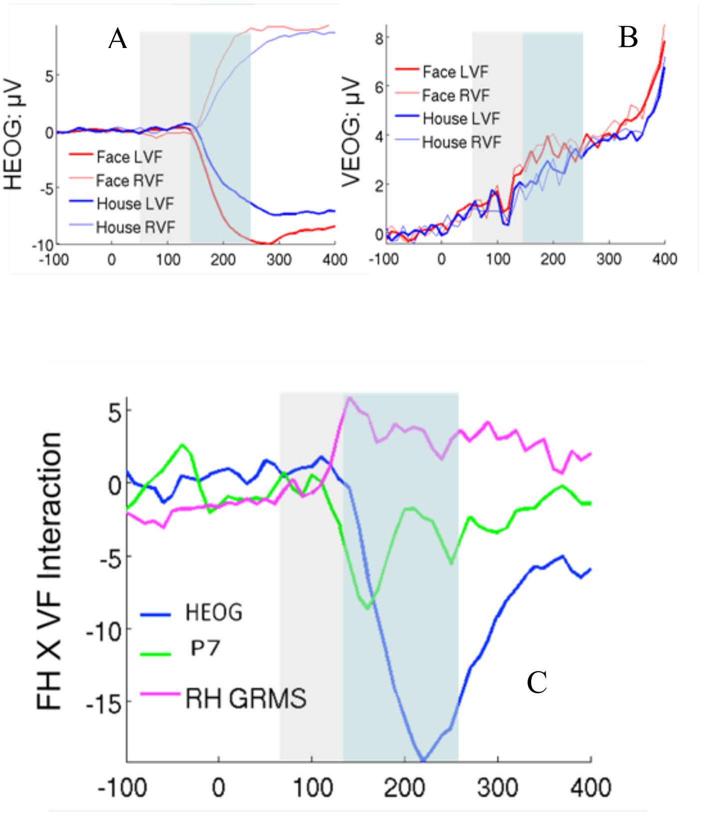


Figure 5-2: HEOG amplitudes for face and houses presented in the LVF and RVF (panel A); Likewise for VEOG (panel B). Panel C represents the plot of the stimulus category and hemifield interaction for the HEOG, P7 and the RH-GRMS.

150-200ms for a saccade to take place (Chapter 1). Note that these effects remain even after rejecting trials in which the potential difference exceeded 80 μV (which should exclude blinks and large eye movements at least), and attempts to reduce the threshold forthe EOG channels (even if only HEOG), in order to remove trials where saccades occurred, resulted in too few remaining trials. Indeed, these saccades occurred frequently across trials and in nearly all subjects, despite the instructions to fixate and the central warning signal at t= 0ms. This suggests that such saccades were occurring in all the experiments reported here, and by extension, most other DVF paradigms (at least where eye-movement is not explicitly measured). Such eye-movements may therefore have confounded the fMRI results, and possibly contribute to the behavioural results (though a reason for the latter is less clear). Fortunately, eye-movements were unlikely to have confounded the earlier timewindows in the present M/EEG data: the early 80-120 ms window that showed a main effect of hemifield effect showed no such effect in the VEOG or HEOG (only a main effect of stimulus category in the HEOG, considered below). This is because this window is before the divergence in HEOG signal related to hemifield (Figure 5-2A).

The second timewindow from 140-190 ms showed a main effect of stimulus category in the VEOG, which was small enough that it may have reflected that part of the N/M170 component that happens to also cause a potential difference between the VEOG electrodes above and below the eye (rather than vertical eye movement per se). However this timewindow is potentially affected by the HEOG hemifield differences. Indeed, the HEOG showed the same, critical interaction between hemifield and stimulus category that was the focus of the previous and present chapter. Hence, the size of this interaction over time was plotted for HEOG (Figure 5-2C) and for channel P7 over which the same interaction was maximal in the EEG data (Figure 5-2C). As it can be seen, the maximum for the HEOG was at ~220ms, whereas the maximum for the EEG data was ~150ms. This latency difference between the two peaks in Figures 5-2 means that it is unlikely that any interaction effects found in the critical 140-190 ms window are a consequence of differential horizontal saccades. However, the same cannot be said of the late timewindow, 200-300ms, where any EEG/MEG effects could be an artefact of differential horizontal eye movement to faces/houses in the left/right hemifield. In fact, the SPMs did show a right-frontal cluster maximal at 240ms, most likely associated with this significant interaction in the HEOG. This late timewindow was therefore not analysed further in the more detailed timewindow ANOVAs below.

5.3.4 Timewindow Results

To investigate the SPM effects in more detail, and explicitly test for interactions with hemisphere, the mean signal across the early (80-120 ms) and mid (140-190 ms) timewindows was extracted for two selected sensors in the left and right hemisphere as Sensors Of Interest (SOI; analogous to the "ROI" analyses of the fMRI data in Chapter 4). These sensors were selected on the basis of independent data, namely those sensors that showed the maximal difference between faces and scrambled faces in our prior study that used the same MEG and EEG set-up (Henson et al., 2008). The ERPs of EEG, magnetometers and gradiometers for both LH (upper part) and RH (lower part) channels can be seen in Figures 5-3, 5-4 and 5-5 respectively. Red lines represent faces and blue lines houses (thick lines for LVF and thin lines for RVF). All the sensors show a P1/N1component, associated with perception of faces, followed by a M/N170 component associated with structural encoding of facial representations (Bentin et al., 1996).

5.3.4.1 EEG

The evoked responses for the left parietal "P7" electrode and its right hemisphere homologue "P8" (selected as above) are shown in Figure 5-3A and 5-3B respectively. The mean signal within each timewindow were submitted to an omnibus four-way ANOVA with factors Hemisphere (P7 vs. P8), hemifield (LVF vs. RVF), stimulus category (faces vs. houses) and repetition condition (first presentation vs. prime/probe in same hemifield vs. prime/probe in different hemifield). For the early 80-120 ms time-window, there was only a significant two-way interaction between hemifield and hemisphere, $F(1,16)=30.2$, $p<0.001$ (no other effects reached significance, $Fs<2.2$, $p>0.15$). The significant interaction reflects the fact that for each hemisphere, the contralateral hemifield showed greater amplitudes than the ipsilateral (Figure 5-3A1 and 5-3B1). For the 140-190ms time window, the four-way interaction between hemisphere, hemifield, stimulus category and repetition was not significant, $F<1$, $p>0.2$, though the three-way interaction between hemisphere, hemifield and stimulus category was, $F(1,16)=41.4$, $p<0.001$. Since repetition did not interact with any other factors, separate two-way ANOVAs were conducted for LH/P7 and RH/P8 with factors hemifield and stimulus category, collapsing across repetition. There was a significant interaction between these two factors in both sensors, $F(1,16) = 27.9$, $p<0.001$, and $F(1,16)=34.9$, $p<0.001$, respectively. Follow on T-contrasts showed that the P7 showed greater amplitude for faces than houses when presented contralaterally (RVF), $t(16)=4.71$,

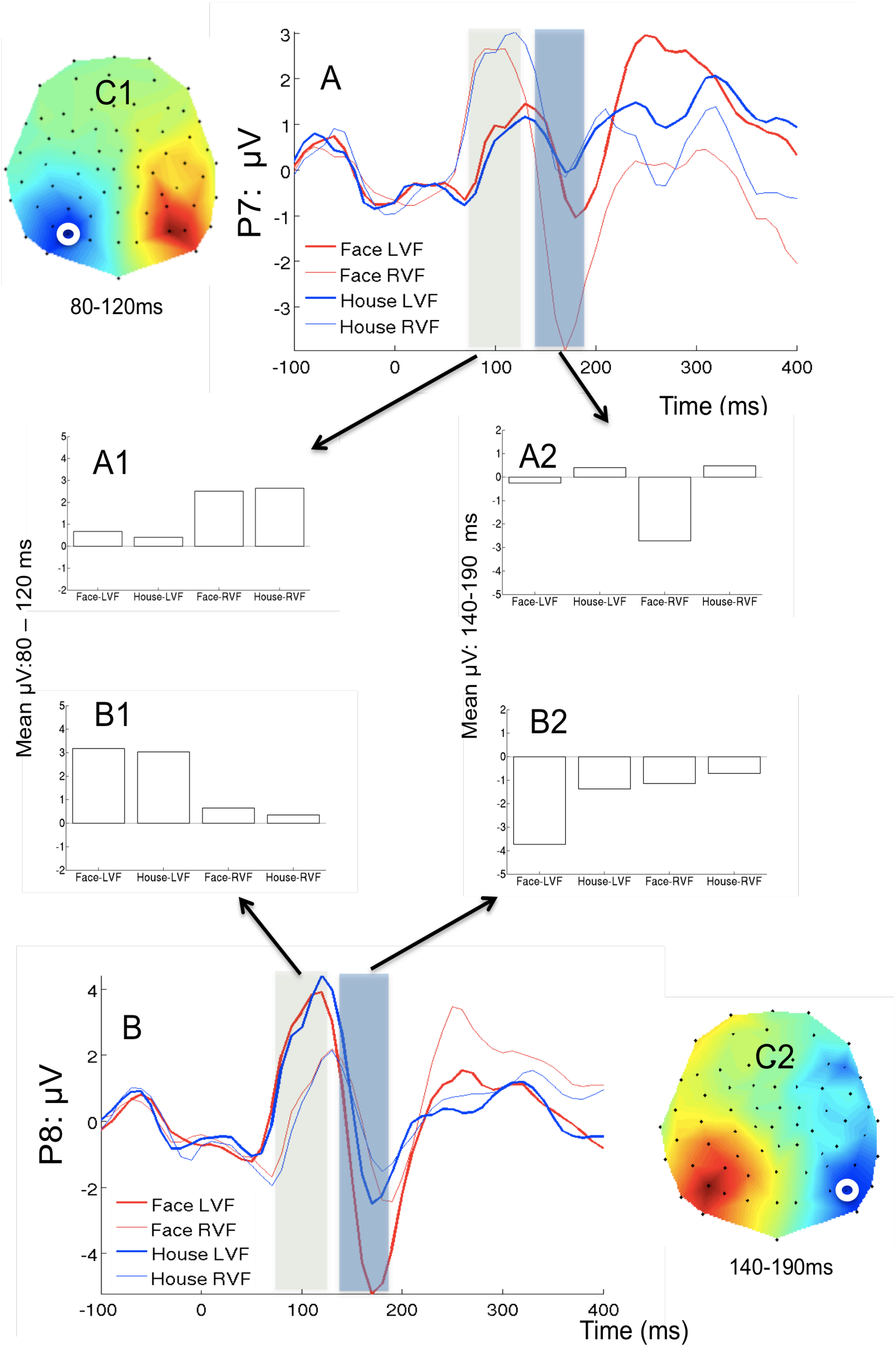


Figure 5-3: EEG evoked waveforms for P7 (panel A) and P8 (panel B) with mean of effects for the early 80-120 ms time window (panels A1 and B1) and the 150-200 ms window (A2 and B2) for each channel. C1 shows the mean sensor level topography for effects of hemifield in the 80-120 ms time window and C2 for the hemifield-by-stimulus category interaction in the 140-190 ms time window (white circles on topographies highlight the selected channels).

p<0.001, but not when presented ipsilaterally (LVF), t(16)=0.16, p=0.87. The same was true for P8 contralateral (LVF) presentations: t(16)=3.79, p<0.001, but not for ipsilateral (RVF) presentations, t(16)=0.63, p=0.53. Hence, the significant three-way interaction reflected that for both channels, contralateral face presentations (LVF for P8 and RVF for P7) showed larger amplitudes for faces than houses.

5.3.4.2 Magnetometers

As with EEG, two magnetometers were selected, based on the maxima for faces minus scrambled faces reported in Henson et al. (2008): a sensor on the left (1521, henceforth termed "LH") and a sensor on the right (2641, henceforth termed "RH"). The evoked fields for each are shown in Figure 5-4A and 5-4B respectively. For the early 80-120 ms time-window, the four-way omnibus ANOVA with factors hemisphere, hemifield, stimulus category and repetition condition only revealed a significant main effect of hemisphere, F(1,16)=18.2, reflecting the reversal of polarity in each hemisphere (Figure 5-4A1 and 5-4B1). For the same omnibus four-way ANOVA in the 140-190 ms time-window, the only interaction that reached significance was the two-way interaction between stimulus category and hemisphere, F(1,16)=42.7, p<0.001. However, this two-way interaction reflects a polarity reversal between the LH and RH sensors, (Figure 5-4A2 and 5-4B2), rather than a difference between faces and houses in each hemisphere (reflecting the nature of the magnetic signal detected by magnetometers, elaborated below). The lack of effects of hemifields in either time-window reflects the fact that magnetometer sensors are not optimal for detecting differences in hemifield (see Figure 5-4C1 and Figure 5-4C2), given that (i) they were defined independently for a face-house difference, and (ii) that magnetometers are highly sensitive to source orientation (more sensitive than EEG). Thus, the maximal difference in the magnetic field over the scalp does not correspond to the likely location of the underlying generator (indeed, if there were a single dipolar source, it would lie midway between the positive (out-going) and negative (in-going) lobes of the magnetic flux). Nonetheless, the hemifield effects for magnetometers were reliable in the SPMs, and the hemisphere effects for MEG are shown more clearly in the following gradiometer RMS analyses, which have better localising power.

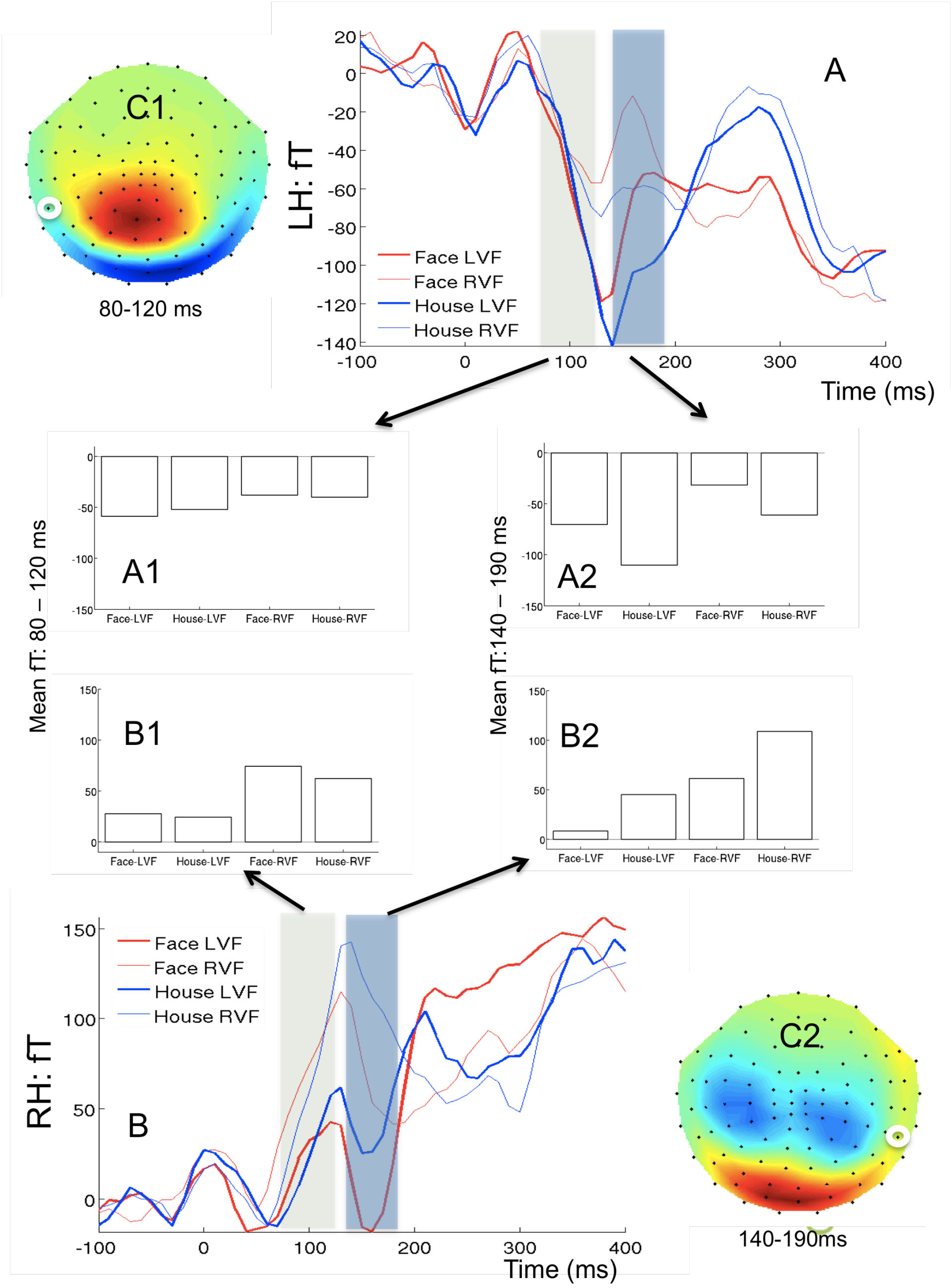


Figure 5-4: Magnetometer evoked waveforms for LH (panel A) and RH (panel B) sensonrs with mean of effects for the early 80-120 ms time window (panels A1 and B1) and the 140-190 ms window (A2 and B2) for each channel. C1 shows the mean sensor level topography for effects of hemifield in the 80-120 ms time window and C2 for the hemifield-by-stimulus category interaction in the 140-190 ms time window (white circles on topographies highlight the chosen channels).

5.3.4.3 Gradiometers

The gradiometer pairs in left and right hemisphere were 1722 and 1723 (henceforth termed “LH”) and 2522 and 2523 (henceforth termed “RH”). The signals of the x- and y- gradients within each pair were combined by taking the root-mean square (RMS), i.e. length of the vector representing the planar component of the magnetic field. This value (also positive) is shown in Figure 5-5A and 5-5B. For the 80-120ms time-window, the highest order significant interaction for the four-way omnibus ANOVA (with factors hemisphere, hemifield, stimulus category and repetition condition) was the two-way interaction between hemisphere and hemifield, F(1,16)=7.52, $p<0.05$. Like with the EEG, for each hemisphere, contralateral presentations showed larger amplitudes than ipsilateral presentations (see Figure 5-5A1 and 5-5B1).

For the 140-190 ms time-window, there was a significant four-way interaction, F(1.45, 23.28)=4.08, $p<0.05$. Follow up three-way ANOVAs for the LH and RH, with factors hemifield, stimulus category and repetition condition showed a reliable three-way interaction for the LH, F(1.96,33.35)=4.31, $p<0.05$, but not for the RH, $F<1.4$, $p>0.2$, which explains the reliable four-way interaction in the omnibus ANOVA. However, these interactions involving repetition were not investigated any further since: (i) they were not found for the SPMs for any sensor, and (ii) they were not specific to faces, and none of the effects survived a Bonferroni correction, given the seven different repetition effects possible in the given design. Given that these repetition effects are likely to reflect a Type I error, further analyses were conducted collapsing across the repetition factor.

As the omnibus four-way ANOVA showed a borderline three-way interaction between hemisphere, hemifield and stimulus category, F(1,16)=4.31, $p=0.05$, further two-way ANOVAs were conducted for the LH and RH separately with factors hemifield and stimulus category. For the LH, the two-way interaction was not significant, F(1,16)=1.68, $p=0.23$. Both the main effects of stimulus category, F(1,16)=12.7, $p<0.01$, and hemifield, F(1,16)=23.1, $p<0.01$ were significant (see Figure 5-5A2), as faces showed larger amplitude compared to houses for both ipsilateral presentations (LVF), t(16)=2.1, $p<0.05$, and contralateral presentations (RVF), t(13)=2.6, $p<0.05$. Importantly however, for the RH sensors, there was a highly significant two-way interaction between hemifield and stimulus category, F(1,16)=26.3, $p<0.001$. Amplitude for faces was larger than houses for contralateral presentations (LVF), t(16)=3.02, $p<0.01$, while the same contrast did not reach significance for ipsilateral presentations (RVF), t(16)=1.95, $p=0.07$. Similar to the OFA analysis in Experiment 7, a T-test was

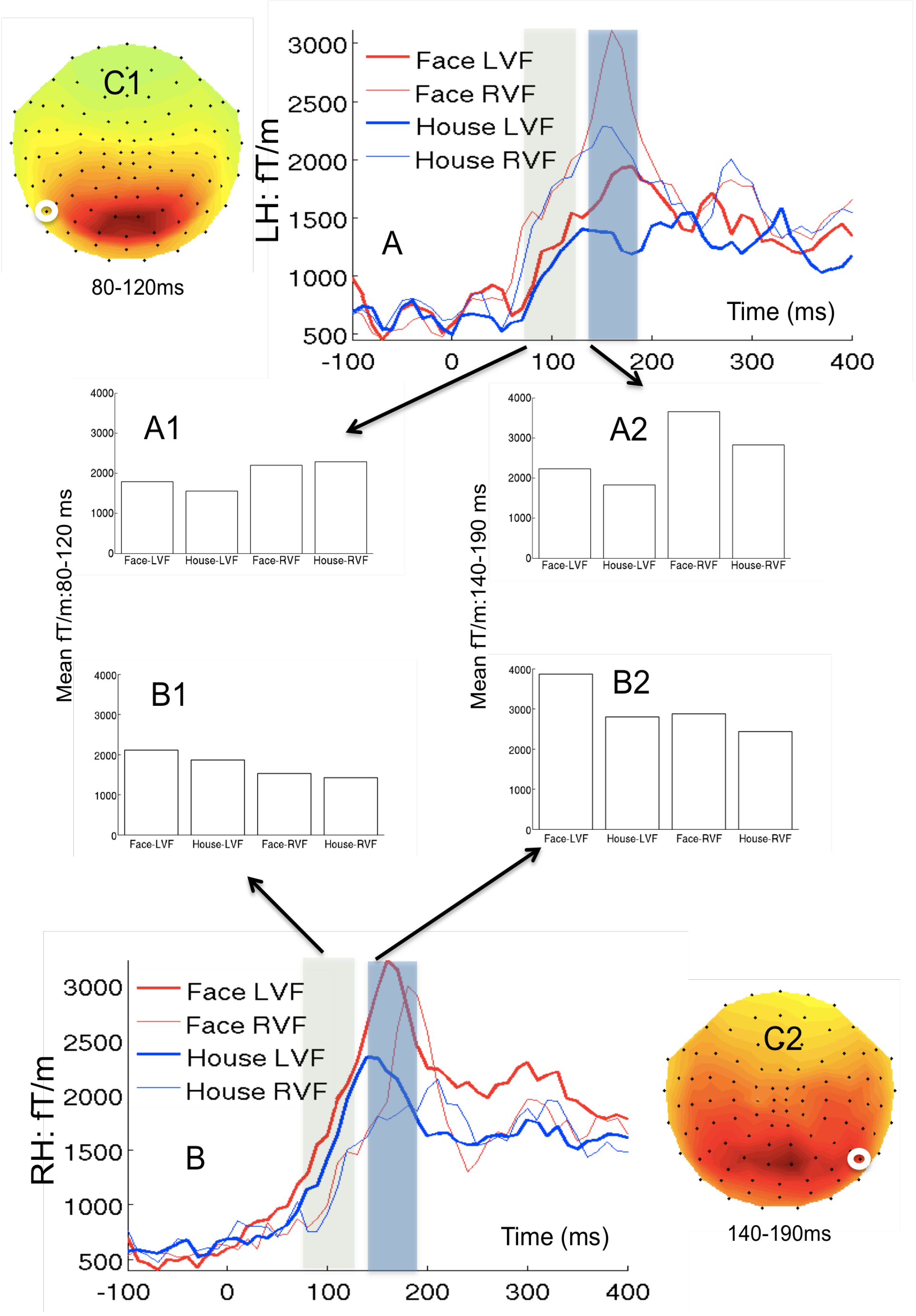


Figure 5-5: Gradiometer RMS evoked waveforms for LH (panel A) and RH (panel B) sensors, with mean of effects for the early 80-120 ms time window (panels A1 and B1) and the 140-180 ms window (A2 and B2) for each channel. C1 shows the mean sensor level topographies for effects of hemifield in the 80-120 ms time window and C2 for the hemifield-by-stimulus category interaction in the 140-190 ms time window (white circles on topographies highlight the chosen channels)

used to compare the face-related activity (faces minus houses) across LH and RH sensors for contralateral presentations (i.e., RVF and LVF respectively). As with the OFA data, any difference did not reach significance, t(16)=0.84, p=0.6, though it is noteworthy that numerically at least, face-related amplitude increases for contralateral stimuli were larger for the RH (1101 fT/m) than for the LH (903 fT/m), similar with the OFA. Finally, visual inspection of the GRMS data in Figure 5-5 revealed a possible latency difference in the emergence of a faces-house differences for LVF and RVF presentations, with the peak difference (and peaks versus baseline) occurring ~20 ms later for ipsilateral than contralateral presentations. Thus, the peaks of the ipsilateral evoked responses were missed by the a priori 140-190 ms timewindow used above, which in turn may have reduced the mean amplitude in comparison to contralateral presentations. Hence, a second analysis was conducted for GMRS with a longer timewindow of 140-220 ms, which captured the peaks of both ipsilateral and contralateral presentations. As with the shorter timewindow, the three-way interaction between hemisphere, hemifield and stimulus category was significant, F(1,16)=8.67, p<0.01, and the two-way hemifield-by-stimulus category interaction was significant for the RH sensor, F(1,16)=9.28, p<0.01, but not the LH sensor, F(1,16)=2.2, p=0.157. Thus the present findings do not appear to be affected by latency differences in the responses evoked by ipsilateral versus contralateral stimuli. As with the shorter timewindow analysis, the difference of contralateral face-related amplitude was not significantly different between the LH and RH, t(16)=0.4, p>0.7, though again numerically the RH (850 fT/m) showed larger face-related amplitude than the LH (687 fT/m).

5.4 Discussion

The data from the present experiment showed a number of findings, the most important of which was the significant interaction between hemisphere, hemifield and stimulus category in the GRMS of the independently-selected gradiometer pairs over left and right occipito-temporal cortices. This interaction, which reflected sensitivity to the hemifield of the face-related response for contralateral presentations in the RH sensor, but not LH sensor, resembles that found for the left and right OFA in the fMRI data of Chapter 4 (cf. Figure 5-5A2/B2 with Figure 4-3E/F). Moreover, these MEG data go beyond the fMRI data in confirming that this interaction happens as early as the earliest divergence between faces and houses (suggesting a bottom-up rather than top-down cause of this RH specialisation), and that the interaction is not an artifact of the differential eye-movement that was detected here for the first time via the EOG channels (see Eye Movement section below).

The EEG and magnetometer data showed a similar interaction between hemifield and stimulus category in the SPM space-time analyses across all channels. The interaction of this effect with hemisphere did not reach significance however for the independently-specified EEG and magnetometer channels. For the magnetometer data, this is understandable given the nature of the magnetic signal measured, which is not maximal directly above the sources (e.g., hemisphere) that generate the effect (see Introduction and Results for further discussion). For the EEG data, the lack of a three-way interaction between hemisphere, hemifield and stimulus category is less likely to be a problem of electrode selection (given that the selected sensors happened to be close to the maxima of the visual-field by stimulus category interaction; Figure 5-3C2). However, it could reflect the greater volume conduction in EEG, where the electrical field generated by neuronal currents is propagated differentially along tissue-types within the cortex, and spatially smeared by the skull/scalp (both consequences of different electrical conductivities for different materials). This volume conduction may have reduced the differences between LH and RH electrodes (e.g., the LH electrode will have picked up relatively more signal from generators in both hemispheres, than did the LH planar gradiometer; likewise for RH sensors).

5.4.1 Hemispheric Differences in the Processing of Lateralised Faces

While there was an interaction between left vs. right hemisphere, faces vs. houses, and left vs. right hemifield, the face-related activity in the RH for LVF presentations was not actually greater than face-related activity in the LH for RVF presentations. Hence, the significant stimulus category-by-hemifield interaction in the RH seems to be driven by the absence of significant face-related activity for ipsilateral (RVF) presentations, while in the LH both ipsilateral (LVF) and contralateral (RVF) presentations elicited significant face-related activity. Although overall the pattern between the OFA (in Chapter 4) and GRMS was similar in terms of the pattern of significant interactions, there was an important difference between the two modalities in the LOFA and left GRMS sensor: in the LOFA, the absence of a significant hemifield-by-stimulus-type interaction was because faces did not produce reliably greater activation than houses for either ipsilateral or contralateral presentations (i.e., there was only a main effect of hemifield); whereas in the LH GRMS data, both ipsilateral and contralateral faces showed higher amplitudes than houses (i.e., there were main effects of both hemifield and stimulus-type). Another interesting aspect of both patterns was that face-related activity for contralateral presentations, though not significantly different, was considerably larger numerically in both modalities. Although the absence of statistical difference does not provide direct neural evidence for the LVF-RH face processing advantage found in the behavioural data of Chapters 2-3, the neural data are still consistent with a LVF specilisation for face processing. This is consistent with the LVF baseline advantage found in the previous Experiments 2-6 of the thesis. Our data also contribute to the limited ERP research that uses DVF to an LVF advantage in structural encoding of faces, also using appropriate control stimuli (see section 1.2.4). Most importantly, there seems to be a convergence of behavioural, fMRI and MEG evidence for a LVF sensitivity in face processing, especially in early processing stages. This is consistent with our RH-SPA hypothesis as both the OFA and the M/N170 are believed to index structural encoding processes. Unfortunately, as with Experiment 7, the neural correlates of how this LVF-RH sensitivity modulates repetition effects was not clear, as no repetition effects were found (see section 5.4.2 below).

One final interesting finding was the early hemifield effect at 80-120 ms (P/M100 component), which reflected maximal responses in contralateral hemisphere (most clearly for EEG and gradiometer RMS), behaving like the V1 ROI in Chapter 4. This was a useful finding as it confirmed that the DVF methodology used in the present experiment ensured that until at least 120 ms post-stimulus activations were highly contralateral. Hence the DVF parameters seem to be successful in enforcing lateralised hemispheric processing of stimuli for at least the initial stages of early visual processing.

5.4.2 Repetition Effects

Unfortunately, no repetition effects were found for M/EEG data, similarly to the efMRI data. The absence of repetition effects eliminates the hypothesis formulated in the previous chapter that repetition effects were not found in efMRI due to the transient nature of such effects, which would not be captured by the temporally slow BOLD signal. Rather, the lateralised primes behaved as if they were unattended, similar to the Henson & Mouchlianitis (2007) fMRI study, in which repetition effects were found for attended but not unattended stimuli. However, in Chapter 3, reliable priming effects for faces were found for a similar paradigm with face stimuli, where both primes and probes were lateralised (Experiments 6 and 7). One possibility is that the tasks used in those experiments in Study phase (Like/Dislike) and Test phase (Male/Female) required a greater depth of processing than the stimulus categorisation task (Face/House) used in the present and previous chapter. For example, participants might quickly learn to perform the face/house discrimination on the basis of low-level visual features like spatial frequency (since houses tend to have more energy in high spatial frequencies, e.g. sharper edges). This would discourage deeper visual analysis. Such strategies may not be possible for the Like/Dislike or Male/Female discriminations, leaving more scope for priming of higher-level visual analyses. This would be consistent with the much slower RTs for the tasks used in the experiments of Chapter 3 (~800 ms) than the efMRI and M/EEG experiments here and in Chapter 4 (~550 ms).

Thus, with the absence of repetition effects, no conclusions can be made for the neural support of the RH-SPA hypothesis formulated in Chapter 3 to explain the behavioural priming effects. This question is addressed in the following chapter, where an M/EEG adaptation of Experiments 6 and 7 was run, using the Like/Dislike and Male/Female rather than Face/House task, in order to increase the probability of obtaining repetition effects.

5.4.3 Eye Movements

One potential caveat, regarding effects later than 120 ms, was the significant horizontal eye-movements found after 150 ms, which also may affect all DVF paradigms (and fMRI results in Chapter 4). Analysis of the HEOG showed a hemifield-by-stimulus category interaction, with a peak at ~220ms. As far as the gradiometer data of the present experiment are concerned, this does not seem to be problematic, as the peak of the same interaction was found at ~150 ms, hence it is unlikely that the significant interaction found in the GRMS for the RH sensor reflected eye movements. Furthermore, SPMs showed that the location of one 240 ms component was more frontal than the 170 ms component, while the other 240 ms component was on the LH, where the stimulus category-by-hemifield interaction on the sensors level was not significant (see gradiometer RMS results). As far the fMRI data were concerned, the hemifield-by-stimulus category interaction was found relatively early in the processing stream, in the ROFA. Given the close resemblance of the GRMS data in the RH sensor and the ROFA data, it is very plausible that the generator of the 150 ms interaction was the ROFA. Future methods for multimodal source analysis, using methods under development

(Henson et al, 2009), will help confirm whether the ROFA is in fact the generator of the M/EEG effects. Note that some localisation efforts indeed show that the N170 corresponds to a lateral occipotemporal region (relative to the OFA), while later components like the N250r to the fusiform gyrus (Schweinberger, Pickering, Jentzsch et al., 2002).

Finally, it is unlikely that eye movements influenced the behavioural data in previous chapters, where there was a LVF advantage in face processing. This is because presentation times were very short (80 ms and 120 ms), hence the face would have disappeared before the eye moved to that part of the screen. One possibility could be that the LVF is more sensitive than the RVF in perceiving an after-image of a face. This seems unlikely however, because backward masking (which would eliminate after-images) has been shown to increase LVF (RH) sensitivity to face processing (Sergent, 1986).

5.5. Conclusions

In conclusion, the present experiment failed to elaborate on the neural correlates of the RH-SPA hypothesis in terms of modulation of repetition effects. However, it did show a greater sensitivity of face-processing in the RH for LVF presentations in early stages of face processing, viz for the M/N170 component, which is associated with structural encoding of faces. This corroborates the fMRI data in Chapter 4, that showed a similar effect for the ROFA, suggesting that it is the possible source of the gradiometer RMS effect. This offers further evidence for the core assumption of the working hypothesis, that the LVF and RH have a central role in the perceptual processing of faces, though it is still not clear how this modulates repetition effects.

Chapter 6: M/EEG Investigation of the RH-SPA Hypothesis Using both Central and Lateralised Probes

This is the final M/EEG experiment to directly test the RH-SPA hypothesis. Although the fMRI and M/EEG data in Chapters 4-5 were successful in demonstrating a relative advantage of the RH in face processing, they did not reveal any repetition effects. As discussed in those chapters, this lack of repetition effects may reflect the relatively "shallow" task (a face/house decision, given that houses were necessary to define face-selective neural responses). The design of the present Experiment 9 was therefore more closely based on the behavioural experiments in Chapter 3, using the same study-test design (i.e., repetition lag) and the same sex task (in the test blocks). To address the issue that lateralised faces do not produce such strong neural responses however (see below), additional conditions were added in which the prime or probe face was central (more akin to Experiments 3-4 in Chapter 2).

6.1 Experiment 9

Experiment 9 was based on Experiments 5-6, with mini-blocks of 8 study trials followed by 12 test trials (8 primed and 4 unprimed). The main difference was that instead of both primes and probes being lateralised, alternating blocks were used with either central primes and lateralised probes, or lateralised primes and central probes. The reason for using centralised stimuli as either primes or probes was to increase the probability of seeing ERP/ERF correlates of repetition effects, given the absence of detectable repetition effects for lateralised stimuli in the fMRI Experiment 7 and previous M/EEG Experiment 8. This absence may have been caused by weaker neural responses to non-central faces (Jeffreys, 1996) or reduced spatial attention (Henson & Mouchlianitis, 2007; see Section 5.4.2). Although this design did not allow direct investigation of within vs. across hemisphere repetition effects (as in Chapters 4 and 5), it could still test the working hypothesis that a RH advantage in structural encoding modulates the effects of repeating (priming) faces. More specifically, this hypothesis predicts that for central visual field (CVF) primes, RVF probes will show greater repetition effects than LVF probes (i.e., priming should be reliable in the CVF-RVF but not CVF-LVF condition), since central primes will be encoded equally by LH and RH, but on repetition, the RH will be already at optimal levels of efficiency.

For the second part of the design, using the opposite situation of lateralised primes and central probes, the RH-SPA hypothesis would predict that, *if* any repetition effects are found, they should be larger from LVF than RVF primes (i.e., reliable priming in the LVF-CVF but not RVF-CVF condition), based on the hypothesis that the LH does not encode faces sufficiently well (as inferred from the lack of priming in the RVF-RVF condition in Experiments 5-6). However, given that CVF probes are processed by both LH and RH, the hypothesis actually predicts no repetition effects in either of these two conditions, because the RH is already optimally efficient in structural encoding (of probes). Nonetheless, these central-probe conditions, which have not been used before in this thesis, were maintained in order to provide a novel test of our hypothesis.

6.2 Methods

6.2.1 Participants

Eighteen right-handed participants (eleven female) were tested, mean age 27 (a superset of the participants in Experiment 8). Four participants were removed due to excessive blinking. Note that the reason these participants were not removed in Experiment 8 is that the present experiment used a longer epoch, from -100 ms to 600 ms (to detect any repetition effects that occurred later in time), and most blinks occurred after 400 ms (the end of the epoch in Experiment 8).

6.2.2 Materials and Design

The material was the same as in Experiments 5 and 6 in Chapter 3 (480 non-famous faces, 240 female, frontal views, hair removed). Given that there were separate predictions for the lateralised primes/central probes and central primes/lateralised probes conditions, the data were analysed in two parts: for central probes, there was a single factor with three levels (i.e., 80 LVF primed, 80 RVF primed and 80 unprimed trials); for lateralised probes, two factors were crossed, hemifield of probe (LVF vs. RVF) and repetition (primed vs. unprimed), with 80 trials per hemifield for primed faces and 40 trials per hemifield for unprimed (given the limited time available).

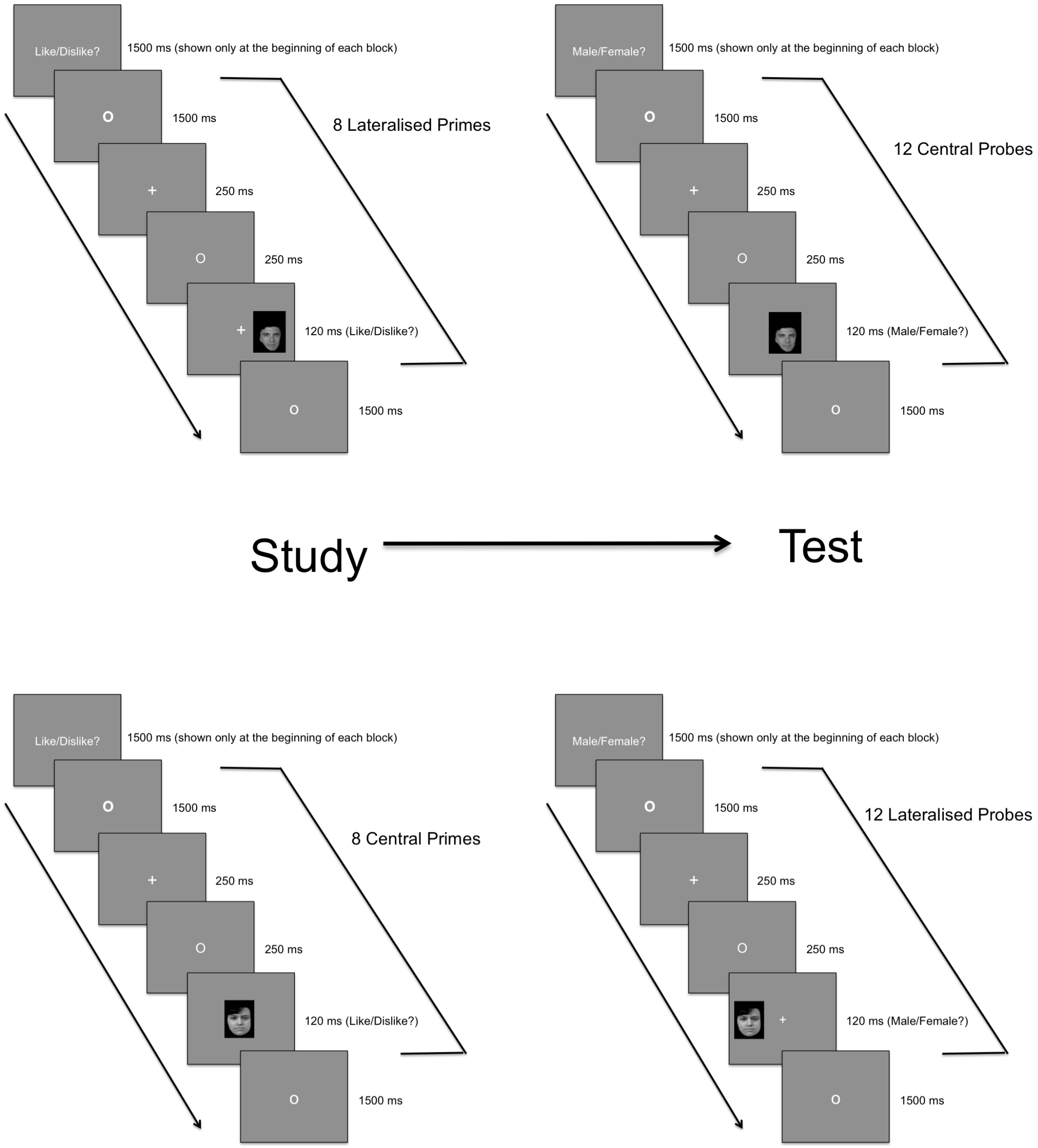


Figure 6-1: Schematic representations of study and test trials for lateralised primes/central probes blocks (top part of figure) and central primes/lateralised probes blocks (bottom part of figure) in Experiment 9

6.2.3 Procedure

As with Experiments 5 and 6, two sessions of ~18mins were run, with no repetition of stimuli across nor within sessions. There were 20 blocks of central probes and 20 blocks of lateralised probes (10 of each per session). Examples of study and test trials for central probes and lateralised probes blocks can be seen in Figure 6-1. Essentially, the procedure was identical with Experiments 3-6, with one difference being separate blocks with central primes / lateralised probes and with lateralised primes / central probes. The study and test tasks, visual angle, bimanual key presses were all maintained as with the previous experiments. The only other main difference was that presentation duration was 120 ms for both primes and probes, compared to 2000 ms for the primes in Experiments 3 and 4. Obviously, since we had a session with lateralised primes, their presentation time needed to be reduced in order to have successful DVF presentations (i.e., less than 200 ms).

6.2.4 M/EEG Data Acquisition and Pre-processing

M/EEG acquisition parameters were identical to those in Experiment 8 (given that this experiment was run on the same participants in the same MEG visit as Experiment 8). Pre-processing was also identical to Experiment 8, except that a longer epoch was used (from -100 ms to +600 ms), in order to check for any repetition effects that emerged later (i.e., closer to the decision rather than early perceptual processing). The number of bad channels ranged across participants from 0-7 in the case of MEG, and 0-13 in the case of EEG), and the mean number of trials after rejection were: (i) for the central probes session: 73 trials for LVF primed, 70 for RVF primed and 72 for Unprimed; and (ii) for the lateralised probes session: 74 trials for LVF probes, 36 trials for LVF unprimed, 72 trials for RVF probes, 32 for RVF unprimed. Another small difference from Experiment 8 is that, for the gradiometer analyses of the lateralised probe conditions, the RMS was taken before averaging across trials, because the uneven number of trials across conditions (with fewer unprimed trials), while for central probes (due to equal numbers across conditions), RMS was taken after average (see section 5.2.5.1 for further discussion).

6.2.5 Behavioural Analysis

Although four participants were removed from the M/EEG analysis because of rejection of a large number of trials due to excessive blinking, those participants were maintained in the behavioural analysis. This was because blinks normally occurred 400 ms after stimulus onset, i.e. significantly after the removal the face from the screen at 120 ms post-onset, and so should not interfere with the behavioural responses. For central probes, a one-way repeated-measures ANOVA was conducted on mean accuracy and RTs, with three levels (LVF primed vs. RVF primed vs. unprimed). For lateralised probes, a two-way repeated measures ANOVA was conducted crossing factors hemifield (LVF vs. RVF) and priming (primed vs. unprimed).

6.2.6 M/EEG Analysis

6.2.6.1 Space x Time analysis

The first step of M/EEG analysis was a space-time SPM approach to localize repetition effects in sensor space and in time (see Experiment 8, Section 5.2.5.1) for details). These SPM analyses used the same ANOVA models as for the behavioral data above, except with a pooled error estimate (Henson & Penny, 2003). In the case of pairwise comparisons of primed and unprimed conditions, an additional model was tested that used a partitioned error (i.e., an error estimate specific to that comparison), to double-check any effects that were not significant using the pooled ANOVA error.

Any clusters that survived p<.05 family-wise error (FWE) for height or extent (using an initial height threshold of p<.001 uncorrrected) using Random Field Theory correction for multiple comparisons across the whole space-time volume were reported. However, given a priori hypothesis about timewindows of interest, this correction was also restricted to those timewindows (anywhere across the scalp); a so-called “Small-Volume Correction” (SVC) in the SPM package). The a priori reasons for these timewindows are detailed below.

6.2.6.2 Timewindows of interest

The first timewindow was 200-300ms, which encompassed the “N250r” component that has previously been shown to be sensitive to short-lag repetition of famous faces in EEG data (Begleiter, Porjesz, & Wang, 1995; Herzmann, Schweinberger, Sommer & Jentzsch, 2004; Itier&Taylor, 2004;Martin-Loeches, Sommer, & Hinojosa, 2005; Pfutze, Sommer,& Schweinberger, 2002; Schweinberger, Huddy, & Burton,2004; Schweinberger, Pfutze & Sommer, 1995; Schweinberger,Pickering, Jentzsch, Burton & Kaufmann, 2002). Though the N250r effect is normally greater for famous than non-famous faces (Begleiter et al., 1995; Engst et al., 2006; Pfütze et al., 2002; Schweinberger et al., 1995, 2002b, 2004), it has been found for non-famous faces when the task is not familiarity-judgment (Henson et al., 2004). It is also normally only found immediate repetitions (Schweinberger et al., 1995; Henson et al., 2004), but we nonetheless thought it would be worth examining for the present short-lag repetition effects.

A second component on which repetition effects are often found is the N400 (Cooper et al., 2007; Schweinberger et al., 2002a), which we tested using a timewindow of 300-500ms. This component is thought to be related to the semantic integration of the prrime and probe, and although larger repetition effects are again usually found for familiar faces (possibly due to the extensive use of a familiarity task, which may defer a "nontarget" status to non-famous faces; Henson et al., 2004), they are also evident with unfamiliar faces (Schweinberger et al., 1995). A later component from 500-700 ms also is found in response to repetition of faces, known as the P600. However this was not used as an SVC here, since it is associated with explicit memory rather than priming (e.g., Henson et al., 2004), hence goes beyond the aims the present experiment.

Note that repetition effects that onset earlier than 200 ms (e.g., on the N/M170 component) are very rarely reported (Bentin & Deouell, 2000; Eimer, 2000b; Engst et al., 2006; Schweinberger et al., 2002b), except for immediate repetition (Campanella et al., 2000; Guillaume & Tiberghien, 2001; Itier & Taylor, 2002), and even then such effects are not always found (e.g., Eimer, 2000b; Schweinberger et al., 2002a). Indeed, a MEG study that systematically varied prime-probe SOAs only found modulation of the M170 for SOAs less than 800 ms (Harris & Nakayama, 2007). A recent study of ours (Henson et al., 2008) found a repetition effect between 100-140 ms, but this was from a (masked) prime that onset only 100 ms before the probe onset (such that the evoked response to the prime overlapped that to the probe, Jeffreys, 1996). Thus no timewindow earlier than 200 ms was used for SVC. Nonetheless, given the lack of repetition effects found in the above timewindows (see Results), in a final analysis we focused on the sensors that were maximally sensitive to faces in Experiment 8, to see whether there were any reliable repetition effects specifically on the M170/N170 components after all.

6.2.6.3 Time Window Analysis

As in Experiment 8, having identified time windows of interest from the SPM analyses, additional ANOVAs were performed on the mean amplitude (with respect to mean pre-stimulus baseline) during these time windows, from selected sensors of interest

(SOI). Unlike in Experiment 8 however, we did not have a priori (i.e., independent) reasons for selecting sensors (particularly in MEG) where short-lag repetition effects for non-famous faces would be maximal; we therefore selected sensors closest to the maxima of the above SPM analyses. Although this sensor selection biases subsequent analyses towards finding a repetition effect, the main purpose of these follow-on analyses was to (i) show complete time-courses for these maxima, and (ii) test for hemispheric differences (as in Experiment 8; see Section 5.3.4).

6.3 Results

6.3.1 Behavioural Results

Mean accuracy and RTs for both central probes and lateralised probes session are summarised in Table 6-1. Note that the RTs were around 800 ms, which is longer than the mean RT for the face/house task in Experiments 7-8 previous experiments, which suggests that the present male/female task encouraged longer/deeper processing of the faces.

	Accuracy (%)		RTs (ms)	
	LVF	RVF	LVF	RVF
Central Probes				
Primed	88 (4.9)	87 (4.7)	699 (114)	720 (116)
Unprimed	88 (5.1)		715 (115)	
Lateralised Probes	LVF	RVF	LVF	RVF
Primed	81 (8.1)	80 (4.9)	727 (97)	727 (113)
Unprimed	84 (6.7)	77 (7.9)	746 (121)	745 (109)

Table 6-1: Mean Accuracy and RTs (N=18) as a function of conditions in Experiment 9 (standard deviations in brackets)

6.3.1.1 Central Probes

Mean accuracy was 88%. The one-way ANOVA across LVF Primed, RVF Primed and Unprimed conditions did not show a significant effect, F<1, p>0.4, hence accuracy data were not analysed further. For RTs, the same ANOVA showed a significant effect, F(1,17)=5.37, p<0.01. Planned pairwise tests of priming relative to the unprimed condition showed reliable positive RT priming for LVF primes, but not for RVF primes (see Figure 6-2A). As explained in Section 6.1, the RH-SPA hypothesis, as currently formulated, actually predicted no priming in either condition (given that CVF primes should be processed by RH, as well as LH, yet the hypothesis proposes that RH is already optimal in structural encoding). Nonetheless, that priming was found from LVF primes rather than RVF primes, is at least consistent with the hypothesis that the RVF is not as efficient at encoding faces so as to cause subsequent priming.

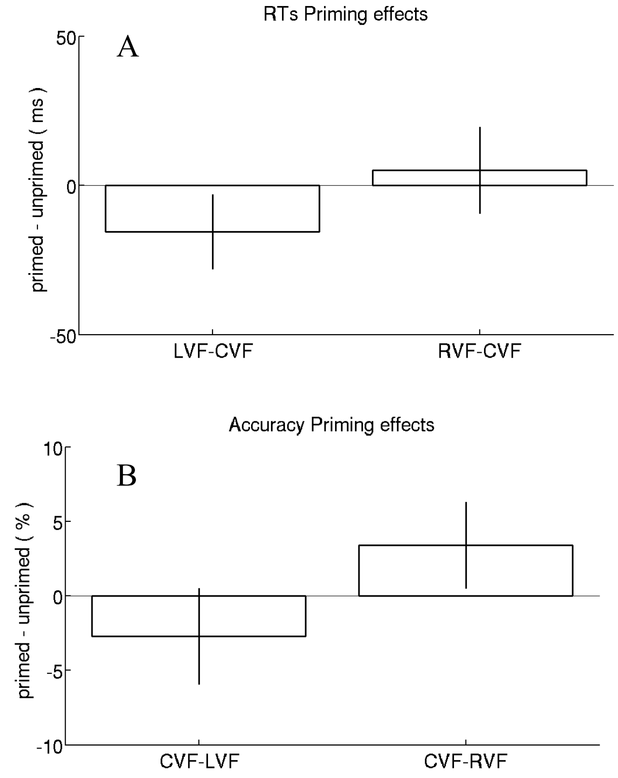


Figure 6-2: Mean (N=18) repetition effects on RTs from Central Probes (and lateralised primes; panel A) and on accuracy for Lateralised Probes (and central primes; panel B). Error bars are one-tailed 95% confidence intervals

6.3.1.2 Lateralised Probes

Mean accuracy was 81%. The two-way ANOVA showed a reliable interaction between hemifield and repetition, F(1,17)=5.09, p<0.01, with RVF, but not LVF probes showing reliable priming (see Figure 6-2B). For RTs, no effects reached significance, Fs<1, except for the main effect of repetition, which approached significance, F(1,17)=4.20, p=0.06.

Analysis of baseline hemifield effects (unprimed stimuli in the LVF and RVF) showed that LVF presentations were significantly more accurate than RVF presentations, t(17)=3.8, p<0.001. This is consistent with the RH advantage in face processing, though again raises the possibility that priming for RVF probes was reduced as a consequence of such baseline effects (see Experiments 3-4 in Chapter 2 and Experiments 6-7 in Chapter 3). There was no reliable baseline difference in RTs, t(17)=0.08, p>0.5.

The accuracy results for lateralised probes support the RH-SPA hypothesis, in that priming was only found for RVF probes, where LH structural encoding is presumed to benefit from prior RH encoding (from the CVF prime). It is unclear why this effect was found on accuracy rather than RTs, given that the analogous effects in Experiments 3-4 (and Experiments 5-6) were on RTs. One reason may be the much shorter prime durations used in this experiment (120 ms) relative to the previous prime durations (2000 ms). Having more accurate representations of a prime face following longer stimulus durations might cause priming to be expressed in RTs rather than accuracy, though this possibility was not explored further in this thesis.

6.3.2 Space x Time SPM results

As with behavioural analysis, Space x Time SPMs were created separately for the central probe and lateralised probes sessions.

6.3.2.1 Central probes

For magnetometer data, the one-way ANOVA showed bilateral occipito-temporal clusters, maximal at 460 ms (suprathreshold from 440 ms to 470 ms), that survived SVC for the N400 timewindow of interest (Table 6-2). The pairwise comparisons of repetition for type of prime suggested that this effect was driven by LVF primes, since a similar effect survived correction for LVF repetition effects (see Figure 6-3A), but nothing survived correction for any timewindow for RVF primes. For EEG and gradiometer RMS data, no effects survived correction for any timewindow.

6.3.2.2 Lateralised probes

For magnetometer data, there was a significant hemifield-by-repetition interaction that survived correction for the N400 timewindow (Table 6-2) in a left temporal cluster, maximal at 410 ms (suprathreshold from 380 to 420 ms). The pairwise comparisons of repetition effects showed a significant cluster with the same coordinates and time as the two-way interaction (see Figure 6-3B) for LVF probes, but no repetition effects survived correction for RVF probes (which is the effect that drives the interaction). This pattern is contrary to the behavioural priming above (which only occurred for RVF probes), and contrary to our working hypothesis (Section 6.1). For EEG and gradiometer RMS data, no effects survived correction for any timewindow.

	N	x	y	t/ms	Z
Magnetometers					
Central Probes					
One-way ANOVA	21	-33	-18	460	3.41*
	25	+39	-15	460	3.36 *
LVF Primed minus unprimed	128	+39	-15	460	3.90 *
Lateralised Probes					
Visual field X Repetition	50	-39	+6	400	3.99 *
LVF probes minus LVF unprimed	16	-39	+6	400	3.41 *

*Table 6-2. Maxima within Space-Time SPMs for Magnetometers that survived: *= SVC correction for 300-500 ms (N400 timewindow). The origin of SPM coordinates is midpoint of a square image created by projecting the sensor positions onto a 2D plane, with x ranging from -48mm (left) to +48mm (right) and y ranging from -39mm (posterior) to +45mm (anterior);" t" refers to the peristimulus time (ms); Z= Z-score; N = number of voxels.*

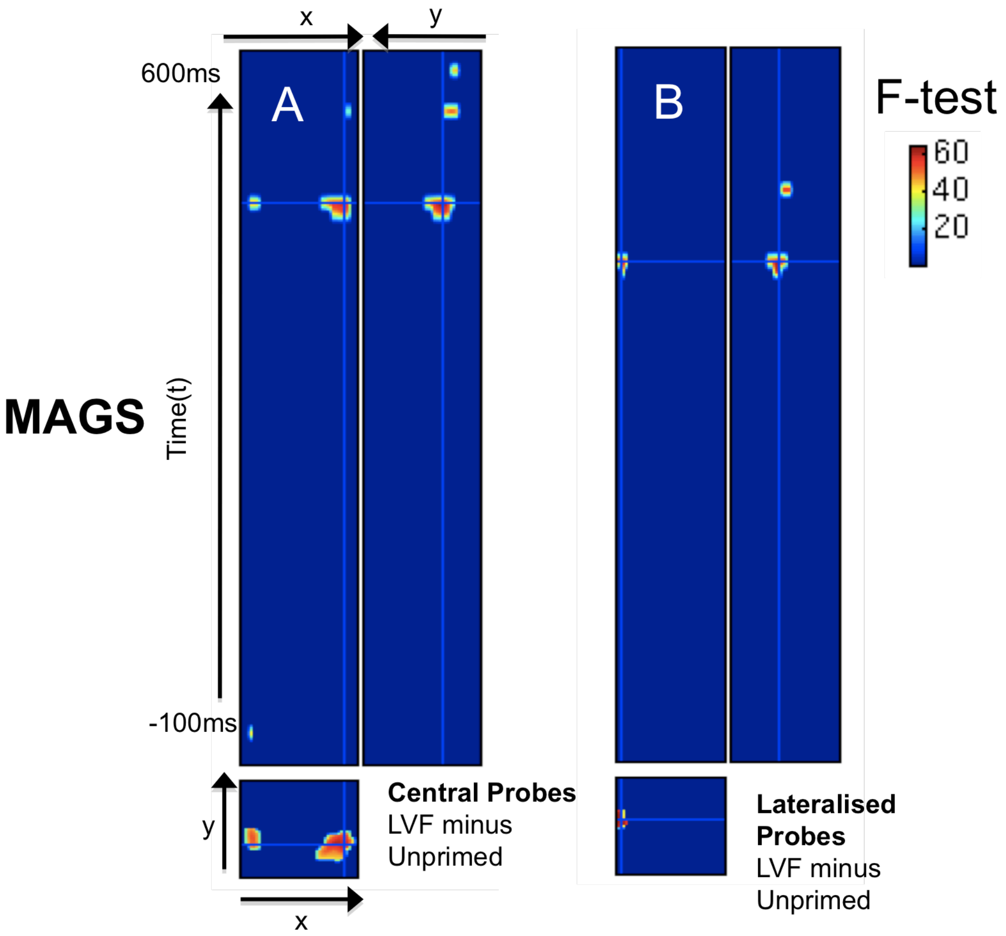


*Figure 6-3. Space-Time SPMs for Magnetometers that survived: *= SVC correction for 300-500 ms for (A) repetition effect for LVF primes, and (B) repetition effect for LVF probes. "t" refers to peristimulus time (ms)*

6.3.3 HEOG and VEOG Results

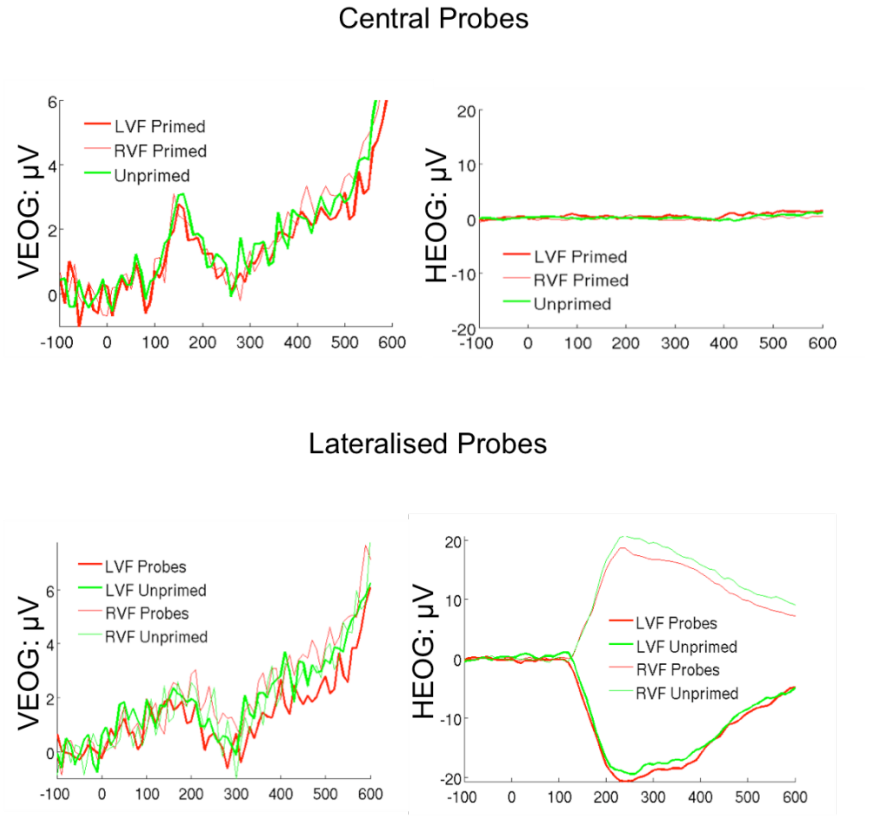
As with Experiment 8, analysis of HEOG and VEOG effects was important, as eye movements could influence repetition effects recorded by M/EEG, which the above analysis showed occurred later than 150 ms (when saccades become evident). In an ANOVA for the 300-500 ms time-window for central probes, there was no significant effect on the HEOG or VEOG; nor was there for pairwise tests of repetition effects for LVF and RVF primes, Fs<1 and ts>0.4 (see Figure 6-4, top panels). For lateralised probes, the two-way ANOVA on the HEOG showed the expected significant main effect of visual field, F(1,13)=25.2, p<0.001. There was also a main effect of repetition, F(1,13)=5.55, p<0.05 (see Figure 6-4, bottom panels). The fact that this repetition effect did not interact with the hemifield of the probe suggests that it is not related to the above repetition effect that was found only for LVF probes in the magnetometer data above (and which showed no sign for RVF probes in Figure 6-5 below), though it remains possible that this magnetometer effect is an artifact of eye-movement (that just failed to reach significance for RVF probes).

6.3.4 Time-window Results

Since only the magnetometer data showed repetition effects in the SPM analyses, only these data were analysed in more detail in terms of sensors of interest.

6.3.4.1 Central Probes

For central probes, the LH sensor 1721 (henceforth termed "LH") was selected


Central Probes

Lateralised Probes

Figure 6-4: VEOG and HEOG evoked waveforms for Central Probes (top panels) and Lateralised Probes blocks (bottom panels)

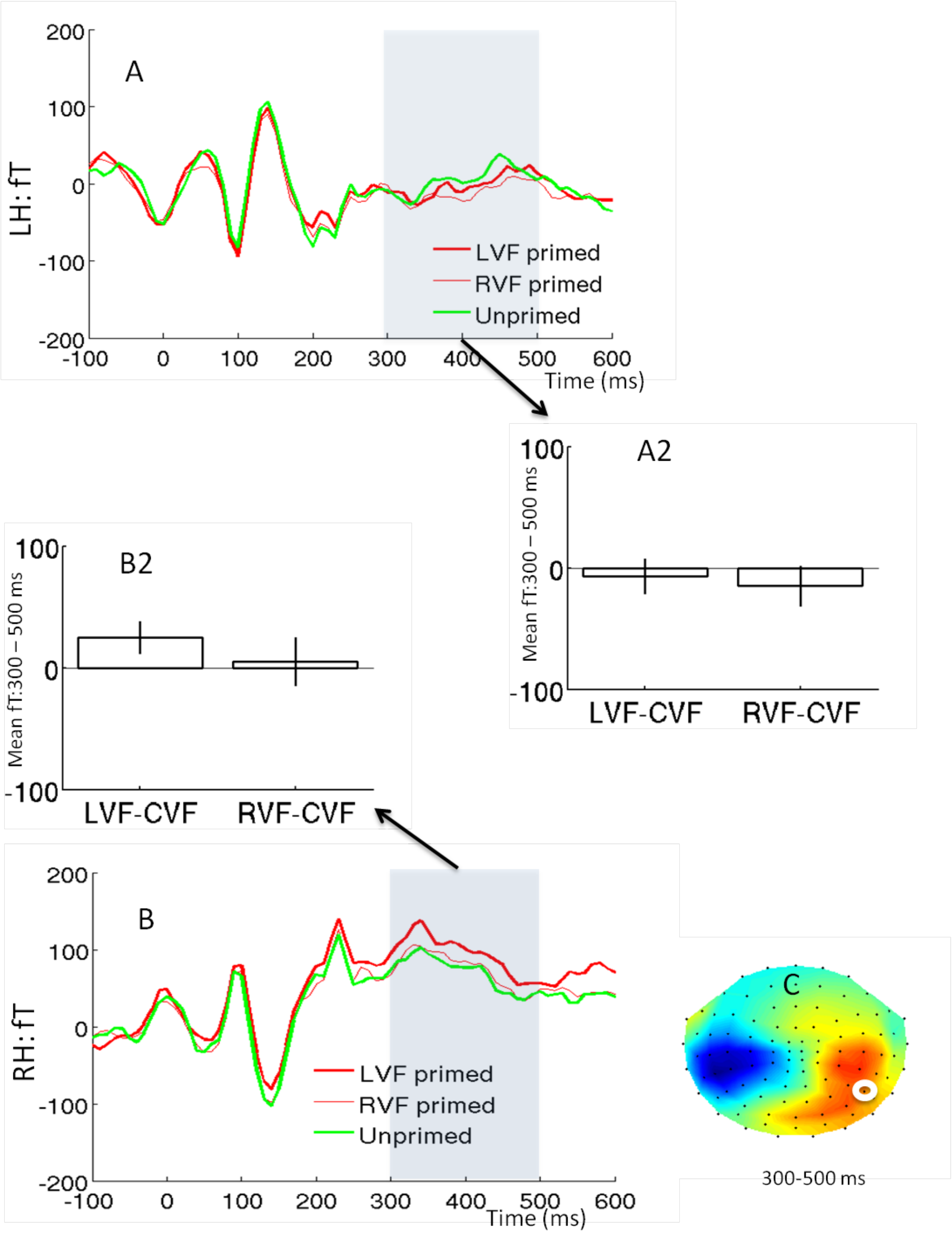


Figure 6-5: Magnetometer evoked waveforms for LH (panel A) and RH (panel B) sensors for the Central Probes blocks of Experiment 9, with mean of effects for 300-500 ms time window (panels A2 and B2; error bars represent 95% two-tailed confidence intervals). Panel C shows the mean sensor level topography for the interaction between hemifield and repetition for the 300-500 ms time-window (white circle highlights the maximal sensor from the SPM analysis).

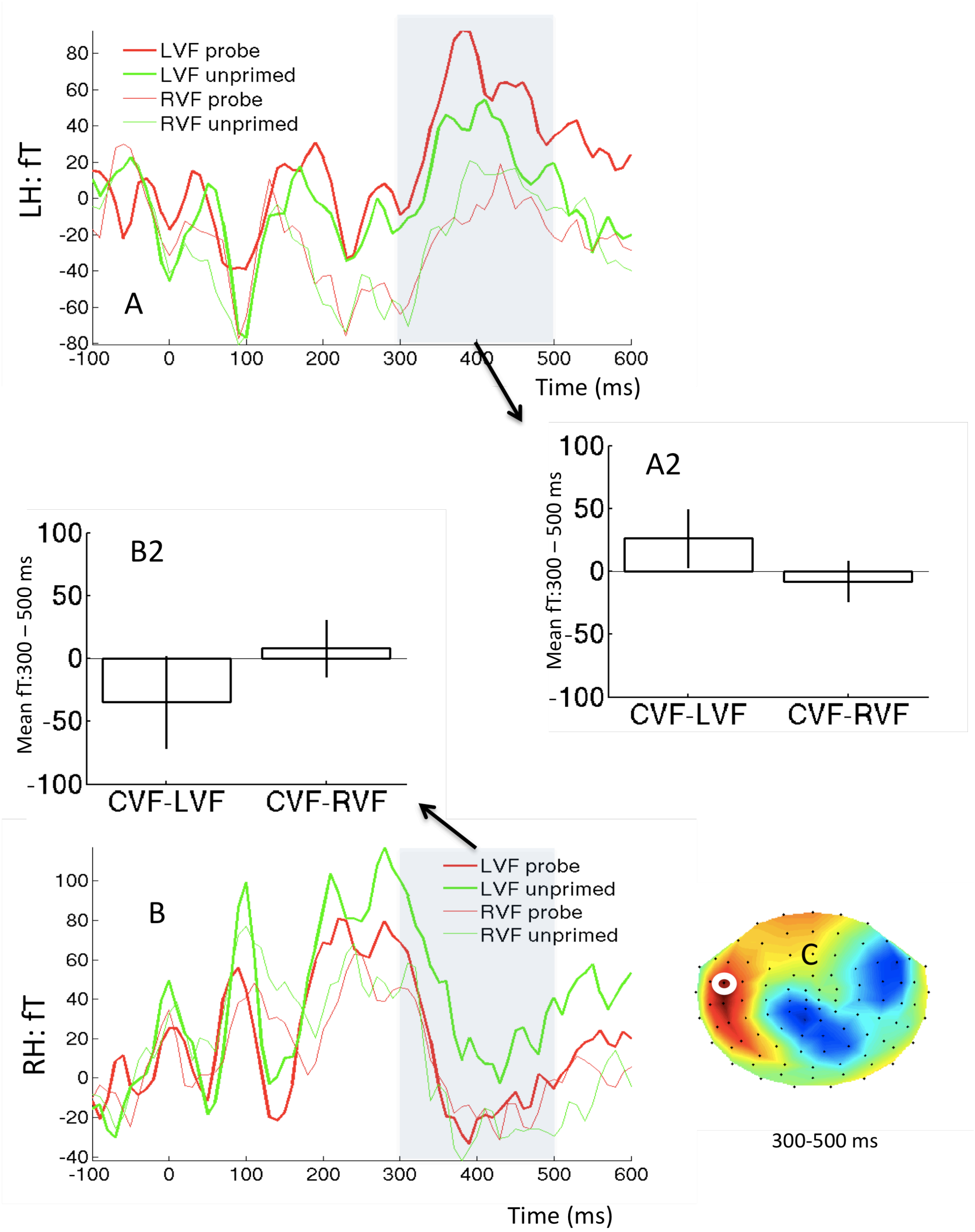


Figure 6-6: Magnetometer evoked waveforms for LH (panel A) and RH (panel B) sensors for the Lateralised Probes blocks of Experiment 9, with mean of effects for 300-500 ms time window (panels A2 and B2; error bars represent 95% two-tailed confidence intervals). Panel C shows the mean sensor level topography for the interaction between hemifield and repetition for the 300-500 ms time-window (white circle highlights the maximal sensor from the SPM analysis).

from the maximum of the SPM main effect contrast, as well its RH homologue 2521 (henceforth termed "RH"). The evoked responses in these channels are shown in Figure 6-5. The mean signals in these sensors over the 300-500 ms timewindow were entered in a 2x3 ANOVA with factors hemisphere (RH vs. LH) and repetition condition (LVF primed vs. RVF primed vs. Unprimed). This showed a hemisphere-by-repetition interaction that approached significance, F(1.65, 216)=3.22, p=0.06. This interaction reflects the fact that there was a reliable repetition effect for LVF primes in the RH sensor but not in the LH sensor, where no repetition effects were found to be significant (see Figure 6-5, panels A2/B2). Analogous ANOVAs on the 200-300 ms timewindow showed no reliable effects.

6.3.4.2 Lateralised Probes

For the lateralised probes analysis, the LH magnetometer sensor 0211 (henceforth termed "LH") and its RH homologue 1321 (henceforth termed "RH") were selected from the maxima of the interaction contrast in the SPM analysis. The evoked responses in these channels are shown in Figure 6-6. A 2x2x2 ANOVA for the 300-500 ms timewindow showed a reliable hemisphere-by-hemifield-by-repetition interaction, F(1,13)=12.7, p<0.05. This reflected the fact that there was a reliable repetition effect for LVF probes in the LH sensor and a trend in the RH sensor (see Figure 6-6, panels A2 /B2). Note that this effect of hemisphere does not reflect true lateralisation, given the nature of the magnetometer signal (see section 5.3.4.2). Analogous ANOVAs on the 200-300ms timewindow showed no reliable effects.

6.3.5 M/N170 effects

Although the SPMs did not show any reliable effects of repetition within either the 200-300 ms or 300-500 ms timewindows in either the gradiometer RMS or EEG data (so sensors could not be selected in the same way that they could for the magnetometer data that did show SPM effects), we performed a final analysis on sensors identified independently from the maxima for the N/M170 component reported in Henson et al. (2008), which were also used Experiment 8.

6.3.5.1 Central Probes

6.3.5.1.1 Gradiometer data

The two-way ANOVA between hemisphere and repetition condition did not show any significant main effects or interactions, Fs<2, ps>0.15 (see Figure 6-7, panels A/ B)

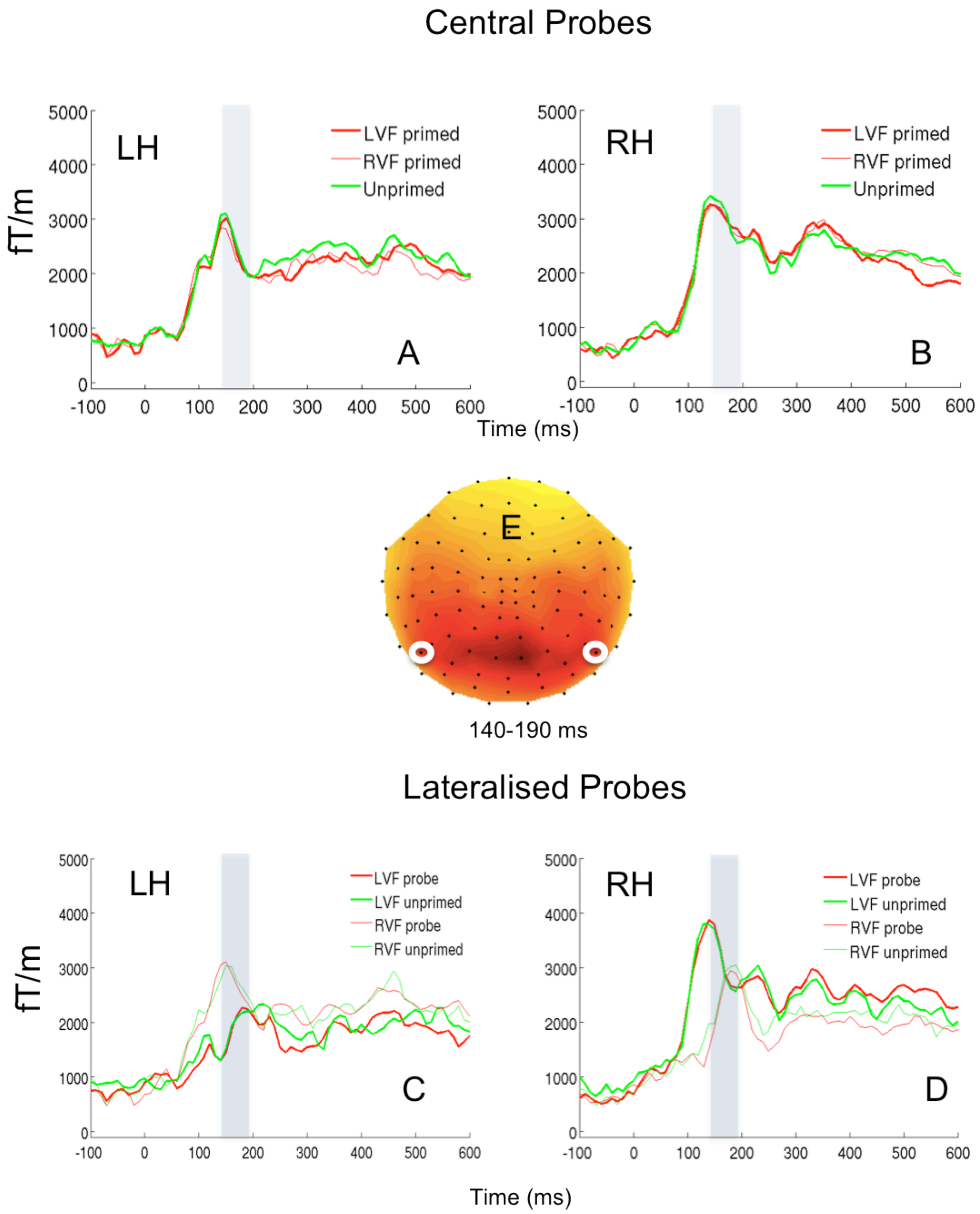


Figure 6-7: Gradiometer RMS evoked waveforms for LH and RH sensors for the Central Probes (panels A and B) and Lateralised Probes blocks (panels C and D) for the M170 component. Panel E shows the mean sensor level topography for the main effect of face presentations within the 140-190 ms timewindow (white circles highlight the selected sensors).

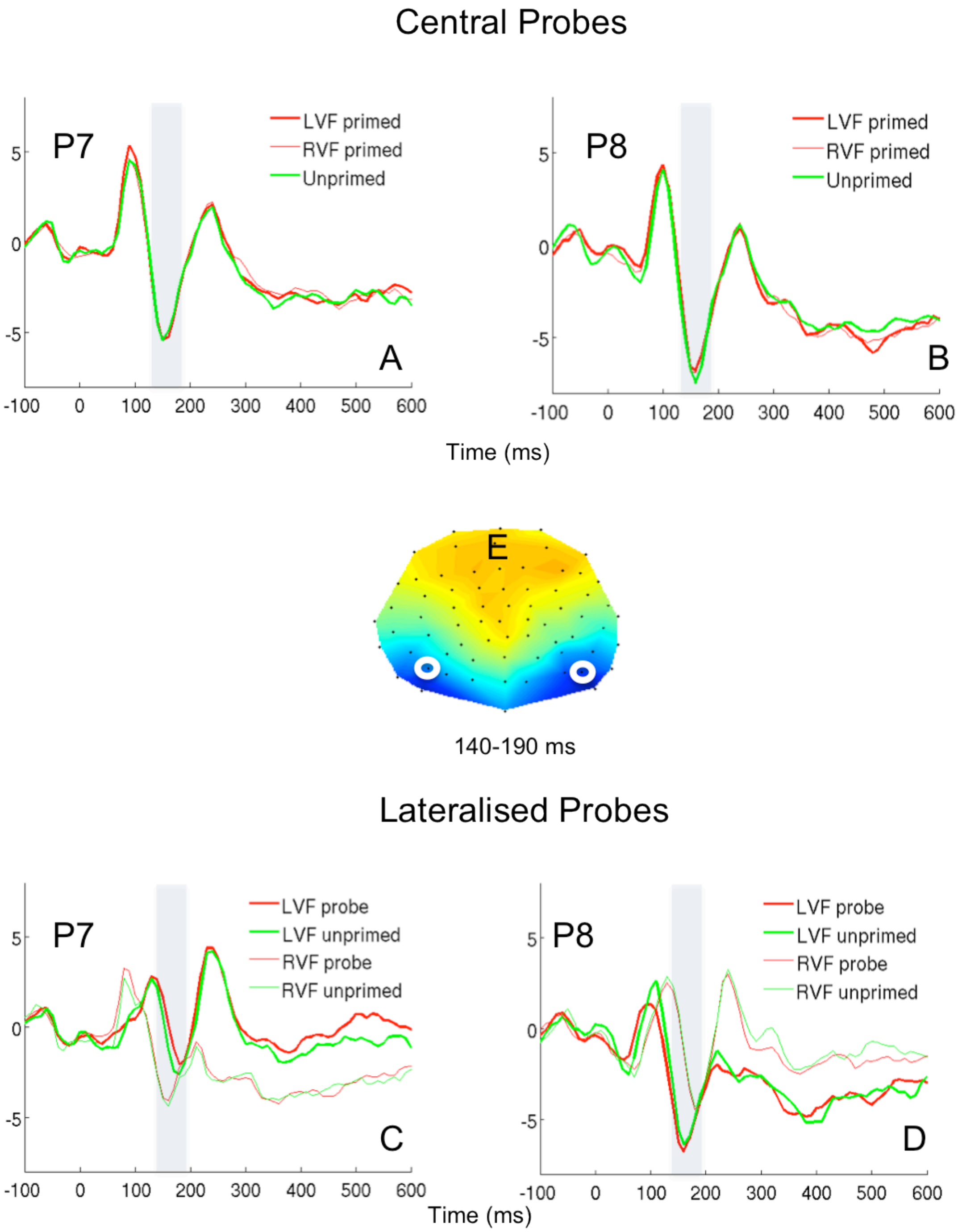


Figure 6-8: EEG evoked waveforms for P7 and P8 sensors for the Central Probes (panels A and B) and Lateralised Probes blocks (panels C and D) for the M170 components. Panel E shows the mean sensor level topography for the main effect of face presentations wtithin the 140-190 ms timewindow (white circles highlight the selected sensors).

6.3.5.1.2 EEG data

The same ANOVA for EEG only showed a main effect of hemisphere, F(1,13)=4.84, $p<0.05$, reflecting larger amplitude for RH (-5.5 μV) than for the LH (-3.7μV; see Figure 6-8, panels A/B). This finding is consistent with extended literature that reports larger N170 amplitudes in the RH for centrally presented faces (see Chapter 1)

6.3.5.2 Lateralised Probes

6.3.5.2.1 Gradiometer data

The three-way ANOVA between hemisphere, hemifield and repetition condition only showed a significant two-way interaction between hemisphere and hemifield, F(1,13)=9.42, $p<0.01$, reflecting larger amplitudes for contralateral stimuli both for the LH and RH sensors (see Figure 6-7, panels C/D).

6.3.5.2.2 EEG data

The same ANOVA for EEG only showed a significant two-way interaction between hemisphere and hemifield, F(1,13.)=16.2, $p<0.01$, reflecting larger amplitudes for contralateral stimuli for both hemispheres (see Figure 6-8, panels C/D)

6.4 Discussion

6.4.1 Behavioural data

The behavioural data showed an interesting pattern of effects. The priming effects for lateralised probes replicated those found in analogous Experiments 3-4 (which also used central primes), in that priming was only found for RVF probes, as also predicted by the RH-SPA hypothesis. Unlike Experiments 3-4 however, this priming effect was found in accuracy rather than RTs. This may reflect the shorter prime duration in the present experiment than in Experiments 3-4, in that an impoverished encoding of primes might lead to greater priming of accuracy. This could be tested in future studies by degrading prime and probe stimuli (e.g., with shorter durations and masks).

The priming effects for lateralised primes and central probes did not conform with the predictions of the current RH-SPA hypothesis, in that, if the RH is already maximally efficient in structural encoding of faces, then central presentations of probes (which should be processed by both hemispheres) should show no priming, regardless of prime visual field. The data however showed reliable priming of RTs from LVF primes (and no reliable priming for RVF primes). Since this combination of lateralised primes and central probes has not been tested before in this thesis, it should be treated with some caution, at least until it is replicated in future. Nonetheless, it is interesting that from the perspective of encoding of the prime, it is consistent with poorer encoding of faces in the LH than RH (a second component of our working hypothesis, which was added to explain the lack of RVF-RVF priming in Experiments 5-6). Note that the combination of lateralised primes and central probes has been tested previously by the studies of Bourne& Hole (2006), Bourne et al. (2009) and Cooper et al. (2007) that were reviewed in Chapter 3. These studies are not directly comparable in terms of procedural details like repetition lag, eccentricity, duration, masking (see Section 3.10), but most importantly, these priming effects were only found for famous faces in a familiarity task. Nonetheless, these studies also only found priming from LVF primes (or at least greater priming from LVF than RVF primes in the Cooper et al study). This issue of famous vs. non-famous faces is revisited in Chapter 7.

6.4.2 Repetition effects in M/EEG data

Unfortunately, despite the reliable behavioural priming effects, any repetition effects in the MEG or EEG data were too weak to be detected, or when they were (in the magnetometer data from 300-500ms), they were difficult to interpret, for example in terms of the hemisphere driving the effect. One reason for finding effects in magnetometers but not planar gradiometers (and possibly not in EEG) is if the neural generators were relatively deep in the brain. Such generators are certainly unlikely to be in the OFA identified in the fMRI data of Experiment 7, since the sensors that showed an analogous interaction between face-processing and hemifield in the MEG and EEG data of Experiment 8 showed no sign of repetition effects in the present MEG or EEG data.

The magnetometer repetition effect from 300-500ms in the central probes conditions was consistent with the behavioural priming effects, in that it occurred only for LVF primes. Unfortunately, the poor localizing power of magnetometers (see Section 5.1) coupled with lack of a hemispheric difference in the SOI analysis of effect magnitude, made it difficult to conclude whether this LVF priming effect was arising in the LH or RH (the topography in fact suggests a mainly midline central source, with a possible additional left occipo-temporal source, but formal source analysis is beyond the scope of the present thesis). The magnetometer repetition effect from 300-500 ms in the lateralised probes conditions, however, was the opposite of the behavioural priming effects, in that it occurred only for LVF probes, rather than for the RVF probes that showed concurrent RT priming. The reason for this is unclear. The magnetometer repetition effect is either a type I error, or reflects neural repetition effects that have nothing to do with those that cause the behavioural priming. Indeed, given its relatively late latency, it is unlikely to reflect the structural encoding of faces that is assumed to underlie the behavioural priming effects according to the RH-SPA hypothesis. The N400 component has been related more to processing of semantic context (see Section 6.2.6.2), which might reflect to post-structural-encoding processing of the pleasantness of the prime faces, or sex of the probe faces.

The lack of repetition effects on the earlier M/N170 and M/N250r components makes the priming effects difficult to relate to the hemispheric asymmetries observed in Experiments 7 and 8. Nonetheless, the lack of such effects is consistent with the majority of the prior literature, in which modulations of the N/M170 are rarely seen for non-immediate repetition (Section 6.2.6.2; cf. the present lags of 2-20 intervening items). It is possible that the RH face-processing advantage observed in OFA and around the N/M170 latency in Experiments 7-8 is a necessary precursor to effects of hemifield on priming, which actually emerge later in time (though perhaps still in “early” visual regions like OFA), owing to re-entrant interactions within or across hemispheres (Henson et al, 2003).

6.5 Conclusions

In conclusion, the behavioural priming data from lateralised probes continued to support the RH-SPA hypothesis, while those from the central probes, if replicated, would suggest additional amendment to this hypothesis may be necessary (as considered in the next chapter). However there were, unfortunately, no clear repetition effects in the MEG or EEG data: no evidence for repetition effects on the M/N170 component that is the most obvious candidate for structural encoding of faces, and only weak evidence for a later effect from 300-500 ms in the magnetometers, but which did not have a clear interpretation, particularly for lateralised probes. The neural correlates of the consistent behavioural effect of hemifield on priming therefore await further studies, perhaps with fMRI and/or with more powerful designs. This issue is again revisited in the next, concluding chapter.

Chapter 7: General Discussion

What are the neural correlates of the Right Hemisphere (RH) advantage for face-processing, and how does this advantage modulate repetition priming effects? These were the two main questions addressed by the present thesis, which used a Divided Visual Fields (DVF) methodology in healthy adults in combination with behavioural and neuroimaging measurements. Through nine experiments, several new findings were made regarding the neural correlates of the LVF-RH face–processing advantage, and a consistent pattern was found in relation to the effects of this hemispheric difference on priming. This chapter starts with a summary of the experiments conducted, followed by sections summarising the main findings from our behavioural and neuroimaging data. An effort was also made to model our behavioural data, based on the findings of the neuroimaging data, in terms of face processing efficiency (Section 7.5). Finally, future possible directions are considered.

7.1 Summary of experiments

Experiments 1-4 in Chapter 2 were conducted to test the Dissociable Neural Subsystems (DNS) model of Marsolek and colleagues, which would seem to predict a greater generalisation of priming across views when probe faces were presented to the RVF (LH) than when presented to the LVF (RH). This prediction was made under the assumption that the LH is more efficient in part-based processing than is the RH, and such part-based processing is necessary in order to observe priming across views of the same visual object (see Introduction to Chapter 2). This prediction has received some support from DVF-priming studies that used visual objects, but has not previously been tested with faces. One possible alternative account of these prior findings is that the objects used were typically nameable, and hence the greater generalisation of priming across views for objects presented to the RVF reflects the well-established LH-advantage in processing verbal (i.e., lexical/semantic) information. Indeed, the prior evidence for a RH-advantage in face-processing raised the possibility that, when using non-nameable (unfamiliar) faces, we might even observe the opposite result to these prior studies, i.e., a LVF rather than RVF advantage in priming across views. Unfortunately however, no convincing evidence was found for an interaction between hemifield and same vs. different face image/view on the amount of behavioural priming across the four experiments. Further discussion of this issue of view effects is given in Section 7.3. However, what Experiments 1-4 did find consistently was greater accuracy and/or faster RTs for initial presentation of faces to the LVF than RVF (i.e., in the unprimed condition). This supports the RH advantage in face-processing. Furthermore, in all experiments, there was priming of accuracy and/or RTs (following central primes) when probes were presented to the RVF, but rarely for LVF probes (see ahead to Table 7-1). This unexpected finding of greater priming when a probe face received preferential processing by the LH (RVF) rather than RH (LVF) was hypothesized to be caused by differential encoding efficiencies by the two hemispheres: RH encoding efficiency is optimal, hence no facilitation occurs after a single repetition; LH encoding efficiency is less than optimal, hence a single repetition induces facilitation. We termed this the “RH Structural Processing Advantage” (RH-SPA) hypothesis.

This hypothesis was directly tested in Chapter 3, where the hemifield of the prime and probe were factorially manipulated. As predicted, Experiments 5 and 6 only found priming when primes were presented to the LVF and probes to the RVF (the LVF-RVF condition). The lack of priming in the other three conditions was explained by processing efficiency already being maximal in the RH (when probes are presented to LVF, i.e., LVF-LVF and RVF-LVF conditions), or when there is no gain from prior LH processing (when primes are presented to RVF, i.e., RVF-RVF and RVF-LVF conditions). A more detailed explanation of this hypothesis, including the case of CVF primes and probes, is given in Section 7.5.

Experiment 7 in Chapter 4 was an event-related fMRI experiment designed to investigate directly the brain localisation of the RH face-processing advantage. Surprisingly, this question does not appear to have been addressed using DVF presentations (only by comparing LH and RH face-related activation to CVF presentations; see Dien et al, 2009). To identify face-related activity, an additional set of house stimuli were used (from Henson & Mouchlianitis, 2007). This experiment revealed an interaction between faces vs. houses and LVF vs. RVF in the right occipital face area (OFA). A similar interaction was not found in the left OFA, or either left or right fusiform face area (FFA), despite a reliable main effect of hemifield or of face vs. houses in these regions respectively. This direct evidence for a RH specialisation for face-processing that is reasonably “early” in the visual ventral stream (i.e., OFA but not FFA) is discussed further in Section 7.2. This experiment also included repetitions within and across hemifields (though with continuous lags of 2 to 16 stimuli, rather than the mini-blocks of Experiments 5-6), but no repetition effects were found either behaviourally, or in the fMRI data. Various reasons for this lack of priming effects, such as the relatively shallow processing of faces required by the face-house classification task (relative to the pleasant-unpleasant or male-female classifications used in Experiments 3-6), were discussed in Chapter 4.

Experiment 8 in Chapter 5 was an M/EEG replication of Experiment 7, in an attempt to localise the RH face-processing advantage in time (i.e., relative to the earliest face-related processing). While any repetition effects again failed to be detected, there was further support for a RH face-processing advantage in that the differential evoked response for faces relative to houses showed a greater effect of hemifield over RH gradiometers than over LH gradiometers. The pattern of this hemifield-by-stimulus-category interaction resembled that across the ROFA and LOFA in Experiment 7, but the MEG data went further in showing that this difference emerged relatively early in time, coincident with the first, classical face-specific effect peaking around 170 ms.

Finally, Experiment 9 in Chapter 6 was a second M/EEG experiment that more closely followed the design of Experiments 5 and 6 (i.e., with the same task and stimuli), with the only difference being the use of central primes / lateralised probes and lateralised primes / central probes (rather than the lateralised prime / lateralised probe conditions in Experiments 5 and 6). Central presentations were used to maximise sensitivity to face-related activity, given prior EEG evidence (Jeffreys, 1996) that the N170 face-related response is reduced for lateralised presentations (even though a N170 was found to lateralised faces vs. houses in Experiment 8, one of the concerns regarding the lack of repetition effects in Chapter 5 was that the N/M170s were too small for reliable modulations by repetition to be observed). The RH-SPA hypothesis predicted priming in the LVF-RVF condition (and possibly the CVF-RVF condition), but not the LVF-CVF or RVF-CVF conditions (since CVF presentations are assumed to be processed in both LH and RH). The prediction of CVF-RVF priming was confirmed behaviourally, but priming was also found for the LVF-CVF condition, which was not expected (interpretation of which is discussed further in Section 7.5). Interestingly, for both the central primes / lateralised probes and lateralised primes/central probes conditions, there was a electrophysiological repetition effect in both the LVF-CVF and CVF-LVF conditions from 300-500 ms, though only in the magnetometer data. This was not expected under our working hypotheses (see Chapter 6 for further discussion). However, the localisation (specifically, the lateralisation) of this MEG effect is difficult to determine on the basis of magnetometer data (which have less localising power then gradiometer data), so the effect could not be easily related to the basic RH face-processing advantage found for ROFA in Experiment 7. Indeed, the lack of any detectable repetition effects for the MEG or EEG data within the sensors and timewindows (M/N170) that showed lateralisation of face-processing in Experiment 8 suggests that the magnetometer repetition effect in Experiment 9 (if real) reflects later, post-perceptual processes, which may not even relate to the behavioural priming, since no behavioural priming was found for the CVF-LVF conditions. Thus the neural correlates of the behavioural priming results remain, unfortunately, unclear.

7.2 LVF-RH advantage in structural encoding of faces

The most consistent and important finding of the present thesis was a RH (LVF) advantage in processing (non-famous) faces. In all experiments, LVF presentations of unprimed faces showed either statistically or numerically faster RTs and increased accuracy than RVF presentations. Most importantly though, the fMRI data in Chapter 4 and gradiometer RMS data in Chapter 5 provided, for the first time, more direct, neural evidence for the hemispheric location (i.e., lateralisation) of this LVF advantage. More specifically, in Chapter 4, a significant hemifield-by-stimulus category interaction was found for the ROFA, but not for the LOFA (cf. Figure 4-3E and F): for the ROFA, contralateral (LVF) presentations showed greater activation for faces relative to houses than did ipsilateral (RVF) presentations; whereas for the LOFA, contralateral (RVF) presentations did not show greater face-related activation than did ipsilateral (LVF) presentations. This suggests that the LVF face-processing advantage occurs relatively early in the ventral visual face-processing stream in the brain. The same pattern of interactions between hemifield and stimulus category was found in Chapter 5 for the RMS of the data from posterior occipitotemporal gradiometers within a timewindow around the M170 component: the RH sensor showed greater activation for faces relative to houses for contralateral (LVF) than ipsilateral (RVF) presentations, but the LH sensor did not - cf. Figure 5-5A2 and B2. Alhough no formal source localization was performed, the location of these sensors means that they are likely to be detecting electrical activity from the OFA. The fact that this lateralization occurs as early as the M/N170 component, which is believed to reflect the earliest onset of face-specific processing (Bentin et al., 1996; see also lack of face-house differences on earlier P/M100 component in Chapter 5), further supports the claim that the LVF face-processing advantage arises at an early stage of face-processing, such as the structural encoding stage of the Bruce and Young (1986) model. Indeed, later stages in the ventral face-processing pathway (such as the fusiform face area (FFA); see Chapter 4 for further discussion) did not show similar evidence of a LVF face-processing advantage.

Note that while a RH face-processing advantage is generally accepted in the literature, no previous neuroimaging study has been able to provide such compelling convergent evidence. While many fMRI studies have reported greater (or more extensive) face-related activation in RH than LH regions (such as FFA), these have used CVF presentations, so do not necessarily imply preferentially visual processing by either hemisphere. Moreover, few of these studies have performed the direct statistical comparisons across hemispheres that were performed here (though see Dien, 2009, for a recent meta-analysis). Experiment 7 is the first fMRI study, to our knowledge, to use the DVF methodology to investigate this issue, and to perform direct comparisons across hemispheres. Our MEG data in Experiment 8 expand the limited ERP/EEG literature (see section 1.2.4) on the LVF face processing advantage, especially with the inclusion of appropriate control stimuli. Furthermore, the relatively low spatial resolution of EEG (as discussed in Chapter 5) makes it less likely to observe significant interactions across LH and RH electrodes. Experiment 8 is the first study, to our knowledge, to combine MEG with the DVF methodology, and more specifically, to be able to use the focal sensitivity of the planar gradient of the magnetic field in order to get more precise localisation and hence more sensitive tests across LH and RH sensors.

Our neuroimaging data for a RH advantage are consistent with prior neuropsychological studies following LH or RH lesions, as described in Chapter 1. More generally, they extend the Haxby et al. (2000) model (as described in Chapter 1). This model posits that the OFA is responsible for early perception of facial features (such as structural encoding), consistent with the present claims, but does not hypothesize any hemispheric differences. Our results also provide direct support for the model proposed by Rhodes (1985; cf. Figure 1-2), which posits that early visuospatial processes (such as those believed to be indexed by the M/N170 component) are right-lateralised.

One limitation of our data is that, although they do provide direct evidence for a RH basis for the LVF face-processing advantage, they do not provide further insights on the precise nature of this advantage. Our operationalisation of face-processing was to compare faces and houses, as is fairly standard in the neuroimaging field. However, faces and houses differ in other ways (such as their spatial frequency content), which may contribute to the neuroimaging results. Indeed, it may even be that the ROFA and N/M170 hemifield effects reflect an advantage of the RH in processing low spatial frequencies. Other alternative explanations are that the RH has an advantage in holistic processing (given that faces are generally accepted to be processed holistically; e.g., Rossion et al., 2000), or even general visuospatial processing. Teasing apart these explanations of the present data will require future experiments (see Section 7.6).

Finally, the precise pattern of face-related activity in Experiments 7 and 8 deserves further consideration. In both the OFA fMRI data and Gradiometer RMS data, the reliable three-way interactions between hemisphere, hemifield and stimulus category suggested only greater differential face-house sensitivity of the RH to hemifield than of the LH: in neither type of data (i.e., fMRI and M/EEG) was there reliable evidence for a greater face-related response in the RH to LVF stimuli than in the LH to RVF stimuli. Nonetheless, there was a numerical difference in this direction for both types of data, consistent with a RH face-processing advantage.[4] This is important for the modelling in Section 7.5.

7.3 Viewpoint effects in face processing

Although viewpoint was not manipulated from Experiment 5 onwards (i.e., not manipulated in the neuroimaging experiments reviewed above), it is worth summarizing the effect of this manipulation on priming that was explored in Experiments 1-4. These experiments were designed for the initial aim of this thesis, which related to the DNS theory of hemispheric asymmetries in visual object processing (see Chapter 2). In general, the lack of reproducible interactions between hemifield, view and priming meant that this initial aim was dropped in favour of more modest tests of interactions between hemifield and priming. The RT data in Experiment 1 did show a pattern consistent with

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[4] There was also a difference in the precise pattern of responses in the LOFA relative to the LH gradiometer data: though both showed the critical interaction between hemifield and stimulus-type, the LOFA showed a main effect of hemifield, but no main effect of stimulus-type, whereas the LH gradiometer showed main effects of both hemifield and stimulus type (cf. Figures 4-3 and 5-5). The reason for this difference – specifically, the lack of a main effect of stimulus-type in the LOFA – is unknown, but may relate to a non-optimal selection of the LOFA (which had to be simply by reversing the x coordinate, since there were no nearby voxels above threshold), or effects in the fMRI data that arise after the MEG time-window, which might have reduced an initial face-house difference.

the DNS theory for famous faces (and there was a borderline effect when collapsing across familiarity in Experiment 2), but this could not be replicated, particularly for non-famous faces, which were deemed important to provide a stronger test of the DNS theory (since famous faces can be named and have associated semantic information, which may cause a LH advantage in extrapolating across views, consistent with DNS theory, but also explicable in terms of a general LH advantage in lexical/semantic processing; see Chapter 2 for further discussion).

It should however be noted that the present Experiments 1-4 may not have been the most sensitive way to test DNS theory. Firstly, priming can be a weak effect, as can effects of hemifield, so to look for modulations of priming and hemifield by a further, third factor (view) is likely to require high statistical power. Indeed, Marsolek's experiments (which also generally use priming to test DNS) typically have over 50 participants (also making them more expensive to port to neuroimaging, which was a consideration for the present thesis). Furthermore, Marsolek's modulations of priming seem to be specific to methodological specifications, such as requiring long-lag, CVF-DVF prime-probe designs, and even male participants (Marsolek & Burgund, 2008 and Marsolek, personal communication). A second problem with using priming is the problem of different levels of baseline (unprimed) performance for LVF vs. RVF stimuli, as discussed and addressed in Chapters 2 and 3. Thus other methods (e.g., adaption, perceptual matching) may be more sensitive tests of DNS.

A second important point is that the core assumption of DNS theory is that the RH has an advantage in holistic processing, while the LH has an advantage in parts-based processing, yet such distinctions may not be as relevant to faces as to other visual objects. For example, Biederman and colleagues have even developed computational models in which faces are processed in a quite different manner from other objects (Biederman & Kaloscai, 1997). More specifically, they believed that the evidence suggests that faces are not deconstructed into "geons" of the type that support view-invariance of visual object recognition. Thus if faces are processed in a unique pathway, independent of other visual stimuli, then faces may not be an appropriate way to test DNS. Having said this, there are related theories about hemispheric differences in face processing, for example claims that the LH encodes and processes individual features (though not as geons), while the RH processes faces holistically (e.g., Goffaux & Rossion, 2006; Rossion et al., 2000). Future (more powerful) tests using view manipulations of faces and the DVF methodology may reveal evidence that can address these theories.

Finally, maybe it is difficult in general to assess viewpoint effects with 2-D, static images of faces. In everyday life, faces are dynamic stimuli, subject to constant changes in view, lighting and expressions. This is unlike other (inanimate) visual objects, that more often tend to be static, hence seen from fixed views. It is possible that differential effects of hemifield might be found when generalising face recognition across changes in dynamic face stimuli.

7.4 Repetition effects for faces and hemifield modulation

The most novel finding of the present thesis was the evidence that the LVF-RH structural encoding advantage modulates priming. Previous studies (i.e., Bourne & Hole, 2006; Bourne et al., 2009) have shown larger priming effects when face primes were presented in the LVF. However, the majority of findings in the present thesis were consistent with a pattern that priming is only found for RVF probes that were primed by LVF (Experiments 5-6) or CVF (Experiments 1-4) primes. Table 7-1 summarizes all these results. One reason for this discrepancy with the studies of Bourne and colleagues could be their use of famous faces (as discussed in Chapter 3). However, even for famous faces, Experiments 1-2 of the present thesis still showed a trend towards greater priming with RVF probes.

One concern was that this pattern of greater priming for RVF probes was an artifact of baseline differences, in that the faster/more accurate processing of LVF probes (consistent with the general RH face-processing advantage considered in Section 7.2 above) might have meant that there is “less room” for behavioural effects of priming to be observed – i.e., that priming might have been equivalent (or even greater) for LVF than RVF probes, but this was masked by measurement limitations (a “range effect”) owing to the baseline differences between LVF and RVF probes. However, this artifactual account was rejected across Experiments 3-6. Firstly, there was no obvious correlation across participants in their amount of priming and the baseline performance. Secondly, hemifield effects remained when priming was expressed as a proportion of baseline performance (rather than an additive effect). But most decisively, the greater priming for RVF than LVF probes remained when baseline performance was manipulated by using different stimulus presentation durations: remaining significant when baseline performance for RVF probes was matched to that of LVF probes (using 120ms vs. 80ms durations respectively) in Experiment 6, and remaining numerically even when baseline

Prime	LVF			CVF			RVF			
Probe	LVF	CVF	RVF	LVF	CVF	RVF	LVF	CVF	RVF	
Experiment										
1				3 28		0 5.5				Familiarity judgement; lag 3 minutes between study and test; prime 3s, probe 80 ms
2				5.5 21		5.5 84				Familiarity judgement; lag 3 s between study and test; prime 3s, probe 80 ms
3				1 3		3 20.5				Sex judgement; 2-12 faces lag, prime 3s; probe 80 ms
4				3 5		2 16				Sex judgement; 2-12 faces lag, prime 3s; probe 80 or 120 ms within groups
5	2* 16*		1* 54				1* 0		1 11	Sex judgement; 2-12 faces lag, prime 80 or 120 ms; probe 80 or 120 ms, between groups
6	2* 15		3.5* 31				4 1		2* 13	Sex judgement; 2-12 faces lag, prime 80 or 120 ms; probe 80 or 120 ms, within groups
9		0 26		3* 19		3 18		1* 5*		Sex judgement; 2-12 faces lag, prime 120 ms; probe120 ms;

Prime	LVF			CVF			RVF			
Probe	LVF	CVF	RVF	LVF	CVF	RVF	LVF	CVF	RVF	
Experiment										
1				5 35		13.5 61.5				Familiarity judgement; lag 3 minutes s between study and test; prime 3s, probe 80 ms
2				18 21		13 84.5				Familiarity judgement; lag 3 s between study and test; prime 3s,

Table 7-1: Repetition effects of Accuracy and RTs across Experiments 1-6 and 9, as a function of prime and probe hemifield. Blue values reflect significant accuracy effects, red values RT effects Top table presents effects of non-famous faces, and bottom table effects of famous faces. Asterices reflect (numerical) priming in opposite direction. Rightmost column summarises main procedural differences across experiments.

performance was actually made better for RVF probes than LVF probes in Experiment 5.

Thus while the greater priming for RVF than LVF probes does not appear to be an artifact of measurement problems (not a range effect), it may reflect a true “saturation” of face processing efficiency in the RH. This was the initial hypothesis developed in Chapter 2 to explain the general lack of priming from CVF primes to LVF probes across Experiments 1-4 (in conjunction with consistent priming for RVF probes): if the RH is already optimal in structural encoding of faces, then it will not show any effects of a prior prime (in either hemifield) – the RH-SPA hypothesis. This hypothesis was then extended in Chapter 3, to explain an additional observation that priming was not observed for RVF probes that were preceded by LVF primes. A second assumption was added to the working hypothesis, namely that the LH cannot process faces efficiently enough for that processing to have any effect on a subsequent probe (even if that probe is presented in RVF, i.e., preferentially processed by the same LH). This extended hypothesis can therefore explain the general pattern shown in Table 7-1 (mainly for non-famous faces): priming is predicted only from LVF or CVF primes (since these can be encoded sufficiently by the RH to potentially cause subsequent priming) to RVF probes (since only the LH can benefit from previous processing in the RH). [5]

While this working hypothesis explains the behavioural data, the precise neural mechanisms that underlie it remain unclear. Foremost, it is unclear whether the priming from LVF/CVF primes to RVF probes arises within the LH (e.g., if some trace of the prime processing were transferred from the RH to LH during, or after, the prime) or within the RH (e.g., if the RH “takes control” of behaviour in this condition). As discussed above, the unfortunate lack of reliable repetition effects in Experiments 7-9 meant that there is no guidance from neuroimaging data on this question. In the next section, we therefore constructed some toy, formal models that try to relate the verbal RH-SPA hypothesis to the basic pattern of neuroimaging data observed for LVF and RVF faces in the LH and RH (to unprimed stimuli).

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[5] As noted in Chapter 6, the hypothesis cannot explain the priming that was found for LVF primes and CVF probes, but this result deserves replication (i.e., in the same way that the conditions in Table 7-1 were replicated).

7.5 Formal models of hemispheric asymmetries in face priming

To make the RH-SPA hypothesis more explicit, and to integrate the behavioural priming findings with the basic neuroimaging findings of hemispheric differences in face processing in Chapters 4-5, a number of toy models were constructed. These models consist of (i) a number representing the "processing efficiency" (where a larger number means more efficient processing) of each hemisphere for LVF, CVF and RVF stimulus presentations (together with a possible upper-limit on this efficiency); (ii) a "behavioural rule" that maps processing efficiency in the two hemispheres to a single behavioural outcome (e.g., RT), and (iii) a "priming rule" that determines how much facilitation of each hemisphere's processing efficiency (for a probe) occurs owing to residual, prior processing (of a prime) in each hemisphere. Before applying these models to the behavioural priming however, the first step of determining the basic processing efficiency of each hemisphere for LVF, CVF and RVF stimulus presentations was constrained by the qualitative pattern of neuroimaging results in Chapters 4-5.

7.5.1 Basic processing efficiency in each hemisphere for each hemifield

The main finding in the OFA fMRI data of Chapter 4, and the right posterior planar gradiometer data around 170ms of Chapter 5, was a three-way interaction between faces vs. houses, left vs. right hemifield, and left vs. right hemisphere. The general, qualitative pattern that seemed to emerge across these two types of data (even if not statistically significant in all cases; see Section 7.2), was that both hemispheres showed more activity for faces than houses, and more activity for contralateral than ipsilateral stimuli, but only the RH showed greater face-related activity for contralateral than ipsilateral stimuli. To model this pattern, three contributions to processing efficiency were modeled:

(i) Greater efficiency for faces than houses in both hemispheres (i.e., the regions within each hemisphere that are considered in the models below are assumed to preferentially process faces).

(ii) Greater efficiency for contralateral than ipsilateral presentations, i.e., basic hemifield effects.

(iii) Greater efficiency for face processing in the RH when faces are presented to the LVF (or CVF). Although the face-house difference for contralateral stimuli was not significantly different for LH versus RH in either the OFA or GRMS data, both showed a numerically greater response to faces (relative to houses) in the RH for LVF presentations than in the LH for RVF presentations (which is also consistent with several prior fMRI studies that used central presentations).

(iv) Finally, for CVF presentations, the processing efficiency of each hemisphere is assumed to be the sum of those for LVF and RVF presentations (consistent with the basic advantage of foveal processing).

These four assumptions produce a pattern like that in Figure 7-1. For DVF presentations, this pattern would predict the three-way interaction between LVF/RVF,

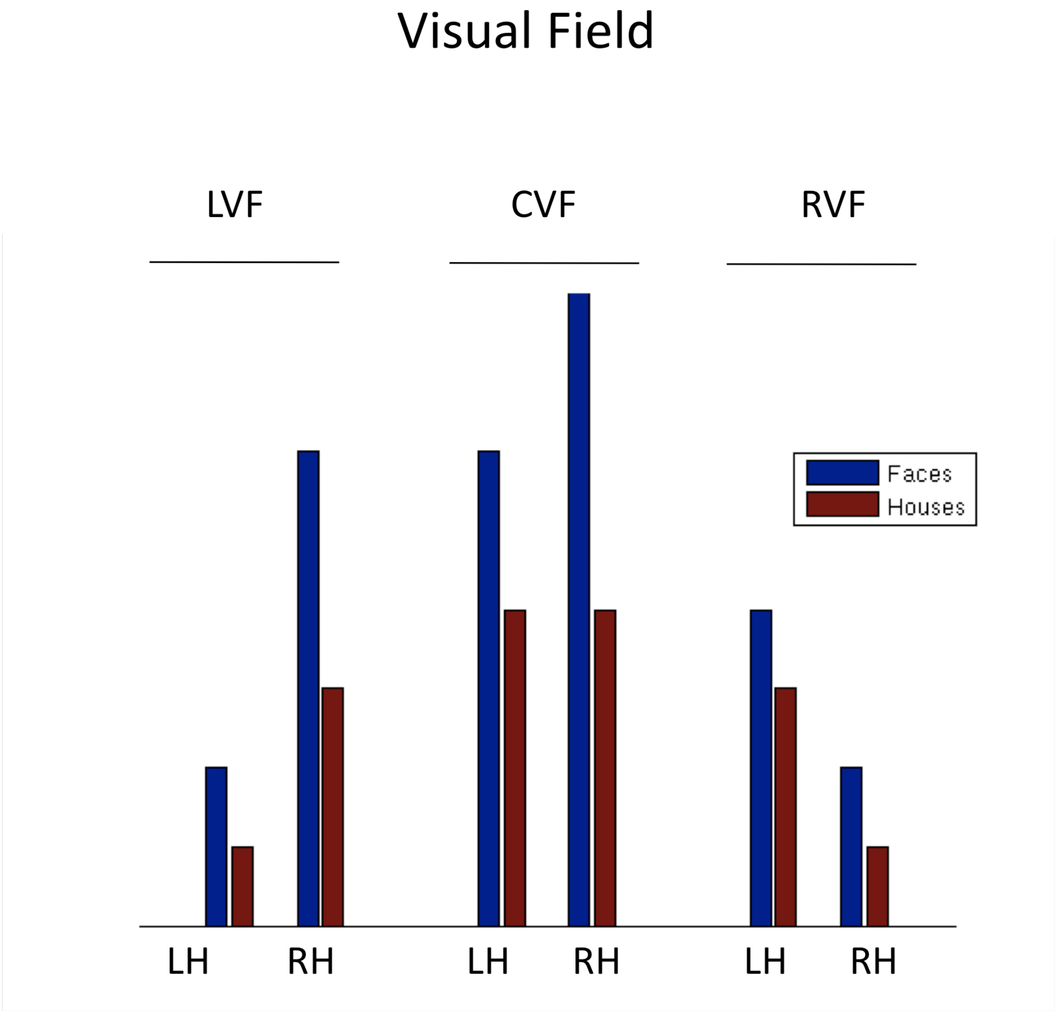

Figure 7-1: Modelled face and house efficiencies as a function of visual field and hemisphere in presumed face-processing regions. In this case, a basic efficiency of 1 was assumed for houses, on top of which was added: a) an additional efficiency of 1 for faces, b) an additional efficiency of 2 for contralateral presentations, and c) an additional efficiency of 2 for RH contralateral presentation of faces. CVF efficiencies were simply the sum of LVF and RVF efficiencies.

LH/RH and face-related activation (faces – houses) as observed in Chapters 4-5. The processing efficiencies for faces in this figure (ignoring houses since these were not used in Experiments 1-6) can then be used in various models that relate these efficiencies to behavioural priming via several further assumptions considered in the following sections. Firstly though, it is necessary to consider the maximal efficiency that can occur in either hemisphere, given that the RH-SPA hypothesis posits that the RH is already optimal in face-processing, in order to explain the lack of priming to LVF probe. Thus one free parameter considered in the models was the maximal efficiency allowed in any hemisphere (i.e., a saturating, upper-bound that constrains any effects of priming).

7.5.2 Relating neural efficiencies to behaviour

The next step is to specify a rule that maps the "neural" processing efficiencies in Figure 7-1 to behavioural measures like accuracy or RTs. Various such rules can be imagined, such as (i) the sum of the LH and RH efficiencies – a type of "hemispheric cooperation" rule – (ii) the maximum of LH and RH efficiencies – a type of "hemispheric race" rule – or (iii) the normalised difference between LH and RH efficiencies (i.e., (LH-RH)/(LH+RH)) – a type of "hemispheric competition/inhibition" rule. Note that relating efficiencies to RTs (rather than accuracy) would of course require an additional inversion of the outcome of this rule, i.e., to explain why higher efficiency leads to lower RTs. A similar inversion could be used if these neural efficiencies were to be mapped directly to fMRI signal, e.g., to explain repetition suppression.

In the simulations presented in the following sections, it was generally the case that the "cooperation" rule did not fit the priming data very well, while "competition/inhibition" rule led to very complex model behaviour that was difficult to predict. Thus we focus on the "race" rule in the models that follow.

7.5.3 The effect of prior processing (priming)

The final step is to add a rule for priming of efficiencies. This rule needs to incorporate both (i) the amount and (ii) the direction of transfer from prior processing in the LH and RH to current processing in LH and RH. The amount seems most naturally expressed as the proportion of processing efficiency of the prime. The direction of hemispheric transfer can then be expressed as a matrix, $\mathbf{P}$, with columns coding "from LH/RH" and rows coding "to LH/RH" (where values of $\mathbf{P}$ are between 0 and 1). Thus, if efficiencies of prime processing are represented as a two-dimensional column vector, $\mathbf{a}$, with a value for LH then a value for the RH, and likewise for a vector **b** representing probe efficiencies (for an identical stimulus), then:

$$\mathbf{b} = \mathbf{a} + \mathbf{P}\mathbf{a}$$

The precise values in **P** do not matter for the present qualitative fits to the modal pattern in Table 7-1 (other than when 0; see below), so here the elements of **P** were either 0 or 0.5. Several examples of **P** can be considered.

If there were no transfer of processing across hemispheres from prime to probe, such that "priming" only occurred within a hemisphere, then **P** would be equal to:

$$\begin{bmatrix} 0.5 & 0 \\ 0 & 0.5 \end{bmatrix}$$

In this case, if the prime were presented to the LVF, such that **a** = [2 6] (from Figure 7-1), then **b** would be [3 9].

Alternatively, one can imagine asymmetric transfer of processing across hemispheres. For example, if only prime processing in the RH had any effect on subsequent probe processing, and this effect transferred equally from RH to LH, then P would be equal to:

$$\begin{bmatrix} 0 & 0.5 \\ 0 & 0.5 \end{bmatrix}$$

In this case, if a LVF prime with **a** = [2 6] (from Figure 7-1) would produce **b** = [5 9].

7.5.4 Three example models

Given the basic assumptions outlined in Sections 7.5.1-7.5.3, many models were explored to see if they could explain the pattern of behavioural priming summarised in Table 7-1. Unfortunately, no model was found that could reproduce the priming that would be expected in every of the 9 combinations of LVF/CVF/RVF primes crossed with LVF/CVF/RVF probes. Nonetheless, to illustrate how the models worked, below we consider three simple models, that progressively get closer to the desired pattern.

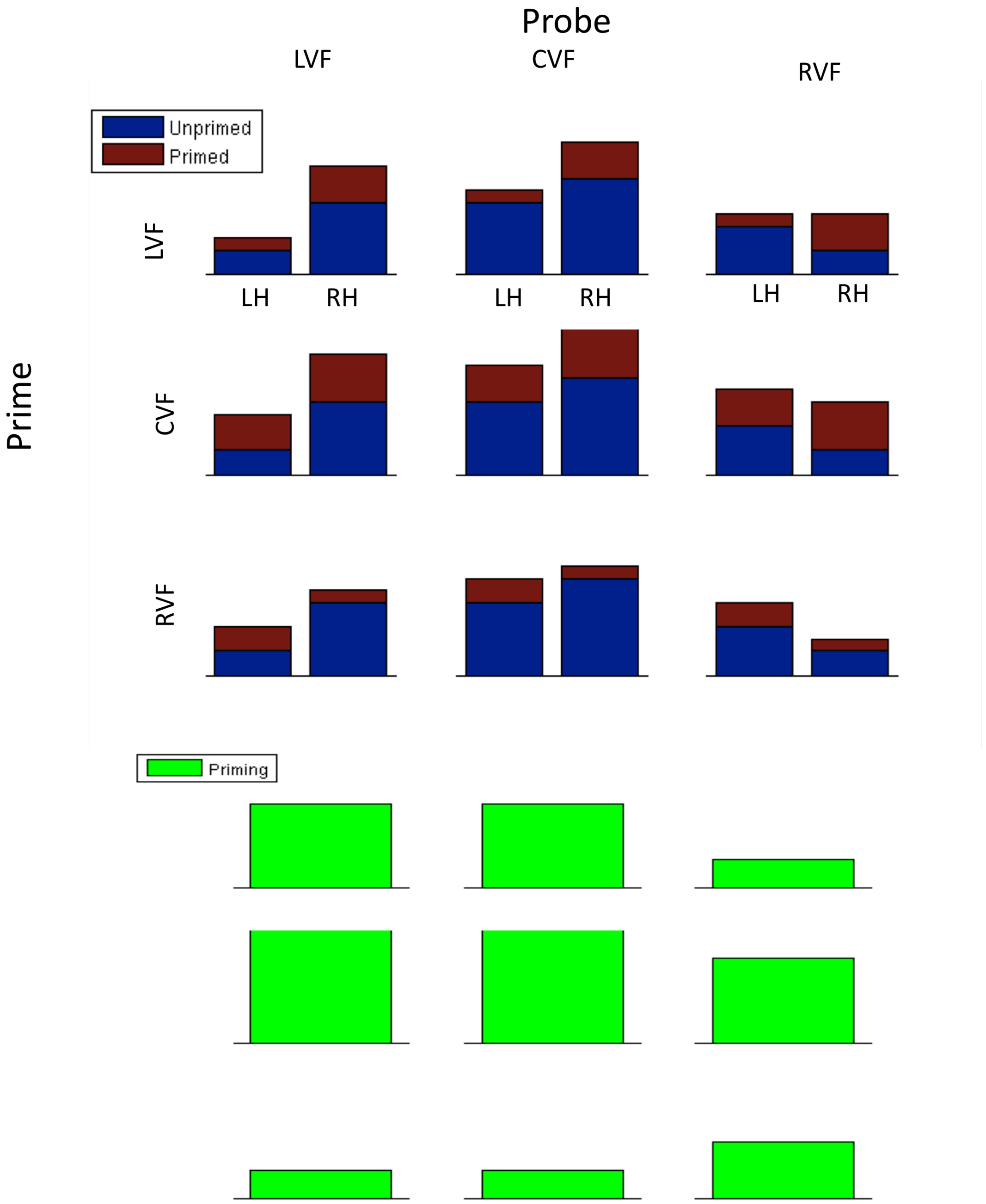

Figure 7-2 Graphic representation of Model 1, as a function of prime and probe hemifield, for the LH and RH. Unprimed efficiencies (equivalent to efficiencies of processing the prime) are in blue, while the boost from priming is indicated in magenta (i.e., efficiencies of probes are the sum of the blue and magenta bars). The resulting behavioural priming that is predicted in each of the 9 conditions that cross prime and probe hemifield are shown in green bars.

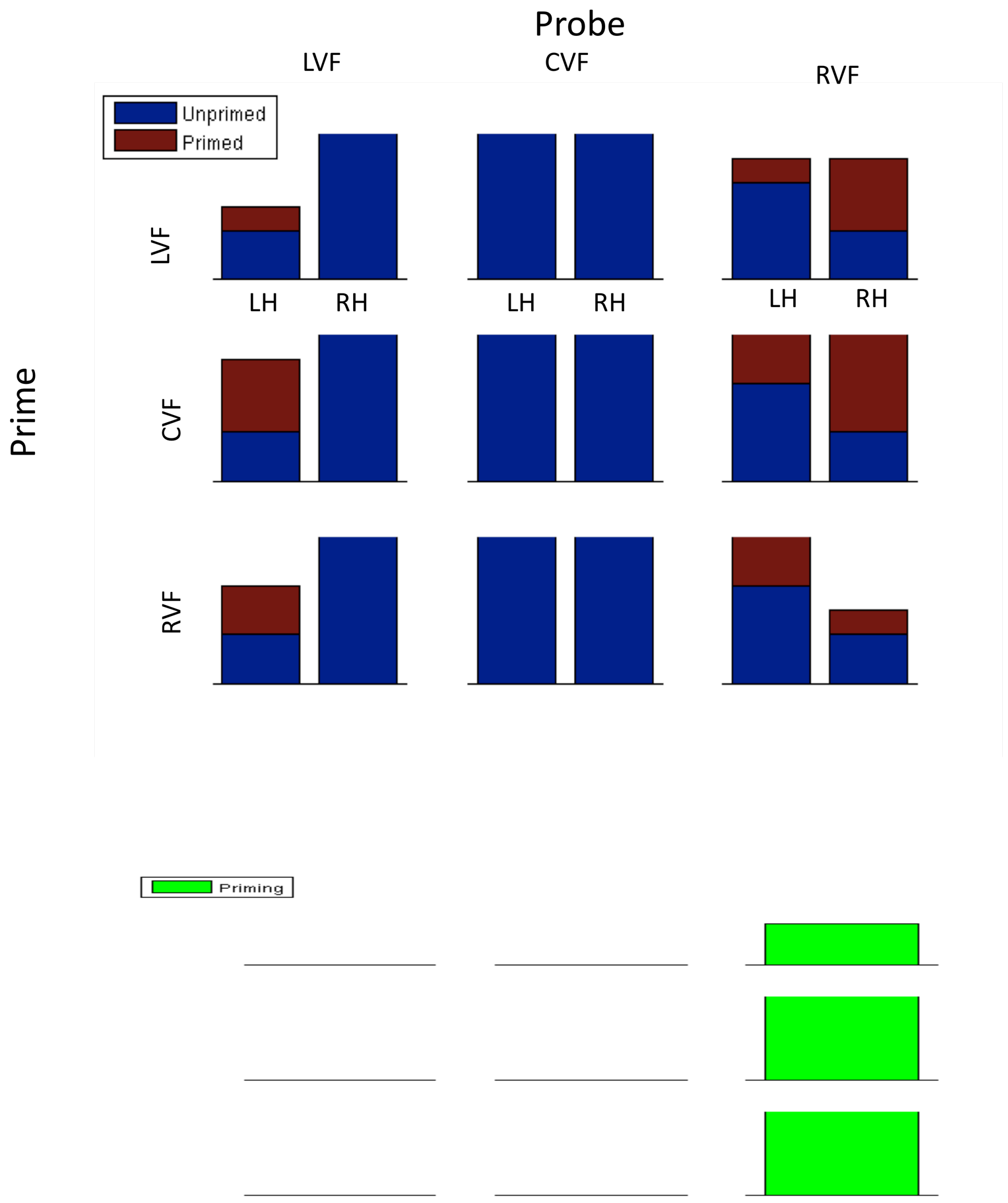

Figure 7-3 Graphic representation of Model 2, as a function of prime and probe hemifield, for the LH and RH. Unprimed efficiencies (equivalent to efficiencies of processing the prime) are in blue, while the boost from priming is indicated in magenta (i.e., efficiencies of probes are the sum of the blue and magenta bars). The resulting behavioural priming that is predicted in each of the 9 conditions that cross prime and probe hemifield are shown in green bars.

7.5.4.1 Model 1: symmetrical, unbounded, hemispheric race

This first model assumed that (i) behaviour was determined by the dominant hemisphere (i.e., by the maximal efficiency across hemispheres), (ii) no saturation of efficiency occurred, and (iii) priming was symmetrical but within-hemisphere only (i.e., **P** = [0.5 0; 0 0.5]). It is not particularly surprising that this simple model, which conveys no hemifield differences other than the basic RH face-processing advantage implicit in Figure 7-1, did not fit the pattern of behavioural priming. As it can be seen in Figure 7-2, this model produced priming in all nine conditions. This happened for two reasons: (i) the model overestimates the contributions of the LH, hence large priming effects are produced for all conditions where primes are presented to the RVF (i.e., RVF-LVF, RVF-CVF and RVF-RVF), and (ii) since RH efficiencies for LVF and CVF are not bounded (i.e., not already optimal), large priming effects were found for all LVF probes. Such priming effects were not found in the behavioural data, hence Model 1 can be rejected.

7.5.4.2 Model 2: symmetrical, bounded, hemispheric race

This model was identical to Model 1, except that an upper bound was placed on the efficiency of face processing in either hemisphere. This bound was equal to the efficiency of LVF faces in the RH in Figure 7-1 (a value of 6 in this example): in other words, as in the RH-SPA hypothesis, it is assumed that the maximal face processing efficiency is that which occurs in the RH to LVF (or CVF) stimuli. As shown in Figure 7-3, this model correctly predicted priming only for RVF probes (i.e., not for LVF probes), which is closer to the pattern in Table 7-1. However, it also predicts priming in the RVF-RVF condition, which was not found in Experiments 5-6. Indeed, Model 2 predicts more priming in the RVF-RVF condition than in the LVF-RVF condition. This is because priming for RVF probes is still largely determined by the efficiency in the LH, an issue addressed in the final model below.

7.5.4.3 Model 3: asymmetrical, bounded, hemispheric race

This model was identical to Model 2, except that the priming rule was now asymmetrical, such that efficiency of prime processing was transferred from the RH to LH, but not vice versa. More precisely, **P** was set to [0 0.5; 0 0.5]. This allowed Model 3 to reproduce the main pattern observed across Experiments 1-6, i.e., priming only for RVF probes after LVF or CVF primes (see Figure 7-4). This happens because the increase in RH efficiency from LVF or CVF primes means that it exceeds the efficiency of the LH for RVF probes, such that the RH now wins the race to control of behaviour. In

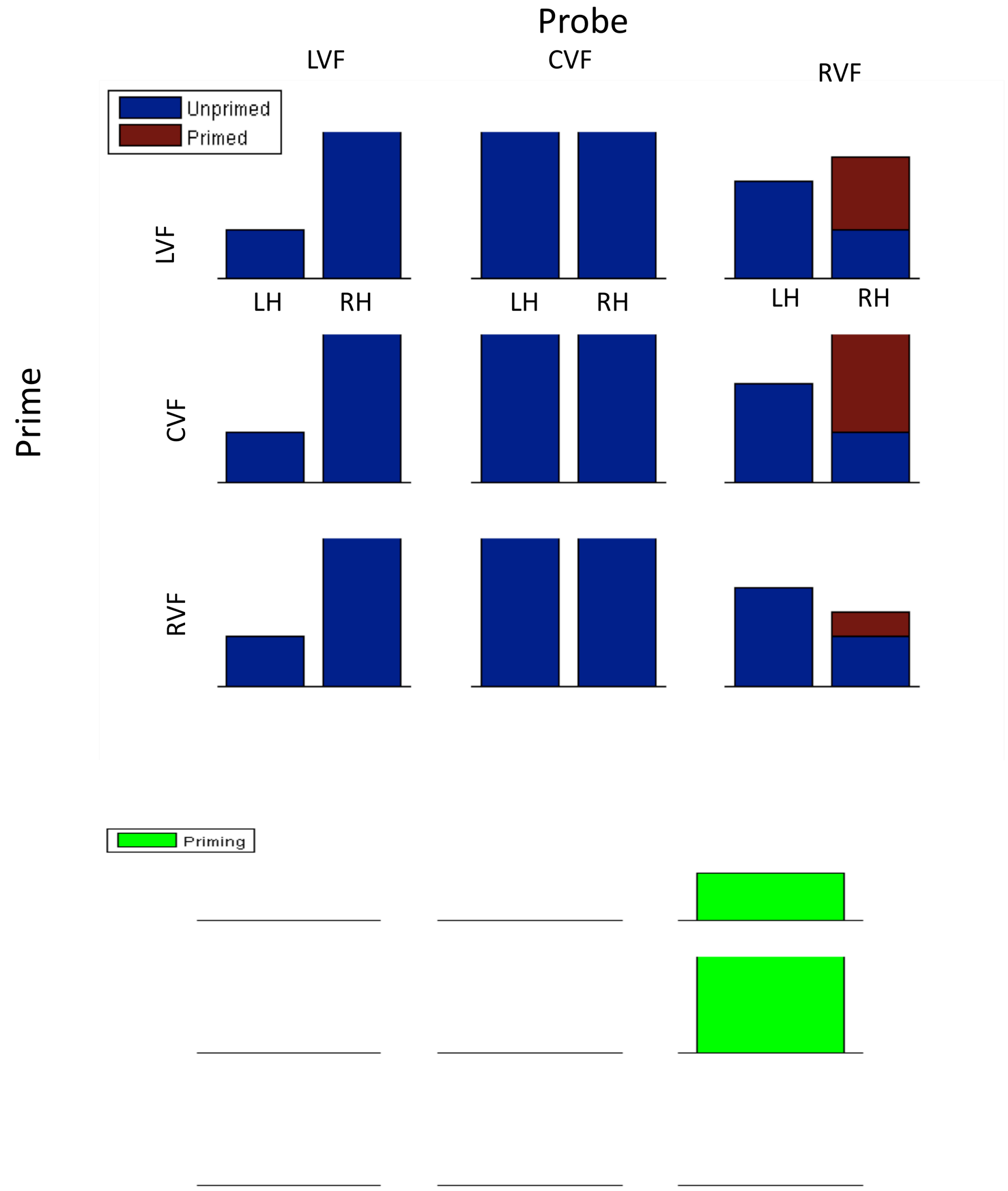

Figure 7-4: Graphic representation of Model 3, as a function of prime and probe hemifield, for the LH and RH. Unprimed efficiencies (equivalent to efficiencies of processing the prime) are in blue, while the boost from priming is indicated in magenta (i.e., efficiencies of probes are the sum of the blue and magenta bars). The resulting behavioural priming that is predicted in each of the 9 conditions that cross prime and probe hemifield are shown in green bars

addition, since the LH does not benefit from RVF primes, no priming was found for the RVF-RVF condition. This model is therefore one instantiation of the RH-SPA hypothesis. Furthermore, it goes beyond that verbal hypothesis in that it interprets the pattern of priming as being driven by the "RH taking-over behaviour", rather than the idea of the simple encoding efficiency differences that was proposed in Chapters 2-3. Thus, one advantage of the present attempts to formalise priming is to highlight such important distinctions. In theory, these two explanations could be tested by neuroimaging evidence for the hemisphere that shows strongest effects of repetition (or greatest correlation with behavioural priming), but unfortunately, as discussed earlier, the neuroimaging experiments in the present thesis were unable to provide such evidence. Nevertheless, the RH contribution for RVF does not seem unlikely given that fMRI studies (though with CVF presentations) do seem to show larger RH repetition effects. For example, Rotshtein et al. (2005) found that the right OFA showed sensitivity for perceptual changes of repeated faces; while several ERP studies showed larger repetition effects in the RH occipital-temporal sites for the N250r component when the probe was a different view of the prime face.

More generally, the idea from Model 3 that RVF performance reflects a process occurring within the RH that elicits facilitation would seem consistent with the claims of the "callosal relay" model that the processes that lead to priming occur within the hemisphere that is specialized (dominant) for a specific process regardless of whether the presentation is ipsilateral or contralateral, as also shown for word priming in the VWFA (Cohen et al., 2002). However, in the absence of spatial and temporal information about these repetition effects, our findings could be compatible with the "direct access" model (Geffen et al., 1971; see Section 1.2.2). This suggests that hemispheric differences for a specific process occur due to differential efficiency of each hemisphere. As we don't know when and where these effects occur, patterns of hemispheric differences that reflect the behavioural priming found in Experiments 1-6 could be different depending whether they occur early or late in the face-processing stream. Finally, Model 3 could also be consistent with a third proposal, the "cell assembly" model, that faces are represented by assemblies that are distributed across both hemispheres and linked by excitatory/inhibitory neuronal connections. Possible hemispheric differences in efficiency then occur due to differences in interhemispheric transfer (Pulvermuller & Mohr, 1996), as in Model 3. It is evident that the issue of the exact process that modulates hemispheric effects of priming cannot be answered by behavioural and modeling data alone.

Neuroimaging data can provide more definite answers on the lateralisation of this process. As mentioned earlier, we failed to find repetition effects in our neuroimaging data, hence this remains an open question for future studies which will employ more powerful designs in regards to repetition effects (see section 7.6).

One possible failure of Model 3 is that it does not predict the priming from LVF primes to CVF probes that was found in Experiment 9. Nonetheless, as discussed in that Chapter, this result would benefit from being replicated. A more serious failure perhaps is that this model does not predict any priming from CVF primes to CVF probes. This condition was not actually included in the present thesis, but there are a number of experiments that have found such priming (using similar tasks, stimuli and lags, e.g., Goshen-Gottstein & Ganel, 2000; Henson et al., 2004). The main reason for this lack of CVF-CVF priming is the bound (saturation) on efficiencies, coupled with the assumption that CVF efficiencies are the sum of LVF and RVF efficiencies. But even if the bound were increased, or if CVF efficiencies were equal to the maximum (rather than sum) of LVF and RVF efficiencies (which is more akin to the "race" rule), it does not seem possible to simultaneously explain CVF-CVF priming and a lack of LVF-LVF priming. Thus there seems to be some other mechanism at work that contributes to priming for CVF stimuli (and it should be noted that the previous examples of CVF-CVF priming cited above used stimulus durations more than 150 ms, since eye-movements were not a concern, which may be another important factor).

7.6 Future Directions

The data from the nine experiments presented in the thesis reveal a complex pattern of results. Although there was substantial evidence from LVF presentation of stimuli that supports a RH advantage in the early stages of face processing, there is a number of issues that could not be addressed in the present thesis, but which future studies might. One important issue concerns the most novel finding reported here, the modulation of priming by hemifield of prime and probe, as reported in Chapter 3 (Experiments 5 and 6) – i.e., that priming was only found when a face was encoded by the LVF and repeated in the RVF, consistent with our RH-SPA hypothesis. One question is whether this effect is truly face-specific, or whether it reflects an advantage in a low-level visual processing that the RH might exhibit when a stimulus is presented parafoveally for a short duration. One way to address this would be to repeat Experiments

5 and 6 with houses. If the LVF-to-RVF priming effect is specific to faces, i.e., houses showed priming but no interaction (or a different type of interaction) with hemifield, that would further support the hypothesis that the present results reflect an advantage specifically in the structural encoding of faces, rather than a general visual processing advantage.

A related question concerns the precise processes that cause a RH advantage in face processing (and hence the modulations of priming by hemifield). For example, LVF presentations have been shown to produce superior processing of low spatial frequencies, while RVF presentations have been shown to produce superior processing of high spatial frequencies (e.g., Sergent, 1982b). Given that the early stages of face processing seem to be dominated by low-frequency/holistic processing (e.g., Goffaux & Rossion, 2006; Schiltz & Rossion, 2006), the RH-SPA hypothesis may actually be a consequence of a RH advantage in processing low spatial frequencies plus the strong dependence of early-processing of faces (relative to other stimuli) on low spatial frequencies. Factorial manipulations of spatial frequency (and/or holistic/configural processing) and face versus non-face stimuli could address such questions.

Furthermore, although the LVF-to-RVF effect was reasonably robust across several experiments, these experiments involved very similar procedures, so it would be interesting and important to show the extent to which the finding generalises across other experimental conditions. This may include the presence of a backward mask immediately after lateralized presentations (which arguably further controls preference hemispheric processing – see Chapter 1 – and may also reduce eye-movements), possibly simultaneous bilateral presentation of stimuli, and a larger range of stimulus durations (other than the 80 and 120 ms used here). A particularly important variable might be the lag between repetitions, in that shorter lags (e.g., immediate repetition) are likely to increase the size of repetition effects (Henson et al., 2004). This would appear important for future neuroimaging studies using fMRI or M/EEG, since Experiments 7-9 in the present thesis did not find strong or compelling effects of repetition (despite concurrent behavioural effects). A design with more repetitions at shorter lags may increase the power to detect the neural correlates of the hypothesised RH structural encoding advantage.

Another significant issue that needs to be addressed is how the RH-SPA hypothesis relates to processing of familiar faces. Experiments 3 onwards were restricted to non-famous faces, in order to control for possible hemispheric differences in lexical/semantic processing – i.e., beyond structural encoding. The return to using familiar faces would be important to reconcile the present LVF-to-RVF priming effects with the different patterns (reported earlier) found by Bourne & Hole (2006), Bourne et al. (2009) and Cooper et al. (2007). There are several procedural differences (other than use of famous faces) that need to be removed in order to conduct a fair comparison, such as the use of a familiarity judgement task, the smaller number of stimuli, etc. Thus one future experiment could use the same design as Experiments 5 and 6, in using a pleasantness task at study and sex-judgement task at test, but with famous faces as well as non-famous faces. If different patterns of priming by hemifield emerge, then this may reflect additional hemispheric lateralisation of post-perceptual processes; whereas, if the same LVF-to-RVF pattern is found for famous faces, then other procedural differences between the present experiments and those of Bourne and colleagues would have to be explored.

7.7 Conclusions

The present chapter draws several conclusions on a number of empirical findings reported throughout the thesis. One of the most novel findings was the modulation of priming effects by hemifield, which led to the initial proposal, and subsequent extension of, the RH-SPA hypothesis. This hypothesis contains two main parts: firstly that the RH is already optimal in structural encoding of faces, so probes presented to the LVF do not show priming, and secondly that the LH is not efficient at encoding faces, so primes presented to the RVF do not produce subsequent priming. Support for this RH advantage in face processing came from functional neuroimaging experiments, which for the first time provided clear statistical evidence of differences in processing faces (relative to houses) across hemispheres, specifically in the Occipital Face Area and in early processing (~170 ms post-stimulus-onset), consistent with the structural encoding phase of the Bruce and Young (1986) model. However, attempts to formally relate the behavioural priming results with the neuroimaging results using toy models were not fully successful, in that the exact pattern of priming one would expect (e.g., in CVF-RVF or even CVF-CVF conditions) could not be produced by these models. Nonetheless, the exploration of differences in hemispheric transfer of priming and different neural-to-behavioural mappings was a valuable exercise, which will inform future theorizing about these modulations of priming by hemifield. Finally, a number of future experiments were considered that could usefully extend and test further the RH-SPA hypothesis..

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APPENDIX

Examples of two views of faces used in Experiments 1 and 2

Famous

Nonfamous

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Examples of Faces used in Experiments 3-4 (frontal views only in Experiments 5-6)

Examples of faces and houses in Experiments 7-9