

Hemispheric Specialisation in the Parietal Cortex and its Effect on Memory and Attention

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List of Abbreviations

ANOVA	Analysis of Variance
AOM	Activation-Orientating Model
AToM	Attention to Memory
BA	Brodmann Area
BOLD	Blood Oxygen Level Dependent
CLS	Complementary Learning Systems
DI	Dissimilarity Index
DMN	Default Mode Network
FEF	Frontal Eye Fields
fMRI	Functional Magnetic Resonance Imaging
FPA	Frontoparietal Attention
IFG	Inferior Frontal Gyrus
IPA	Implicit Primed Attention
IPL	Inferior Parietal Lobule
LoVF	Lower Visual Field
LPC	Lateral Parietal Cortex
MDS	Multidimensional Scaling
MLB	Manual Line Bisection
MNI	Montreal Neurological Institute
MTL	Medial Temporal Lobe
PCC	Posterior Cingulate Cortex
ROI	Region of Interest
SEF	Supplementary Eye Fields
SLF	Superior Longitudinal Fasciculus
SPL	Superior Parietal Lobule
TMS	Transcranial Magnetic Stimulation
UpVF	Upper Visual Field

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Abstract

The University of Manchester, Oliver J. Gray, Doctor of Philosophy (PhD)

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Healthy individuals tend to preferentially allocate attention to the left visual field (the pseudoneglect effect). This tendency has been closely linked with hemispheric specialisation of the right frontoparietal attention network (FPA) (including the lateral parietal cortex (LPC)). However, evidence is presented here showing that engaging semantic processing (left hemisphere specialised) during object recognition induces a right visual field bias, a reversal of the pseudoneglect effect. Other factors have also previously been shown to modulate the pseudoneglect effect; e.g. target and observer proximity, and horizontal stimulus length. A forced perspective misperception mechanism that directly links these effects is introduced here for the first time. These findings provide important developments in our understanding of LPC processing in spatial attention allocation. Though LPC engagement has been widely observed in neuroimaging studies of episodic memory retrieval, the functional role it plays in memory has been the subject of intense debate. This debate is first addressed through a detailed systematic review of inferior parietal lobule (IPL) activations observed in previous fMRI studies of episodic memory. More consistent engagement of the right hemisphere IPL was observed during perceptual memory experiences than during semantic/conceptual memory experiences. The left hemisphere IPL demonstrated the opposite effect. The debate is further addressed by an fMRI study investigating the neural bases of retrieval of detailed perceptual experiences without engaging semantic/conceptual memory processing. As predicted, memory-related processing produced right IPL activation, and deactivation in the left IPL. Finally, a previously unrecognised association between the hemispheric lateralisation of IPL processing in perceptual memory retrieval and a memory advantage for items encoded on the left side of space is presented. Critically, this advantage is independent of perceptual pseudoneglect effects. Significant correlations between memory tasks provide a mechanistic link between representational pseudoneglect and the hemispheric specialisation of memory retrieval processing. This body of research is discussed with reference to hemispheric specialisation and the functional organisation of the IPL and the LPC, in attention and memory.

Declaration

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this, or any other university or other institute of learning.

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Chapter 1: Introduction

On December 2nd, 1977, N.V. had a stroke. Neurological examination revealed spatially selective impairments in N.V.'s perception. When presented with a symmetrical pattern of 13 dots, he touched all dots on the right, ipsilesional side of space whilst completely neglecting the left, contralesional side of space. This perceptual difference could not be overcome despite prompting by the examiner. Rudimentary neuroimaging revealed a lesion in the right hemisphere that was approximately 4cm in diameter. This lesion affected grey and white matter space in the postero-temporal and inferior parietal areas.

The patient was also asked to describe the features of two highly familiar locations from memory (the Piazza del Duomo, Milan, and his studio where he had spent much of his life). For each location, the patient was asked to adopt two specific perspectives, e.g. (1) facing the church in the piazza from the other side of the square, and (2) facing the square with his back to the church. In describing these scenes, the patient described considerably more features on the right, ipsilesional side of space than on the left, contralesional side. This occurred irrespective of the perspective taken by the participant. Moreover, the experimenters describe the absent-minded and annoyed tone adopted by the patient when describing the few features recalled from the left side of space.

This case study, adapted from Bisiach & Luzzatti (1978), describes the features of unilateral representational neglect. This condition and case study provide compelling evidence that unilateral hemispatial neglect patients, who display impairments in describing contralesional perceptual space, have impaired non-sensory and non-motor neural mechanisms. In other words, their difficulties cannot be fully explained by impairment of visual, auditory, or action processes. More interestingly for this thesis, the representative deficits observed here showed an example of an interaction between the brain systems controlling memory and those controlling attention, and demonstrated the necessity of their interaction for healthy human behaviour.

Primarily distinct fields of research have developed our understanding of the neural underpinnings of memory and attention. Two, or more, groups of a single species of organism can develop into very different species when isolated from each other (Darwin, 1859). Like the very different features of the Galápagos finches that have evolved as a function of isolation imposed by the ocean, the fields of attention and memory have been seemingly isolated, lacked

interaction, and developed distinct perspectives on the processing of the brain. The fields of memory and attention have both produced techniques that are extremely adept at assessing the neural mechanisms associated with their respective processes. However, the techniques developed by one field have, until now, not been effectively and creatively adapted to reveal the idiosyncratic characteristics and features of the other field.

The following sections will first introduce the fields of memory and attention. Increasing focus will then be dedicated to the lateral parietal cortex (LPC), a brain area that is fervently discussed in both fields. I will present my novel ideas regarding the hemispheric specialisations of the LPC before describing the experimental procedures that were developed and employed to explore these perspectives.

An Introduction to Memory

'Memory' describes our ability to encode, retain, and reconstruct previous experiences (Hebb, 1949; Squire, 2004). Memory can be delineated further to describe processes that are qualitatively and mechanistically distinct. *Declarative* memory refers to the conscious retrieval of experiences. *Procedural* or *non-declarative* memory is another umbrella term referring to the subconscious processing that allows for procedural, perceptual, and non-associative learning as well as classical conditioning. These systems have differing rules of operation and brain areas processing their unique functions. *Fig 1.1* illustrates a simple taxonomy of mammalian long-term memory systems that clearly distinguishes between the declarative and non-declarative aspects of memory (Squire, 2004).

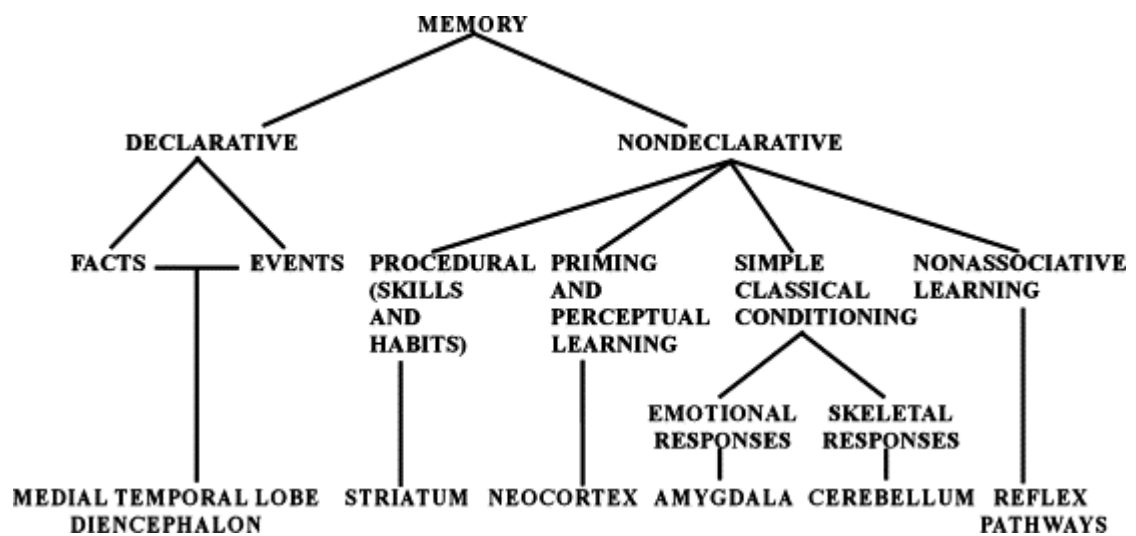


Figure 1.1: The delineation of memory into distinct qualitative and mechanistic processes. Different areas of the brain and nervous system are thought to underpin these different memory subtypes (Squire, 2004).

Episodic Memory

The declarative aspect of memory was further theoretically delineated into semantic and episodic memory by Tulving (1972). A central aspect of this thesis focuses on the episodic aspect of the memory taxonomy. Episodic memory requires the individual to 'mentally time-travel' to re-experience the event in order to recall the information. This has been aptly described as memory for the 'what, where, and when/which' of an event (Eacott & Easton, 2007). Remembering details (location, people, food) of your 21st birthday party, and to some degree

mentally re-experiencing the occasion is an episodic form of memory that has been termed recollection. Familiarity memory is another form of episodic memory. In contrast to recollection, familiarity memory does not involve recall, but instead memory is based on a feeling of re-experience. In contrast to episodic memory, semantic memory supports the accumulated knowledge of facts, ideas and concepts formed by many experiences. Critically, semantic memory is independent of learning from any one specific event. For example, generally knowledge of the capital of Italy is not dependent on memory for a specific occasion when you learned the fact. Some aspects of semantic memory are addressed in this thesis and as a result, the classification of memories as strictly semantic or episodic is questioned.

As highlighted by *Fig 1.1*, declarative memory is processed within the medial temporal lobe (MTL) and the diencephalon. A network of brain areas within the MTL, the diencephalon and the wider cortex have been shown to play crucial and distinct roles in the processing of episodic memory encoding, consolidation, and retrieval. The following section will detail these regions and their well understood contributions to memory.

The MTL

The critical role of the MTL in declarative memory was first identified through observation of “grave loss” of memory for events following bilateral resection of the MTL in patient H.M (Scoville & Milner, 1957). The observation that less extensive MTL damage was associated with less severe amnesic effects indicated that the components of the MTL are collectively involved in the processing of episodic memory. The contribution of each of the constituent elements of the MTL to the episodic retrieval process has remained a highly contentious issue in cognitive neuroscience since these original observations (Jeneson, Kirwan, Hopkins, Wixted, & Squire, 2010; Mayes, Montaldi, & Migo, 2007; Montaldi & Mayes, 2010; Squire, Stark, & Clark, 2004).

The MTL is a collection of cytoarchitecturally distinct but highly interconnected areas of cortex. It consists of the hippocampus and the cortical areas surrounding the hippocampus, collectively known as the parahippocampal gyrus (Van Hoesen, 1995). The hippocampus is a hierarchical arrangement of processing units. These units consist of the dentate gyrus, the subiculum, and the three CA (*cornu Ammon*) subfields (CA1, CA2, CA3) comprising the hippocampus proper. The perirhinal, entorhinal, and parahippocampal cortices comprise the parahippocampal gyrus that surrounds the hippocampus. The perirhinal cortex receives input

from inferior temporal areas (TE and TEO) and V4 (Buffalo, Bellgowan, & Martin, 2006; Squire et al., 2004). This connectivity has been proposed to support the perirhinal cortex's role in coding the identity of different stimuli (Aggleton & Brown, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007). In contrast, the parahippocampal cortex shows connectivity with cingulate and retrosplenial cortex, as well as the posterior parietal cortex (Buffalo et al., 2006). The processing of spatial information in the parahippocampal cortex is thought to reflect this connectivity (Eichenbaum et al., 2007). The entorhinal cortex receives input from the parahippocampal and perirhinal cortex and provides the major input to the hippocampus (Buffalo et al., 2006). The hippocampus integrates this spatial and identity information (Eichenbaum et al., 2007). The connectivity of the MTL is illustrated in Fig 1.2.

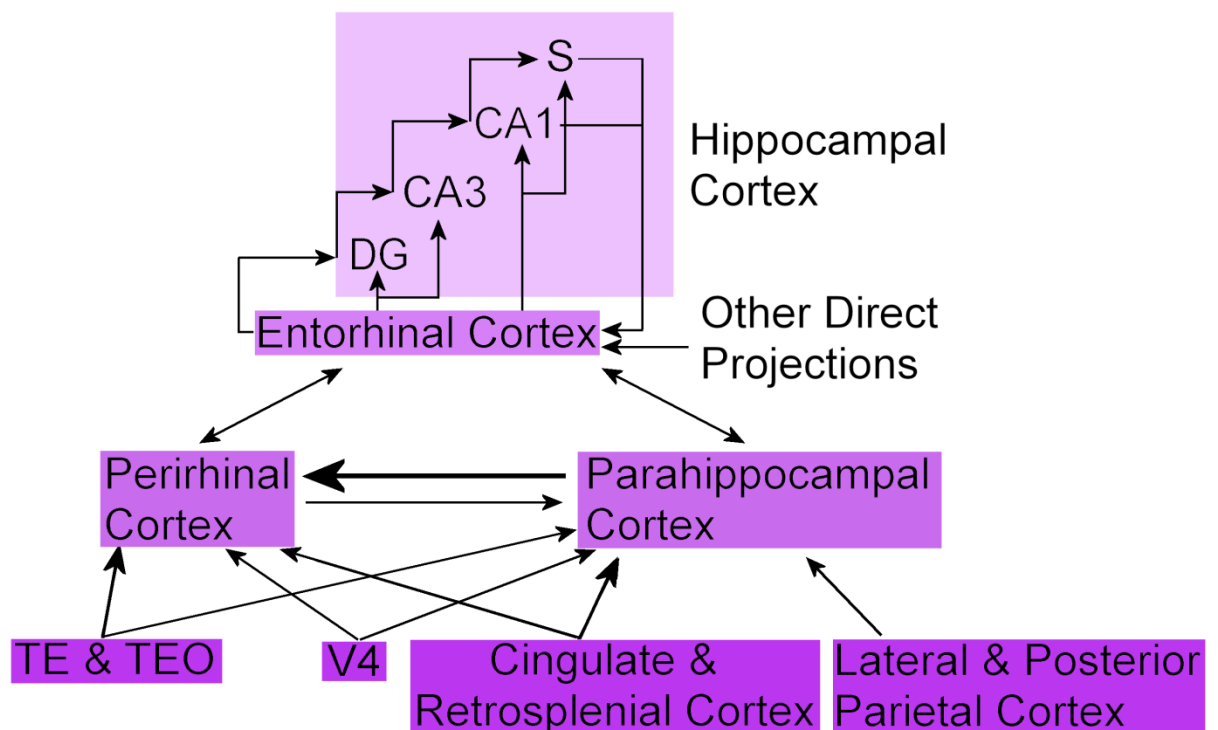


Figure 1.2: An illustration of the anatomical regions of the MTL episodic memory network and its major connectivity. Semantic inputs are not shown but include the lateral temporal cortex, temporal pole and frontal regions (Buffalo et al., 2006; Mayes et al., 2007; Squire et al., 2004).

Identification of the functional roles of the hippocampal formation has been helped through explorations of its role in supporting spatial representations. Hippocampal *place cells* that exhibit spatially-dependent, viewing direction-independent firing patterns (O'Keefe, Burgess, Donnett, Jeffery, & Maguire, 1998), as well as, *grid cells* - representing Euclidean 3D space (entorhinal cortex) (Hafting, Fyhn, Molden, Moser, & Moser, 2005), *head-direction cells* (found in

the anatomical circuit connecting the presubiculum and mammillary bodies via the anterior thalamus), and *boundary vector cells* (subiculum and parahippocampal cortex) (Hartley, Burgess, Lever, Cacucci, & O'Keefe, 2000; Lever, Burton, Jeewajee, O'Keefe, & Burgess, 2009) have been observed in different nodes of the MTL memory network (Byrne, Becker, & Burgess, 2009). Collectively, these cell types have been proposed to enable our memory of space and its contents. The concept of space, how it is processed by particular brain mechanisms, and its modulatory effects on these mechanisms will be discussed throughout this thesis.

The MTL and Recognition Memory

Healthy individuals are very adept at identifying the re-presentation of a stimulus that was previously encountered (Brady, Konkle, Alvarez, & Oliva, 2008). The process that enables this accuracy of recognition has been broken down into qualitatively distinct components (Mandler, 1980). Recollection is characterised by the conscious access to additional information accompanying the previous experience with the stimulus. In contrast, familiarity memory denotes a subjective feeling or knowledge that the stimulus has previously been encountered, but critically without the conscious retrieval of additional information. For example, I may be convinced by my feeling of familiarity that I know a man that I see on a 142 bus to East Didsbury. I am convinced that I know him despite not being able to bring to mind the man's identity or where I have met him previously. After an effortful memory search, I may gain recall that he is the manager at my favourite Mexican food restaurant in Manchester and further recall the conversation we had the previous week about guacamole (adapted from an example by Mandler, 1980). The dual process model of recognition memory proposes that recollection and familiarity are distinct memory functions that are processed by distinguishable brain regions both within and outside the MTL.

The Complementary Learning Systems (CLS) computational model (Norman & O'Reilly, 2003) has demonstrated the necessity for a dual process model to account for recognition memory functions. In this model, a hippocampal system produces non-overlapping representations based on the distinct stimulus characteristics (*pattern separation*). In contrast, a cortical system codes and stores the similarities and overlap between environmental inputs. The output of this cortical system resembles that of the perirhinal cortex. A critical prediction of this dual process model is that the hippocampus is not involved in the processing of familiarity memory.

Though the dual process model of recognition memory has previously been contested (Dede, Squire, & Wixted, 2013; Squire, 2004; but see Kafkas & Montaldi, 2012; and Montaldi & Mayes, 2010), the multitude of investigations revealing evidence of a dual process system (Kafkas & Montaldi, 2012, 2014; Montaldi, Spencer, Roberts, & Mayes, 2006; Skinner & Fernandes, 2007; Yonelinas, Otten, Shaw, & Rugg, 2005) has convinced most researchers of the presence of biologically distinguishable mechanisms supporting recollection and familiarity.

Prefrontal Cortex

At both encoding and retrieval, effective remembering requires active management of sensory information that is both perceived and retrieved. Interactions between prefrontal cortex and hippocampus have been proposed to facilitate this management, and direct the encoding and retrieval of memory representations (Eichenbaum, 2017). The prefrontal cortex has been shown to exert this control in memory retrieval through suppression of unwanted, irrelevant, or interfering memories (Guise & Shapiro, 2017; Shimamura, Jurica, Mangels, Gershberg, & Knight, 1995). Different areas within the prefrontal cortex process distinct aspects of this control mechanism and damage to these regions leads to deficits in multiple aspects of remembering and a wide variety of other cognitive abilities (Szczepanski & Knight, 2014). In addition, direct interactions between the prefrontal cortex and the hippocampus through the fornix support the prefrontal cortex role in mnemonic management (for reviews, see Eichenbaum, 2017; Jin & Maren, 2015; Simons & Spiers, 2003).

Parietal Cortex

The functions of the parietal cortex are diverse and often critical to normal cognition. Posterior to the central sulcus lies a strip of cortex processing somatosensation (Brodmann area (BA) 1, 2, 3 - Brodmann, 1908). Further posterior to this strip is the posterior parietal cortex. This cortex can be grossly divided into lateral and medial regions. The medial portion of the posterior parietal cortex comprises the precuneus (the medial aspect of BA 7). The precuneus, along with adjacent non-parietal, posterior cingulate and retrosplenial cortex (BA 29 and 30) are considered parts of the core recollection network defined by Aggleton & Brown (2006). The precuneus plays a central role in mental imagery and the adoption of an egocentric perspective during recall of an episodic memory (Brodt et al., 2016; Freton et al., 2014). The retrosplenial cortex seems to play a significant role in contextual learning and extinction of conditioned responses (Todd &

Bucci, 2015). The posterior cingulate cortex (PCC) is also engaged during retrieval of autobiographical memories. It also shows activations related to the majority of tasks that demand attention, and is a node of the default mode network (DMN) that demonstrates general task-independent activations. The PCC has therefore been hypothesised to perform a general state tuning of the brain towards particular functions, e.g. episodic memory (Leech & Sharp, 2014). Damage to these medial aspects of the parietal cortex has been linked to impairments of episodic memory (Haramati, Soroker, Dudai, & Levy, 2008; Leech & Sharp, 2014).

The lateral parietal cortex (LPC) has been commonly described anatomically using two nomenclatures based on neuronal cytoarchitectonics. Brodmann's cytoarchitectural map of the brain is the most common of these nomenclatures (Brodmann, 1909). The LPC is divided into dorsal and ventral regions by the intraparietal sulcus (IPS). Dorsal to the IPS is the superior parietal lobule (SPL - BA 5 and 7). The ventral aspect of the LPC is referred to as the inferior parietal lobule (IPL), and consists of the supramarginal gyrus (BA 40), and angular gyrus (BA 39). At the anterior border of the supramarginal gyrus is (listed dorsally to ventrally) the postcentral gyrus (BA 2), and parietal operculum. The SPL is dorsal to the supramarginal gyrus, and the middle temporal gyrus (BA 21) and temporoparietal junction (TPJ) lie ventrally. The angular gyrus lies posterior to the supramarginal gyrus and TPJ, and has common dorsal and ventral neighbours. The posterior boundary of the angular gyrus is made clear by the anterior occipital sulcus. These cortical areas have been more recently confirmed using modern structural magnetic resonance imaging (MRI) segmentation software (Wild, Heckemann, Studholme, & Hammers, 2017).

von Economo & Koskinas, (1925) described the parietal cortex as Parietal (P) A, PB, PC, etc. and designated PE, PF, PG to the LPC. In combination, these three regions roughly cover the LPC as described by Brodmann but assigns alternative borders to its substructures. The use of these von Economo & Koskinas (1925) delineations have recently regained some favour for describing differences between subregions of LPC (Kwok & MacAluso, 2015). However, descriptions based on Brodmann assignments remain overwhelmingly popular (Hutchinson, Uncapher, & Wagner, 2009; Sestieri, Shulman, & Corbetta, 2017) and may be more informative when considering hemispheric lateralisation of brain functions. As a result, Brodmann descriptions are adopted throughout the remainder of this thesis. The intraparietal sulcus (IPS) was originally under described by both Brodmann, (1909) and von Economo & Koskinas (1925). More recently, five

discrete cortical subdivisions were observed within the IPS with discernible functional characteristics first in non-human primates¹ (collated and reviewed in Grefkes & Fink, 2005), and subsequently, in humans² (Swisher, Halko, Merabet, McMains, & Somers, 2007). These regions play a critical role in the processing and judgment of visuospatial attention, eye movements and object-related motor actions in space (Grefkes & Fink, 2005; Orban, 2016; Silver & Kastner, 2009; Swisher et al., 2007). The anatomical delineations of the LPC are illustrated in Fig 1.3A.

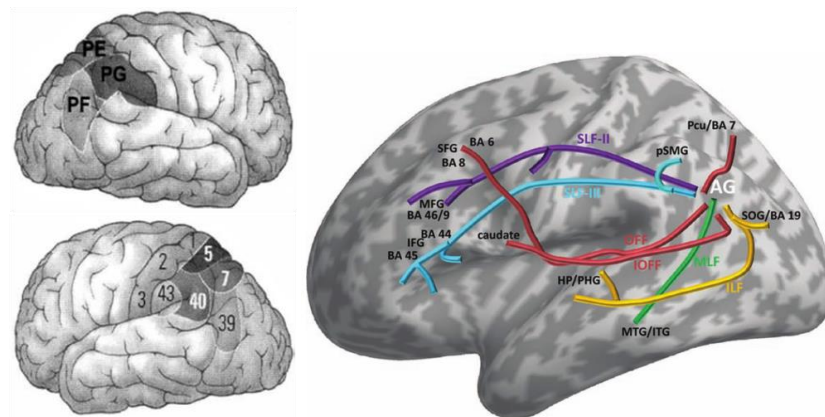


Figure 1.3: **A)** Illustrations of the anatomical delineations of the parietal cortex according to (upper) von Economo & Koskinas (1925) and (lower) Brodmann, (1909) (figures from Jäncke, 2007). **B)** A simplified view of the connectivity of the angular gyrus with other brain regions is displayed (Seghier, 2013). Though there are some differences in strength and exact innervation, the supramarginal gyrus utilises many of the same fasciculi as the angular gyrus (Kwok & MacAluso, 2015; Parlatini et al., 2017). SLF-I connects the SPL with dorsal aspects of the frontal lobe and is omitted in this illustration (Parlatini et al., 2017).

The parietal cortex is a heterogeneous cortical region with many anatomical connections that reflect its wide range of functional processes. Anatomical white matter tracking studies in both non-human primates and humans have revealed complex association tracts that reflect this diverse connectivity. Frontoparietal connections include the three superior longitudinal fasciculi (SLF). The dorsal branch (SLF-I) connects regions of the SPL with dorsal aspects of frontal lobe, including the frontal eye fields (FEF) and supplementary eye fields (SEF). The middle branch (SLF-II) joins regions of the IPL and IPS with aspects of the superior and middle frontal gyri. The

¹ Non-human primate parietal areas - AIP - anterior intraparietal area, VIP - ventral intraparietal area, MIP - medial intraparietal area, LIP - lateral intraparietal area, CIP - caudal intraparietal area.

² Human IPS subdivisions with non-human primate homologues in brackets- IPS1 (LIP), IPS2 (LIP), IPS3, IPS4, IPS5 (VIP).

IPL is connected with the inferior frontal gyrus via the ventral branch of the SLF (SLF-III) (Parlatini et al., 2017; Seghier, 2013). Critically, these frontoparietal connections form an integral part of the frontoparietal attention (FPA) network (Marshall, Bergmann, & Jensen, 2015; Sestieri, Corbetta, Romani, & Shulman, 2011) that will be discussed throughout this thesis.

As well as these frontoparietal links, the parietal cortex also has strong connectivity with other nodes of the core recollection network (*Fig 1.3B*). The IPL has extensive and direct reciprocal connections with the parahippocampal and entorhinal cortex, and the hippocampal formation via the inferior longitudinal fasciculus (Seghier, 2013). In addition, the occipito-frontal fasciculus provides a direct connection between the IPL and precuneus (Seghier, 2013). The location of the IPL and these connections with the core recollection network are consistent with an integrative role for the IPL in episodic memory processing.

Spatial Attention Allocation and the LPC

Evidence in the following section is largely underpinned by the work of Reuter-lorenz et al., (1990). They conducted a series of behavioural experiments that produced various hemispheric competitions for attention across visual space and manipulated activity in the attention network of each hemisphere. Despite controlling for the difference in acuity between the fovea and peripheral receptors, and optic angle, their results indicated that the tendency to allocate attention was consistently biased towards the visual space that was contralateral to the most active FPA network. The Activation-Orientating Model (AOM) they proposed provided the basis for further investigations (Loftus & Nicholls, 2012; McCourt, Freeman, Tahmahkera-Stevens, & Chaussee, 2001) and mechanistic accounts (Corbetta & Shulman, 2002, 2011) of how the brain allocates attention across perceptual space.

Unilateral hemispatial neglect (UHN)

UHN is a condition characterised by an inability to attend and report stimuli from contralesional space, and an inability to autonomously disengage attention from ipsilesional space (review Corbetta and Shulman, 2011). In drawing objects or scenes, UHN patients illustrate an egocentric bias to only report features of ipsilesional space (*Fig 1.4A*). Some patients display an object-centred neglect syndrome where they can report all objects in a scene but only attend to the ipsilesional side of those objects. These subtypes of UHN are generally anatomically distinguishable (egocentric UHN - ventral attention network damage, object-centred impairment - temporal lobe damage) (Verdon, Schwartz, Lovblad, Hauert, & Vuilleumier, 2010) and only the first, more common subtype is focussed on here.

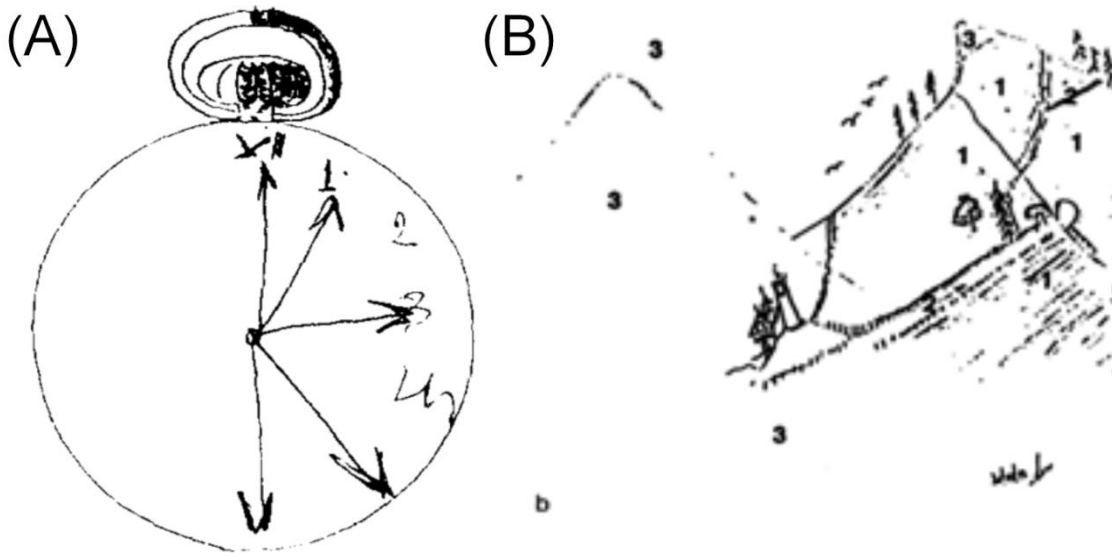


Figure 1.4: Examples of the characteristic lateralisation biases observed in UHN patients. **A)** UHN patients frequently only report the details of objects in ipsilesional visual space (Bisiach, Capitani, Luzzatti, & Perani, 1981). **B)** When asked to report or draw the features of a memory UHN patients will only provide details of the ipsilesional side of representational space (Beschlin, Cocchini, Della Sala, & Logie, 1997)

Investigation into the mechanisms driving UHN has attracted much interest due to the direct implications that findings could, and have had for patients (for meta-analysis of effectiveness of different treatment strategies see Yang et al., 2013). Earlier work on UHN sought to characterise and compare the effect with reference to hemianopia (Reuter-lorenz et al., 1990) and other early visual deficits. UHN has been thoroughly characterised with the use of many different paradigms. Demonstrations of normal sensitivity to image contrast (Spinelli, Guariglia, Massironi, Pizzamiglio, & Zoccolotti, 1990), standard identification of low level image features (Driver & Mattingley, 1998), identical visually evoked potentials to controls (Di Russo, Aprile, Spitoni, & Spinelli, 2008), and blood oxygen level dependent (BOLD) activation of striate and extra-striate areas in response to stimuli in the neglected field (Rees et al 2000), have demonstrated that UHN is not driven by failure of early visual processing. Rather, these studies suggest the grounding of UHN lies in attention allocation processing differences across the two hemispheres.

As well as neglecting the contralesional information in perceptual space, UHN patients also exhibit a deficit in recalling features of contralesional space. For example, when asked to imagine themselves in a very familiar location (well known to them before lesion onset), UHN

patients will recall far more features of the ipsilesional than the contralesional side of space (*Fig 1.4B*). When asked to adopt their opposite egocentric perspective (after a distracter task or a long break), UHN patients will recall previously omitted features of the scene and fail to provide features that were previously remembered (Bisiach & Luzzatti, 1978). Representational UHN has also been demonstrated in geographical map labelling (participants will omit labelling or identification of contralesional locations), and tactile maze exploration (in the absence of visual input, patients fail to locate a small target object in the contralesional but not ipsilesional tactile space) (Beschin et al., 1997).

Perceptual UHN almost invariably co-occurs with representational UHN. In fact, just one example of a patient with representational without perceptual UHN has been reported in the literature (to the author's knowledge) (Beschin et al., 1997). The patient in this case study was unimpaired in perceptual UHN assessments including line, letter, and star cancellation, horizontal line bisection, auditory and tactile extinction and predominantly unimpaired in visual extinction (a deficit was observed only during a high attentional load condition). In contrast, the patient was severely impaired in the previously described representational UHN assessments. The patient also exhibited an interesting distinction between working memory and long-term memory. Whilst being able to describe features of a complex scene from short term memory, the patient was severely impaired after both a 15 minute and 2 day delay. The imaging techniques used to assess the patient were limited to just a computerised tomography (CT) scan. As a result, it is not possible to accurately delineate the areas of damage and cortical sparing beyond observing that the patient had a substantial lesion in the right parietal lobe. However, the distinction between short and long term memory provides evidence that whilst non-MTL, and non-prefrontal brain regions critically involved in episodic retrieval were damaged, those dedicated to perceptual attention allocation were most probably intact as immediate performance was normal. Moreover, the case provides the first evidence that long-term memory retrieval processes supported by the right parietal cortex are involved in the processing of the contralateral side of remembered space. Despite the uniqueness of this patient and the caution that should be maintained in interpreting their impairments, the combination of the findings of this case study are both interesting and potentially informative for this thesis.

UHN can be caused by damage to any of a number of cortical areas. Brain insult to regions in the parietal and frontal lobes that include, but are not limited to, the IPS, IPL, and inferior frontal

gyrus (IFG) are the most frequently causes of UHN. The areas that are most commonly associated with neglect are displayed in *Fig 1.5*. Furthermore, UHN patients also frequently have damage to white matter tracts such as the SLF and occipito-frontal fasciculus (Thiebaut de Schotten et al., 2005, 2011; Verdon et al., 2010). Correspondence between lesion site and behavioural deficits in UHN has been shown to be extremely variable. More recently, however, network integrity and functional connectivity have been found to correlate well with behavioural impairments and symptom recovery in UHN (Baldassarre et al., 2014; He et al., 2007; Ramsey et al., 2016). Lesions of the right hemisphere FPA network are more likely to result in UHN than left FPA lesions (Corbetta & Shulman, 2011; Kinsbourne, 1970; Mesulam, 1981, 1999; Ramsey et al., 2016). The source of this hemispheric difference in the effect of brain insult to the FPA network led to two competing theories of attention allocation (Heilman & Van Den Abell, 1980; Kinsbourne, 1977; Mesulam, 1981). Interestingly, through the technological developments that have advanced neuroimaging, research has only recently been able to provide integrative models that seem to be resolving this mechanistic dichotomy.

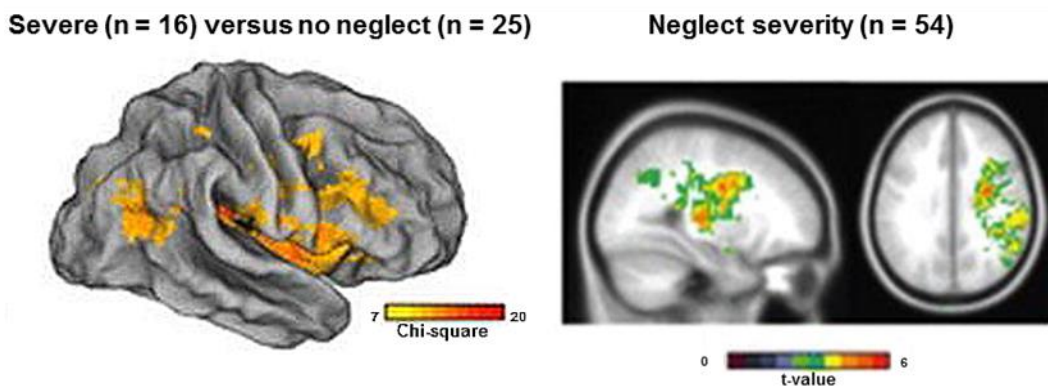


Figure 1.5: A representation of the brain lesions where damage is most consistently associated with UHN (Corbetta & Shulman, 2011). Note that regions with damage consistently associated with UHN are limited to the right hemisphere ventral attention network (VAN).

Neuroanatomical Models of Attention Allocation

The 'right hemisphere dominance' theory suggests that the left hemisphere is engaged solely in processing attention allocation in the right hemifield, whereas the right hemisphere is engaged in processing information in both hemifields (Heilman & Van Den Abell, 1980; Mesulam, 1981). Thus damage to attention centres in the left hemisphere could be compensated for by the right hemisphere but not vice versa. This accounted for the hemispheric differences in UHN producing damage.

The 'interhemispheric competition' theory was an alternative mechanism proposed to account for the spatial attention allocation features of the brain. This theory focussed on the role of inhibition between the two hemispheres of the brain in the governance of attention allocation (Kinsbourne, 1970, 1977). According to this model, each hemisphere contains homologous attention processing regions that work in opposition. Input to the attention network of one hemisphere leads to its stimulation. This increased activity subsequently enables greater power of inhibition over the contralateral hemisphere. Healthy attention allocation was argued to be achieved by the modulation of a careful balance between the attention networks of each hemisphere. This theory predicted that the right hemisphere would exhibit an inherent dominance over the left hemisphere during the processing of visuospatial attention (when the input to each hemisphere is equal). This unequal inhibitory strength accounted for the hemispheric difference in brain damage that produces UHN.

Corbetta & Shulman, (2002, 2011) proposed that attention allocation is controlled by a dorsal (DAN), and a ventral (VAN), attention network. They argued that these networks receive sensory input and following the processing of attention allocation, feed back to the primary sensory systems (Corbetta & Shulman, 2002, 2011; Szczepanski, Konen, & Kastner, 2010; Vuilleumier et al., 2010). The DAN includes the SPL, IPS, FEF, and SEF, and enables voluntary shifting of attention across space. Hemispheric lateralisation in the DAN has not been directly observed and its characteristics are more easily accounted for by the interhemispheric competition theory of attention allocation. The other FPA network, the VAN, includes the IPL, TPJ and IFG. The VAN is heavily lateralised to the right hemisphere and responds to stimuli in both hemifields. The demonstration of VAN lateralisation provides the evidence supporting the right hemisphere dominance theory of attention allocation.

The cortical nodes of the DAN are recruited when subjects respond to cues to shift the locus of their attention, voluntarily guide their eye movements, and when attention is allocated in line with a task relevant goal. Interestingly, the IPS also contains topographic maps of contralateral space. The presence of these maps reflects the important role of the DAN in directing attention to specific locations in space (Corbetta & Shulman, 2002). The DAN shows purely contralateral accountability without right hemisphere specialisation. This contradicts the proposal by the right hemisphere dominance theory of attention allocation (the right hemisphere FPA network allocates attention bilaterally, whilst the left does so contralaterally) (Heilman & Van Den Abell, 1980; Mesulam, 1981). Instead, the processing characteristics of the DAN are better accounted for by the inter-hemispheric competition theory of attention allocation. Current opinions view the hypoactivation of the right DAN, and hyperactivation of the left DAN (due to lack of right DAN inhibition) caused by right hemisphere damage, as the primary cause of spatial attention allocation deficits in UHN (Corbetta & Shulman, 2011).

As primary nodes of the VAN, the right TPJ and IPL are consistently activated during reflexive detection and orientation towards relevant information (Chambers, Payne, & Mattingley, 2007; Shulman et al., 2009, 2010). The right IFG is additionally involved in the reorientation of attention to unattended or unexpected stimuli (Shulman et al., 2009). Damage to the right VAN causes impairment of these functions across the visual field (Corbetta & Shulman, 2011). The right VAN is engaged by stimuli across both hemifields and has thus been referred to in the Corbetta and Shulman attention model as 'non-spatial'. However, the activation and integrity of the VAN does have consequences for spatially-specific attention allocation. For example, damage to the VAN that produces UHN is associated with lower arousal/alertness that is not observed in patients with parietal damage without UHN (Corbetta & Shulman, 2011). The right VAN is thought to be highly connected with the arousal/alertness network. Indeed in states of high arousal, UHN patients with right hemisphere damage show a reduction in the severity of their UHN (I. H. Robertson, Mattingley, Rorden, & Driver, 1998; I. H. Robertson, Tegnér, Tham, Lo, & Nimmo-Smith, 1995). This is the first of much evidence that highlights the importance of the interaction between the right hemisphere lateralised, 'non-spatial' functions of the VAN and the non-lateralised, spatially selective DAN.

Damage to the right hemisphere VAN is the most common damage associated with UHN. The Corbetta & Shulman (2002, 2011) model proposes that ordinarily the right VAN drives the right

DAN and maintains the tonic balance of attention allocation bias across the hemifields. As such, damage to the right hemisphere VAN greatly reduces the VAN drive of the right DAN causing a state of hypo-activity and reduced inhibition of the left hemisphere. This model provides an account for both the non-spatial and spatial characteristics of UHN and the association between damage to the right hemisphere and UHN. This mechanism also demonstrates the close link between the VAN and DAN. This mechanistic link underpins my proposals regarding the effects of hemispheric differences in IPL activation on measures of spatially specific attention allocation and memory retrieval in healthy individuals.

Since the proposal of the neuroanatomical model of attention allocation, the focus of more recent work has turned to characterising the mechanistic features of the DAN and VAN. In many cases, this has focussed on the lateralisation tendencies of these networks. For example, after reviewing the effect of transcranial magnetic stimulation (TMS) on a number of spatial attention allocation paradigms (line bisection (Szczepanski & Kastner, 2013), distractor interference (Chambers, Stokes, Janko, & Mattingley, 2006), spatial orienting (Duecker, Formisano, & Sack, 2013), and spatially-specific phosphene detection (Silvanto, Lavie, & Walsh, 2006)), Duecker & Sack (2015) proposed a revision of the Corbetta & Shulman (2002, 2011) model of attention. These studies showed a consistent role for the right FEF in spatial attention processing in both hemifields. In contrast, the left FEF was implicated in only the processing of contralateral stimuli. This hemispheric difference in hemifield engagement better reflects Heilman's right hemisphere dominance model rather than Kinsbourne's interhemispheric competition model. This conflicted with the Corbetta (2002, 2011) proposal that the activity of the DAN is controlled by interhemispheric inhibition and is not intrinsically lateralised. Thus, the hybrid model of attention control (*Fig 1.6*) was proposed to encompass these subsequent conclusions (Duecker & Sack, 2015). This proposed that modulatory connectivity exists between the right FEF and left PPC (in addition to the traditional right FEF-right PPC DAN connectivity) that reflects Heilman's right hemisphere dominance theory. The hybrid model also stressed the existence of interhemispheric competition between the PPC of each hemisphere.

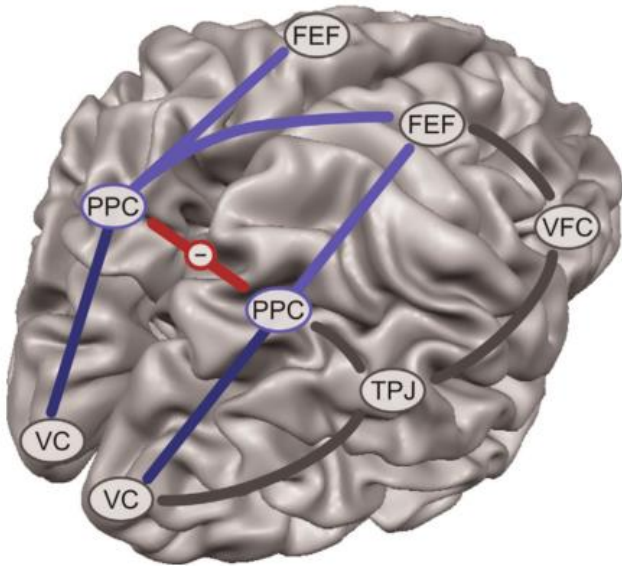


Figure 1.6: A schematic representation of the interactions between the nodes of the DAN in the hybrid model of attention control. Note the interhemispheric inhibition that characterises the connectivity between the superior aspects of the posterior parietal cortex (PPC) that reflects Kinsbourne's opponent processing model. Also see the bilateral processing engagement of the right frontal eye field (FEF) that is characteristic of Heilman's right hemisphere dominance theory. The visual cortex (VC), temporo-parietal junction (TPJ) and ventral frontal cortex (VFC) are included as nodes of the VAN for completeness (Duecker & Sack, 2015).

The views and theoretical proposals presented thus far have primarily drawn on data from patients with UHN. The following section will provide an insight into attention allocation in the healthy brain.

Pseudoneglect

The characteristics of the mechanisms supporting the allocation of attention have been thoroughly investigated with a variety of different techniques (intraoperative electrical stimulation (Thiebaut de Schotten et al., 2005); electroencephalography (EEG) (Benwell, Harvey, & Thut, 2014; Learmonth, Benwell, Thut, & Harvey, 2017); functional MRI (fMRI) (Petitet, Noonan, Bridge, O'Reilly, & O'Shea, 2015; Zago et al., 2017); neurostimulatory techniques (Chambers et al., 2007; Hilgetag, Theoret, & Pascual-leone, 2001; Petitet et al., 2015)). The line bisection test (Fig 1.7A; Hughes, Bates, & Aimola Davies, 2004; Reuter-Lorenz et al., 1990;

Thiebaut de Schotten et al., 2005), the landmark task (Fig 1.7B; Benwell, Harvey, et al., 2014; Benwell, Thut, Grant, & Harvey, 2014; Fink, Marshall, Weiss, Toni, & Zilles, 2002) and greyscale task (Fig 1.7C; Loftus & Nicholls, 2012; Nicholls & Roberts, 2002; Thomas, Loetscher, & Nicholls, 2014) all require the subject to produce a stimulus centric comparison of the left and right sides of an image and have proven sensitive to differences in functional specialisation across the hemispheres. Many of these techniques will be described below, or later in the thesis. In addition, patients with UHN produce extremely biased judgements on all of the tests described above (Di Russo et al., 2008).

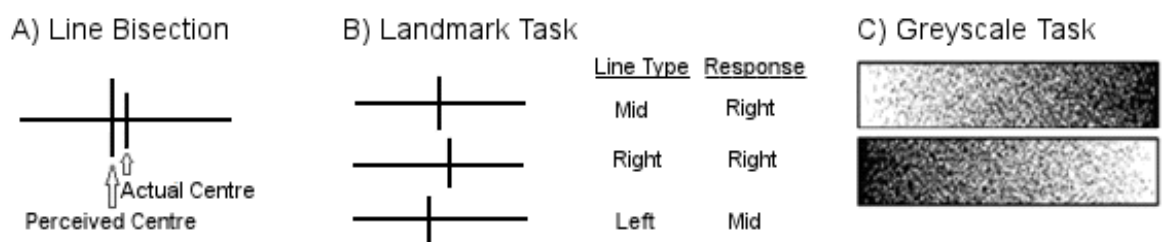


Figure 1.7: A) An example of a MLB response that is characteristic of pseudoneglect (Anderson, 1996). B) An example of three responses to three different line type presentations that epitomise pseudoneglect (Reuter-lorenz et al., 1990). C) An example greyscale task presentation stimulus. Under the influence of pseudoneglect, subjects would be more likely to select the bottom square when asked which stimulus was darker (Loftus & Nicholls, 2012).

The pseudoneglect effect was first observed and described by Bowers & Heilman (1980). Attention research has since shown that items on the left side of perceptual space are processed more quickly, judged to be larger, more numerous, or brighter than items in the right hemifield (Learmonth, Gallagher, Gibson, Thut, & Harvey, 2015). A wealth of evidence has confirmed the existence of the pseudoneglect effect since its first observation. Evidence pertaining to the pseudoneglect effect was collated in a meta-analysis that observed a substantial (estimated mean $d = 1.024$) left spatial processing advantage in a multitude of free-viewing laterality tasks (Voyer, Voyer, & Tramonte, 2012).

The line bisection task requires the subject to use a straight vertical line to perfectly bisect a straight horizontal line. Upon inspection of the line on the body's midline, each side of the line

falls into the hemifield processed by the contralateral hemisphere. When completing this task, the majority of individuals will consistently place the vertical line to the left of the actual centre of the horizontal line (see *Fig 1.7* for example; for a review of the pseudoneglect effect and the line bisection task, see ref. Jewell & McCourt, (2000)). In a similar way to the line bisection task, the landmark task presents pre-bisected lines to the subject, and asks them to indicate whether the vertical line was in the centre, or to the left or right of the true midline of the horizontal line (though exact instructions do vary (Fink et al., 2002)). Subjects generally overestimate the size of the left side of the horizontal line and indicate that the line was to the right of its true position. The landmark task, developed to provide a comparable task to the MLB with a reduction in motor processing dependency, has enabled a constrained and flexible tool for investigating the different aspects of attention allocation processing (Cavézian, Valadao, Hurwitz, Saoud, & Danckert, 2012).

The tendency of healthy individuals to preferentially allocate attention to the left side of visual space, (the pseudoneglect effect) has been shown to reflect the specialisation of the right hemisphere attention centres for processing visuospatial information (Benwell, Harvey, et al., 2014; Gitelman et al., 1999; Heilman & Van Den Abell, 1980; Mesulam, 1981, 1999; Nicholls, Hobson, Petty, Churches, & Thomas, 2017). Corbetta & Shulman (2002, 2011) updated this conjecture and proposed that the right lateralised VAN (engaged by stimulation across both hemifields) drives activity in the DAN spatially specific within the contralateral hemifield and the spatial pseudoneglect attention bias. Though the nature of the interaction between these networks was not clearly understood at the time, more recent work has provided strong evidence in support of this proposal. For example, Thiebaut de Schotten et al., (2011) showed that the difference in the size of the SLF II (which provides direct connections between the VAN and the DAN (Schmahmann et al., 2007; Thiebaut de Schotten et al., 2011)) across the hemispheres is strongly positively correlated with the individual extent of the pseudoneglect bias.

The association between alertness and spatial orienting of attention in UHN patients (in states of high arousal, right hemisphere damaged UHN patients show less severe ipsilesional biases) introduced earlier also seems to be an important modulator of the pseudoneglect effect. Extended periods of time on task (~1 hour - linked to reduced alertness) were associated with a graduated shift away from the leftward, pseudoneglect attention bias towards the right side

(Newman, O'Connell, & Bellgrove, 2013). In addition, healthy elderly participants show both reduced arousal/alertness and a reduction in the pseudoneglect effect (or a small rightward bias under certain conditions) (Schmitz & Peigneux, 2011). The further observation that orientation to the left visual field could be augmented by exposure to high intensity blue light (associated with increased activation of the locus coeruleus/noradrenergic arousal system) has helped to confirm the association between these systems (Newman et al., 2016).

A number of other factors have also been shown to modulate the pseudoneglect effect (generally reducing or eliciting a small rightward bias). The mechanisms that enable modulation by these factors are generally less clearly understood than the interaction between alertness and spatial lateralisation. In a MLB or landmark task, the length of the horizontal line that is bisected significantly affects the extent and sometimes direction of the observed lateralisation bias (Benwell, Harvey, et al., 2014; McCourt & Jewell, 1999; Veronelli, Vallar, Marinelli, Primativo, & Arduino, 2014). In these studies, bisection of shorter lines (subtending $<2^\circ$ visual angle, ~ 2 mm) resulted in reduced leftward, and sometimes small rightward biases. In addition, the distance at which perceptual judgements (such as in the MLB or landmark task) are made impacts upon the pseudoneglect effect. There is a rightward shift in attention allocation from the left side as judgements are made at greater distances from the viewer (peri- versus extra-personal space) (Lane, Ball, & Ellison, 2015; Longo & Lourenco, 2006; Longo, Trippier, Vagnoni, & Lourenco, 2015; Lourenco & Longo, 2009; McCourt & Garlinghouse, 2000). The vertical location of stimulus presentation also modulates the lateralisation bias of attention allocation. Larger pseudoneglect effects have been observed with perceptual judgements in the upper visual field than in similar judgements in the lower visual field (McCourt & Jewell, 1999; Nicholls et al., 2012; Thomas, Castine, Loetscher, & Nicholls, 2015). In chapter 3 of this thesis, evidence is presented that characterises the similarities between the line length, vertical location, and proximity effects. For a more detailed review of factors that modulate the pseudoneglect effect but fall outside the scope of this thesis, see (Jewell & McCourt, 2000).

Representational pseudoneglect is a term currently used to describe a bias of spatial processing in the absence of direct perceptual input. The seminal work (referred to earlier) by Bisiach & Luzzatti (1978) found that healthy individuals recalled more items from the left side of a highly familiar remembered scene (the Piazza del Duomo) than the right. The existence of the representational pseudoneglect effect has been confirmed in more focussed studies (Aniulis,

Churches, Thomas, & Nicholls, 2016; Brooks, Sala, & Logie, 2011; Darling, Logie, & Della Sala, 2012; Della Sala, Darling, & Logie, 2010; Friedman, Mohr, & Brugger, 2012; McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007). In a replication of the Piazza del Duomo study, the representational effect was linked to the allocation of attention to a mental image of the remembered space (McGeorge et al., 2007). This proposed mechanism has since been substantiated by further evidence of bias in mental imagery in working memory (Della Sala et al., 2010). In addition, healthy individuals also underestimate the mean average from a set of numbers. When completing this task, an individual will arrange the set of numbers in ascending size order from left to right. The underestimation of the mean number in the set has been linked to a leftward bias in the allocation of attention to this internally generated mental number line (Göbel, Calabria, Farnè, & Rossetti, 2006; Rusconi, Dervinis, Verbruggen, & Chambers, 2013).

Although, the representational pseudoneglect effect has been observed in a diverse set of paradigms, and has potentially wide reaching implications for studies of spatial memory, the effect has yet to be fully investigated with neuroimaging methods. As a result, the neural mechanisms that support the representational and perceptual pseudoneglect effects have largely been assumed to be analogous. However, this assumption is likely to be an overly simplistic perspective. Darling et al. (2012) performed a computerised line bisection task in a within-subjects comparison of perceptual (the line was visible throughout the trial) and representational (the line was bisected after it was presented and subsequently removed from the screen) lateralisations. This study observed a strong group level representational pseudoneglect effect in the absence of a perceptual bias. In addition to the difference between these group level attention biases, there was no correlation between the degree of bias on the perceptual and memory tasks. This absence of correlation across representational and perceptual lateralisation biases was replicated by Brooks, Darling, Malvaso, & Della Sala (2016), but has, to the author's knowledge, not been observed outside of mental number lines (a bias that is closely linked to mental imagery of an internally generated number line rather than memory) (Longo & Lourenco, 2007). This evidence collectively suggests that similar but distinct systems (rather than the varying engagement of one system) may be engaged by perceptual and representational tasks. The unique case, described earlier, of spared perceptual attention allocation occurring alongside representational UHN (Beschin et al., 1997) provides further evidence of these distinct mechanisms with common lateralisations.

There is an ongoing debate regarding the role of the LPC in episodic memory retrieval. This interesting and rapidly developing field of research may offer insight into the potential distinction between the neural mechanisms supporting representational and perceptual pseudoneglect. The following section will assess the LPC and episodic memory retrieval debate and consider its implications for both lateralisation effects.

The LPC and Episodic Memory Retrieval

A fascinating disconnect has now existed for 15 years between the view of cognitive neuroscience and clinical neuropsychology regarding the role of the LPC in episodic memory. Neuroimaging studies of episodic memory clearly show LPC activity with remarkable consistency (Simons & Mayes, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). In contrast to the clear amnesic effects of lesions to the prefrontal and MTL cortices, many clinical studies have concluded that damage to the LPC does not produce memory deficits (Simons & Mayes, 2008). In contrast, clinical neuropsychological investigations of the LPC have traditionally focussed on visual and spatial attention, or visually guided action (Committeri et al., 2007; Harvey & Rossit, 2012; Heilman & Van Den Abell, 1980; Kinsbourne, 1977; Verdon et al., 2010).

The association between the LPC and episodic memory retrieval was first observed through investigations of event-related potentials (ERP) in recognition memory paradigms. A phasic, positive deflection in the amplitudes of ERPs was observed during correctly recognised 'old' (previously encountered) when compared to correctly rejected 'new' (items not previously encountered). The terms 'parietal old/new effect' or the 'retrieval success effect' were subsequently coined to describe this observation (this literature is reviewed in Rugg & Curran (2007)).

fMRI investigations have yielded significant insight into the parietal old/new effect. A wide variety of stimuli have been employed to show that the parietal old/new ERP effect occurs as a function of LPC activity. Although a range of memory processes have revealed LPC activations, the region has been associated with recollection-based memory with greatest consistency (Simons et al., 2008). This has been demonstrated using various recognition paradigms, including the traditional old/new memory test (Hutchinson, Uncapher, & Wagner, 2015; Weis, Klaver, Reul, Elger, & Fernández, 2004), remember/know (Angel et al., 2016; Dennis, Bowman, & Vandekar, 2012; Frithsen & Miller, 2014; Sharot, Delgado, & Phelps, 2004), and source recollection paradigms (Cansino, Maquet, Dolan, & Rugg, 2002; Duarte, Henson, & Graham, 2011; Frithsen & Miller, 2014; Ragland, Valdez, Loughhead, Gur, & Gur, 2006). Activations in the LPC have also been observed during paradigms assessing familiarity memory (Daselaar, Fleck, & Cabeza, 2006; Frithsen & Miller, 2014; Kafkas & Montaldi, 2012; Yonelinas et al., 2005). Interestingly, the *perception* of oldness in a recognition judgement seems to modulate activity in

the LPC. As such, LPC activity patterns during trials with correct recognition of previously encountered (old) items (classified as hits) can be extremely similar to trials in which previously unobserved (new) items are misidentified as previously encountered items (classified as false alarms). The same is also true of old items that are reported to be new (misses) and correctly identified new items (correct rejections). In contrast to this activity that is dependent on perceived oldness, hits, false alarms, correct rejections and misses produce distinguishable activity in the MTL (Montaldi et al., 2006).

Wagner and colleagues (2005) proposed a number of mechanisms that could explain the memory-related activations in the parietal cortex. The dependence of parietal activity on the perception of memory, rather than objective oldness provided the impetus for the conception of the *mnemonic accumulator hypothesis*. This theory suggests that the parietal regions integrate memory information from other regions involved in the retrieval process and allow comparison of memory strength against a criterion. In cases where the accumulated memory signal summates to surpass the criterion, the memory probe or retrieved information would be reported as remembered. Contrastingly, memory probes that return retrieval signals falling below the criterion would be reported as new. The mnemonic accumulator hypothesis assumes that recollection and familiarity memory are represented by a unitary memory strength signal in the parietal cortex. Though this is consistent with some views of these memory types (Wixted, 2007), the dual processes model proposes that recollection and familiarity are underpinned by distinct processes (Montaldi et al., 2006). However, it is possible that the parietal cortex is an area that does not conform to dual processing mechanisms and instead represents a shared memory strength signal (Simons & Mayes, 2008).

The *output buffer hypothesis* (Wagner et al., 2005) is another theory of LPC memory function and provides a neural basis for the memory buffers thought to be required for working memory (Baddeley, 2003). According to this model, retrieved information is temporarily stored in a form conducive to decision making. This hypothesis was based on the additional activation observed in the LPC that is elicited by recollection compared to familiarity memories. The effect of perceived oldness in the LPC led quickly to scepticism of the output buffer hypothesis (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Simons & Mayes, 2008). The perceived oldness effect observed in the LPC describes the equivalence of LPC signalling for remembered items irrespective of the accuracy of memory retrieval. One would expect that correctly remembered

items should be accompanied by more information than incorrectly remembered items. The equivalence of LPC processing for correctly and incorrectly remembered items violates this pattern of activity that would be expected by output buffer hypothesis.

Amongst other reasons, that will be described shortly, interpretation of neuroimaging findings of LPC function has been contentious because of the range of cognitive processes that are known to draw on coarsely analogous areas. In the same review by Wagner and colleagues (2005), the *attention to internal representations hypothesis* was first speculatively suggested to address the apparent presence of multiple LPC functions. This highlighted the possibility that a common area of LPC cortex was involved in the distribution of attention to both external (in perception) and internal (in memory) retrieval. Through further explorations and development (Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008), this proposal was linked more closely with the functionally segregated model of attention allocation processing in the DAN and VAN (Corbetta & Shulman, 2002, 2011). The *attention to memory (AToM)* account of LPC function integrated this dorsal/ventral functional dissociation and proposed distinct roles in memory for each aspect of LPC (Cabeza et al., 2008). This model proposed that the SPL maintains and guides the attempt of memory retrieval according to task goals. In contrast, reflexive orienting to the relevant and potentially unanticipated contents of retrieval would be dependent on the IPL.

Activations in different aspects of the LPC have been linked to distinct roles within the retrieval process. Earlier investigations of episodic memory retrieval linked the SPL and IPS to the processing of the feeling of oldness or familiarity memory (Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Wheeler & Buckner, 2004; Yonelinas et al., 2005). Later studies found that the fundus and lateral bank of the IPS demonstrated the activity patterns similar to those traditionally associated with familiarity memory (Daselaar et al., 2006; Yonelinas et al., 2005). This was further refined to link these IPS activations to the subject's perception of the oldness of a stimulus (Hutchinson et al., 2014, 2015). In contrast, activation patterns in the SPL and medial border of the IPS were distinct from this pattern of perceived oldness activity. Instead, these regions were associated with processing the degree of decision uncertainty (in both perceived oldness and novelty judgements) in a recognition judgement (Hutchinson et al., 2014, 2015).

The role of the SPL in the DAN (Corbetta & Shulman, 2002, 2011) described earlier has, in this case, aided the interpretation of memory-related SPL activations. Hutchinson et al. (2015) identified increased connectivity between the SPL and ventral occipital cortex during uncertain

memory decisions that corresponded with the view that the SPL governs top-down modulation of goal directed attention. In the context of a recognition memory test, this uncertainty-related connectivity was said to reflect greater effort to perceive more details of the recognition cue and thus aid the memory decision (Hutchinson et al., 2015).

Many of the subsequent investigations of the involvement of the LPC in memory have focussed and elaborated on the early theories proposed by Wagner and colleagues (2005). One of the most poignant examples of this work showed a distinct dissociation between subregions within the LPC that were active during the processing of attention and episodic memory (Hutchinson et al., 2009). This meta-analysis showed that the lateral bank of the IPS was strongly associated with top-down maintenance of memory retrieval goals. In contrast, the medial bank of the IPS was more closely related to the similar processing in attention. A similar distinction was also observed with bottom-up processing related activity. Reflexive orienting to memory information was observed primarily in the angular gyrus, whereas perceptual attention allocation signals were closely linked to the TPJ and supramarginal gyrus. Further evidence in support of this proposal was subsequently provided in a within-subjects fMRI comparison of memory and perceptual attention allocation (Sestieri, Shulman, & Corbetta, 2010). This same comparison demonstrated inversely related activity in LPC regions linked to perception and memory. The perceptual task was associated with increased BOLD activity in perceptual LPC regions and decreased BOLD activity in memory regions. The converse pattern was observed in the memory task.

In a conceptual elaboration of the output buffer and mnemonic accumulator hypothesis, the angular gyrus has been proposed to contain (Vilberg & Rugg, 2008) or provide a convergent hub for the integration (Shimamura, 2011) of retrieved information. This function has been linked to enabling vivid remembering of episodes. This role in vivid remembering is supported by the increase in angular gyrus activity that is observed with greater amounts of episodic retrieval content (Vilberg & Rugg, 2007). More recent evidence also suggests that the angular gyrus assimilates retrieved information into a form accessible to declaration, decision making, or further processing but does not store representations as an output buffer. Firstly, the angular gyrus consistently shows initial but transient activity akin to the temporal dynamics of the MTL (Sestieri et al., 2011). Secondly, neuropsychological and non-invasive brain stimulation, that interferes with cortical processing, indicate that vivid memory that includes multiple features

may be dependent on the angular gyrus (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Yazar, Bergström, & Simons, 2017).

As described earlier, the traditional clinically-driven view of LPC function does not include the processing of episodic memory (Simons & Mayes, 2008). Deficits in non-memory functions (that result from damage to the LPC (such as perceptual UHN)) have most likely obscured the observation of impairments of memory processing. In addition, to the author's knowledge, no investigations have been able to investigate brain insult specifically affecting only one of the anatomically-adjacent perceptual and memory LPC regions that were discussed above. Potentially because of these methodological difficulties, investigations that have employed patients with LPC damage have revealed mixed findings, ranging from no differences to clear memory impairments.

Initial neuropsychological studies using patients did not reveal clear effects of LPC damage on memory. For example, patients exhibited comparable memory performance to healthy control subjects on a test of source memory using words and images of famous faces (Simons et al., 2008). Around the same time, an Old/New recognition test of words, pictures, and sounds also failed to differentiate between patients and healthy controls (Haramati et al., 2008). These initial studies suggested that the LPC was not critical to the episodic retrieval process. However, this was challenged by subsequent studies that assessed more vivid memories with greater perceptual richness. When freely recalling details of autobiographical memories, patients with bilateral parietal lesions provided descriptions that were impoverished and lacked specificity compared to healthy controls. Questioning with specific probes alleviated this diminished memory retrieval (Berryhill et al., 2007). Similar studies that assessed detailed memories observed similar deficits in rich, vivid retrieval in patients with bilateral and unilateral lesions (Davidson et al., 2010; Simons, Peers, Mazuz, Berryhill, & Olson, 2010).

The angular gyrus has been identified as a core node of the default mode network and activation in the region has been linked to a wide range of behaviours relative to fixation (Bellana, Liu, Anderson, Moscovitch, & Grady, 2016; Seghier, 2013). As a result, the functional relevance of angular gyrus activations has been questioned. Subsequent investigations of the LPC memory problem have utilised non-invasive neurostimulation techniques to address these questions. TMS disruption of processing in the angular gyrus elicited a reduction in participants' confidence supporting recollections (Yazar, Bergström, & Simons, 2014). A similar TMS approach observed a

shift in source memory attributions and memory accuracy (Sestieri, Capotosto, Tosoni, Luca Romani, & Corbetta, 2013). Another TMS investigation of angular gyrus function recently provided further evidence of a causal relationship of the region with episodic memory (Yazar et al., 2017). In this study, TMS was used to disrupted angular gyrus processing and temporarily induce a deficit in the retrieval of episodic memories that relied on information from multiple, but not single modalities. This added substantial evidence supporting the theory that the angular gyrus is involved in the integration of episodic memory information during retrieval. Single modality conditions are heavily associated with angular gyrus activity. It is therefore slightly surprising that single modality memory was not impaired by the TMS.

As explained earlier (Spatial Attention Allocation & the LPC), the processing of reflexive detection and orienting in the VAN is highly lateralised to the right hemisphere (Corbetta & Shulman, 2002, 2011). Interestingly, the activity of the IPL in memory processes shows the opposite lateralisation tendency (Capotosto et al., 2017; Ciaramelli et al., 2008; Hutchinson et al., 2009; Wagner et al., 2005). The effect that the highly right hemisphere lateralised functioning of the VAN has on the DAN and attention allocation has been well characterised through exploration of the pseudoneglect effect. In stark contrast, current models of the LPC role of episodic memory do not provide any account of the effects of hemispheric specialisation of LPC activity. Though considerable evidence supports an anatomical and, to some degree functional dissociation between the parietal networks supporting attention and memory, the idea that common lateralisation characteristics may support these functions and allow for insightful access to mechanistic processes has not been well considered.

Aims and Objectives

This thesis characterises the functions of the LPC through targeted behavioural, theoretical, and neuroimaging assessment of hemispheric lateralisation.

Studies that have sought to characterise the role of the LPC in attention and pseudoneglect do not fully reflect the complexity of our environments. These experiments frequently present simple, reductionist stimuli as cues, probes, and targets to challenge the allocation of attention across perceptual space. This highly spatial approach minimises any potential impact of object recognition and semantic processing on the hemispheric balance of processing power. In addition, the memorability of these stimuli is highly limited by the detail and variability of these impoverished stimuli. In stark contrast, the vast majority of investigations of the role of the LPC in memory employ semantically engaging words, object images, faces, scenes, or a combination of the above. The following chapters seek to address the impact of these methodological differences on LPC processing and utilise the experimental features of each previously distinct cognitive strand of research to aid the investigation of the other.

In *Chapter 2*, an adapted version of the line bisection task and a newly developed implicit primed attention task (used to investigate attention allocation) were modified to effectively assess the impact of object and semantic processing on hemispheric lateralisation for the first time. The three experiments in this chapter (experiment 2.1 - line/object bisection, 2.2 - abstract shape bisection, 2.3 - implicit primed attention) were the first step in demonstrating a hemispheric specialisation in the LPC that was highly dependent on the semantic or perceptual nature of the system input. Furthermore, the findings provide the impetus for a shift in investigative approach towards studying attention in ways that better reflect environmental complexity.

Chapter 3 presents convergent evidence from an fMRI and a behavioural experiment (additional analysis of experiment 2.1) that further develops our understanding of the idiosyncratic features of attention allocation mechanisms in the brain. For the first time, similarities in the way that lines and objects are processed are revealed and utilised to provide a better perspective on the neural basis of the line length and target-observer proximity attention effects. This chapter provides another example of investigating pseudoneglect and attention with materials more

commonly associated with memory experiments.

Chapter 4 focuses on the role of the IPL in memory retrieval. A systematic review of the lateralisation of IPL activations in fMRI studies of episodic memory retrieval was performed. This investigated the possibility that the hemispheric lateralisation of memory retrieval is dependent on the content/requirements of the memory. More specifically, we asked whether retrieval of more richly perceptual memories is associated with greater right hemisphere IPL activations, and does the left hemisphere IPL process the integration of semantic and/or conceptual memory retrieval? The findings of this review are presented in *Chapter 4* along with an fMRI investigation of the functional correlates of perceptual episodic memory (the memory test phase of the fMRI study (experiment 3.2)). In this fMRI experiment, we provide the first direct comparison of the activity profiles of each IPL during a highly perceptual, and minimally semantic, episodic retrieval task.

The effects of hemispheric lateralisation of the IPL on behavioural measures of episodic memory retrieval processing are explored in three experiments in *Chapter 5* (experiment 5.1 - modified version of the behavioural paradigm used in the fMRI experiment 4.2, experiment 5.2 - tactile cued recall task, experiment 5.3 - spatially-specific autobiographical recall task). We provide novel insight into the contribution of episodic memory retrieval mechanisms to the representational pseudoneglect effect and establish further evidence supporting the functional role of right hemisphere retrieval mechanisms in episodic retrieval.

Chapter 6 summarises and further discusses the contribution made by the research in this thesis to our current understanding of spatial attention and memory retrieval processing. Ideas for the future directions that research should take to better understand these systems are also presented. One particular focus of this chapter is the development of novel behavioural manipulations that can provide meaningful insight into the mechanistic underpinnings of the brain. These manipulations are developed with consideration of the limitations and requirements of neuroimaging. This will enable a convergent approach to answering the future questions related to hemispheric specialisations of function, the role of the LPC in attention and memory, and the translation of our understanding of these mechanisms to ecologically realistic environments.

References

- Aggleton, J. P., & Brown, M. W. (2006). Interleaving brain systems for episodic and recognition memory. *Trends in Cognitive Sciences*, 10(10), 455-463. <http://doi.org/10.1016/j.tics.2006.08.003>
- Anderson, B. (1996). A mathematical model of line bisection behaviour in neglect. *Brain*, 119(3), 841-50. <http://doi.org/10.1093/brain/119.3.841>
- Angel, L., Bastin, C., Genon, S., Salmon, E., Fay, S., Balteau, E., ... Collette, F. (2016). Neural correlates of successful memory retrieval in aging: Do executive functioning and task difficulty matter? *Brain Research*, 1631, 53-71. <http://doi.org/10.1016/j.brainres.2015.10.009>
- Aniulis, E., Churches, O., Thomas, N. A., & Nicholls, M. E. R. (2016). Representational pseudoneglect for detecting changes to Rey-Osterrieth figures. *Experimental Brain Research*, 234(11), 3381-3387. <http://doi.org/10.1007/s00221-016-4735-0>
- Baddeley, A. (2003). Working memory: looking back and looking forward. *Nature Reviews Neuroscience*, 4(10), 829-39. <http://doi.org/10.1038/nrn1201>
- Baldassarre, A., Ramsey, L. E., Hacker, C. L., Callejas, A., Astafiev, S. V., Metcalfe, N. V., ... Corbetta, M. (2014). Large-scale changes in network interactions as a physiological signature of spatial neglect. *Brain*, 137(12), 3267-3283. <http://doi.org/10.1093/brain/awu297>
- Benwell, C. S. Y., Harvey, M., & Thut, G. (2014). On the neural origin of pseudoneglect: EEG-correlates of shifts in line bisection performance with manipulation of line length. *NeuroImage*, 86, 370-80. <http://doi.org/10.1016/j.neuroimage.2013.10.014>
- Benwell, C. S. Y., Thut, G., Grant, A., & Harvey, M. (2014). A rightward shift in the visuospatial attention vector with healthy aging. *Frontiers in Aging Neuroscience*, 6, 113-124. <http://doi.org/10.3389/fnagi.2014.00113>
- Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: bilateral damage causes impaired free recall of autobiographical memory. *The Journal of Neuroscience*, 27(52), 14415-23. <http://doi.org/10.1523/JNEUROSCI.4163-07.2007>
- Beschin, N., Cocchini, G., Della Sala, S., & Logie, R. H. (1997). What the Eyes Perceive, The Brain Ignores: A Case of Pure Unilateral Representational Neglect. *Cortex*, 33, 3-26. [http://doi.org/10.1016/S0010-9452\(97\)80002-0](http://doi.org/10.1016/S0010-9452(97)80002-0)
- Bisiach, E., Capitani, E., Luzzatti, C., & Perani, D. (1981). Brain and conscious representation of outside reality. *Neuropsychologia*, 19, 543-51.
- Bisiach, E., & Luzzatti, C. (1978). Unilateral neglect of representational space. *Cortex*, 14, 129-133. [http://doi.org/10.1016/S0010-9452\(78\)80016-1](http://doi.org/10.1016/S0010-9452(78)80016-1)
- Bowers, D., & Heilman, K. M. (1980). Pseudoneglect: Effects of hemisphere on a tactile line bisection task. *Neuropsychologia*, 18(4-5), 491-8. [http://doi.org/10.1016/0028-3932\(80\)90151-7](http://doi.org/10.1016/0028-3932(80)90151-7)
- Brady, T. F., Konkle, T., Alvarez, G. A., & Oliva, A. (2008). Visual long-term memory has a massive storage capacity for object details. *PNAS*, 105(38), 14325-14329. <http://doi.org/10.1073/pnas.0803390105>

- Brodman, K. (1909). *Vergleichende Lokalisationslehre der Grosshirnrinde*. Leipzig: Johann Ambrosius Barth.
- Brod, S., Pöhlchen, D., Flanagin, V. L., Glasauer, S., Gais, S., & Schönauer, M. (2016). Rapid and independent memory formation in the parietal cortex. *PNAS*, 113(46), 13251-13256. <http://doi.org/10.1073/pnas.1605719113>
- Brooks, J. L., Sala, S. Della, & Logie, R. H. (2011). Tactile rod bisection in the absence of visuo-spatial processing in children, mid-age and older adults. *Neuropsychologia*, 49(12), 3392-3398. <http://doi.org/10.1016/j.neuropsychologia.2011.08.015>
- Buffalo, E. A., Bellgowan, P. S. F., & Martin, A. (2006). Distinct roles for medial temporal lobe structures in memory for objects and their locations. *Learning & Memory*, 13(5), 638-643. <http://doi.org/10.1101/lm.251906>
- Byrne, P., Becker, S., & Burgess, N. (2009). Remembering the past and imagining the future: a neural model of spatial memory and imagery. *Psychological Review*, 114(2), 340-375. <http://doi.org/10.1037/0033-295X.114.2.340.Remembering>
- Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: an attentional account. *Nature Reviews Neuroscience*, 9(8), 613-625. <http://doi.org/10.1038/nrn2459>
- Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain Activity Underlying Encoding and Retrieval of Source Memory. *Cerebral Cortex*, 12(10), 1048-1056. <http://doi.org/10.1093/cercor/12.10.1048>
- Capotosto, P., Baldassarre, A., Sestieri, C., Spadone, S., Romani, G. L., & Corbetta, M. (2017). Task and Regions Specific Top-Down Modulation of Alpha Rhythms in Parietal Cortex. *Cerebral Cortex*, 27(10), 4815-4822. <http://doi.org/10.1093/cercor/bhw278>
- Cavézian, C., Valadao, D., Hurwitz, M., Saoud, M., & Danckert, J. (2012). Finding centre: ocular and fMRI investigations of bisection and landmark task performance. *Brain Research*, 1437, 89-103. <http://doi.org/10.1016/j.brainres.2011.12.002>
- Chambers, C. D., Payne, J. M., & Mattingley, J. B. (2007). Parietal disruption impairs reflexive spatial attention within and between sensory modalities. *Neuropsychologia*, 45(8), 1715-1724. <http://doi.org/10.1016/j.neuropsychologia.2007.01.001>
- Chambers, C. D., Stokes, M. G., Janko, N. E., & Mattingley, J. B. (2006). Enhancement of visual selection during transient disruption of parietal cortex. *Brain Research*, 1097(1), 149-155. <http://doi.org/10.1016/j.brainres.2006.04.084>
- Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, 46(7), 1828-1851. <http://doi.org/10.1016/j.neuropsychologia.2008.03.022>
- Committeri, G., Pitzalis, S., Galati, G., Patria, F., Pelle, G., Sabatini, U., ... Pizzamiglio, L. (2007). Neural bases of personal and extrapersonal neglect in humans. *Brain*, 130(2), 431-441. <http://doi.org/10.1093/brain/awl265>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201-15. <http://doi.org/10.1038/nrn755>
- Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. *Annual Reviews Neuroscience*, 34, 569-99. <http://doi.org/10.1146/annurev-neuro-061010-113731>

- Darling, S., Logie, R. H., & Della Sala, S. (2012). Representational pseudoneglect in line bisection. *Psychonomic Bulletin & Review*, 19(5), 879-83. <http://doi.org/10.3758/s13423-012-0285-z>
- Darwin, C. R. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2006). Triple Dissociation in the Medial Temporal Lobes: Recollection, Familiarity, and Novelty. *Journal of Neurophysiology*, 96(4), 1902-1911. <http://doi.org/10.1152/jn.01029.2005>
- Davidson, P. S. R., Anaki, D., Ciaramelli, E., Cohn, M., Alice, S. N., Murphy, K. J., ... Levine, B. (2010). Does lateral parietal cortex support episodic memory? Evidence from focal lesion patients. *Neuropsychologia*, 46(7), 1743-55. <http://doi.org/10.1016/j.neuropsychologia.2008.01.011.Does>
- Dede, A. J. O., Squire, L. R., & Wixted, J. T. (2013). A novel approach to an old problem: Analysis of systematic errors in two models of recognition memory. *Neuropsychologia*, 52C, 51-56. <http://doi.org/10.1016/j.neuropsychologia.2013.10.012>
- Della Sala, S., Darling, S., & Logie, R. H. (2010). Items on the left are better remembered. *Quarterly Journal of Experimental Psychology*, 63(5), 848-55. <http://doi.org/10.1080/17470211003690672>
- Dennis, N. A., Bowman, C. R., & Vandekar, S. N. (2012). True and phantom recollection: An fMRI investigation of similar and distinct neural correlates and connectivity. *NeuroImage*, 59(3), 2982-2993. <http://doi.org/10.1016/j.neuroimage.2011.09.079>
- Di Russo, F., Aprile, T., Spitoni, G., & Spinelli, D. (2008). Impaired visual processing of contralesional stimuli in neglect patients: A visual-evoked potential study. *Brain*, 131(Pt 3), 842-854. <http://doi.org/10.1093/brain/awm281>
- Driver, J., & Mattingley, J. B. (1998). Parietal neglect and visual awareness. *Nature Neuroscience*, 1, 17-22. Retrieved from http://www.nature.com/neuro/journal/v1/n1/abs/nn0598_17.html
- Duarte, A., Henson, R. N. A., & Graham, K. S. (2011). Stimulus content and the neural correlates of source memory. *Brain Research*, 1373, 110-123. <http://doi.org/10.1016/j.brainres.2010.11.086>
- Duecker, F., Formisano, E., & Sack, A. T. (2013). Hemispheric differences in the voluntary control of spatial attention: Direct evidence for a right-hemispheric dominance within frontal cortex. *Journal of Cognitive Neuroscience*, 25, 1332-1342. <http://doi.org/10.1162/jocn>
- Duecker, F., & Sack, A. T. (2015). The hybrid model of attentional control: New insights into hemispheric asymmetries inferred from TMS research. *Neuropsychologia*, 74, 21-29. <http://doi.org/10.1016/j.neuropsychologia.2014.11.023>
- Eacott, M. J., & Easton, A. (2007). On Familiarity and Recall of Events by Rats. *Hippocampus*, 17, 890-897. <http://doi.org/10.1002/hipo.20325>
- Eichenbaum, H. (2017). Memory: Organization and Control. *Annual Review of Psychology*, 68(1), 19-45. <http://doi.org/10.1146/annurev-psych-010416-044131>
- Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The Medial Temporal Lobe and Recognition Memory. *Annual Review of Neuroscience*, 30, 123-152. <http://doi.org/10.1021/nl061786n.Core-Shell>

- Fink, G. R., Marshall, J. C., Weiss, P. H., Toni, I., & Zilles, K. (2002). Task instructions influence the cognitive strategies involved in line bisection judgements - evidence from modulated neural mechanisms revealed by fMRI. *Neuropsychologia*, 40, 119-30. [http://doi.org/10.1016/S0028-3932\(01\)00087-2](http://doi.org/10.1016/S0028-3932(01)00087-2)
- Freton, M., Lemogne, C., Bergouignan, L., Delaveau, P., Lehericy, S., & Fossati, P. (2014). The eye of the self: Precuneus volume and visual perspective during autobiographical memory retrieval. *Brain Structure and Function*, 219(3), 959-968. <http://doi.org/10.1007/s00429-013-0546-2>
- Friedman, A., Mohr, C., & Brugger, P. (2012). Representational pseudoneglect and reference points both influence geographic location estimates. *Psychonomic Bulletin & Review*, 19(2), 277-284. <http://doi.org/10.3758/s13423-011-0202-x>
- Frithsen, A., & Miller, M. B. (2014). The posterior parietal cortex: Comparing remember/know and source memory tests of recollection and familiarity. *Neuropsychologia*, 61(1). <http://doi.org/10.1016/j.neuropsychologia.2014.06.011>
- Gitelman, D. R., Nobre, A. C., Parrish, T. B., Labar, K. S., Kim, Y., Meyer, J. R., & Mesulam, M. (1999). A large-scale distributed network for covert spatial attention: Further anatomical delineation based on stringent behavioural and cognitive controls. *Brain*, 122, 1093-1106. <http://doi.org/10.1093/brain/122.6.1093>
- Göbel, S. M., Calabria, M., Farnè, A., & Rossetti, Y. (2006). Parietal rTMS distorts the mental number line: simulating "spatial" neglect in healthy subjects. *Neuropsychologia*, 44, 860-8. <http://doi.org/10.1016/j.neuropsychologia.2005.09.007>
- Grefkes, C., & Fink, G. R. (2005). The functional organization of the intraparietal sulcus in humans and monkeys. *Journal of Anatomy*, 207(1), 3-17. <http://doi.org/10.1111/j.1469-7580.2005.00426.x>
- Guise, K. G., & Shapiro, M. L. (2017). Medial Prefrontal Cortex Reduces Memory Interference by Modifying Hippocampal Encoding. *Neuron*, 94(1), 183-192.e8. <http://doi.org/10.1016/j.neuron.2017.03.011>
- Hafting, T., Fyhn, M., Molden, S., Moser, M. B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, 436(7052), 801-806. <http://doi.org/10.1038/nature03721>
- Haramati, S., Soroker, N., Dudai, Y., & Levy, D. A. (2008). The posterior parietal cortex in recognition memory: A neuropsychological study. *Neuropsychologia*, 46(7), 1756-1766. <http://doi.org/10.1016/j.neuropsychologia.2007.11.015>
- Hartley, T., Burgess, N., Lever, C., Cacucci, F., & O'Keefe, J. (2000). Modeling place fields in terms of the cortical inputs to the hippocampus. *Hippocampus*, 10(4), 369-379. [http://doi.org/10.1002/1098-1063\(2000\)10:4<369::AID-HIPO3>3.0.CO;2-0](http://doi.org/10.1002/1098-1063(2000)10:4<369::AID-HIPO3>3.0.CO;2-0)
- Harvey, M., & Rossit, S. (2012). Visuospatial neglect in action. *Neuropsychologia*, 50(6), 1018-28. <http://doi.org/10.1016/j.neuropsychologia.2011.09.030>
- He, B. J., Snyder, A. Z., Vincent, J. L., Epstein, A., Shulman, G. L., & Corbetta, M. (2007). Breakdown of Functional Connectivity in Frontoparietal Networks Underlies Behavioral Deficits in Spatial Neglect. *Neuron*, 53(6), 905-918. <http://doi.org/10.1016/j.neuron.2007.02.013>
- Hebb, D. O. (1949). The Organization of Behavior. *The Organization of Behavior*, 911(1), 335. <http://doi.org/10.2307/1418888>

- Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, 30, 327-330. <http://doi.org/10.1212/WNL.30.3.327>
- Henson, R. N. A., Rugg, M. D., Shallice, T., Josephs, O., & Dolan, R. J. (1999). Recollection and familiarity in recognition memory: an event-related functional magnetic resonance imaging study. *The Journal of Neuroscience*, 19(10), 3962-3972. Retrieved from <http://eutils.ncbi.nlm.nih.gov/entrez/eutils/elink.fcgi?dbfrom=pubmed&id=10234026&retmode=ref&cmd=prlinks%5Cnpapers3://publication/uuid/73A80DE2-9E23-4115-8A1C-F48EBC1563C4>
- Hilgetag, C. C., Theoret, H., & Pascual-leone, A. (2001). Enhanced visual spatial attention ipsilateral to rTMS-induced "virtual lesions" of human parietal cortex. *Nature Neuroscience*, 4, 953-7.
- Hughes, L. E., Bates, T. C., & Aimola Davies, A. (2004). Grasping at sticks: pseudoneglect for perception but not action. *Experimental Brain Research*, 157(3), 397-402. <http://doi.org/10.1007/s00221-004-1958-2>
- Hutchinson, J. B., Uncapher, M. R., & Wagner, A. D. (2009). Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. *Learning & Memory*, (650), 343-356. <http://doi.org/10.1101/lm.919109.16>
- Hutchinson, J. B., Uncapher, M. R., & Wagner, A. D. (2015). Increased functional connectivity between dorsal posterior parietal and ventral occipitotemporal cortex during uncertain memory decisions. *Neurobiology of Learning and Memory*, 117(18), 71-83. <http://doi.org/10.1016/j.nlm.2014.04.015>
- Hutchinson, J. B., Uncapher, M. R., Weiner, K. S., Bressler, D. W., Silver, M. A., Preston, A. R., & Wagner, A. D. (2014). Functional heterogeneity in posterior parietal cortex across attention and episodic memory retrieval. *Cerebral Cortex*, 24(1), 49-66. <http://doi.org/10.1093/cercor/bhs278>
- Jäncke, L. (2007). Neuroanatomy of the Parietal Cortex. In F. Mast & L. Jäncke (Eds.), *Spatial Processing in Navigation, Imagery and Perception* (pp. 1-440). <http://doi.org/10.1007/978-0-387-71978-8>
- Jenson, A., Kirwan, C. B., Hopkins, R. O., Wixted, J. T., & Squire, L. R. (2010). Recognition memory and the hippocampus: A test of the hippocampal contribution to recollection and familiarity. *Learning & Memory*, 17(1), 63-70. <http://doi.org/10.1101/lm.1546110>
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, 38(1), 93-110. [http://doi.org/10.1016/S0028-3932\(99\)00045-7](http://doi.org/10.1016/S0028-3932(99)00045-7)
- Jin, J., & Maren, S. (2015). Prefrontal-Hippocampal Interactions in Memory and Emotion. *Frontiers in Systems Neuroscience*, 9(December), 1-8. <http://doi.org/10.3389/fnsys.2015.00170>
- Kafkas, A., & Montaldi, D. (2012). Familiarity and recollection produce distinct eye movement, pupil and medial temporal lobe responses when memory strength is matched. *Neuropsychologia*, 50(13), 3080-93. <http://doi.org/10.1016/j.neuropsychologia.2012.08.001>
- Kafkas, A., & Montaldi, D. (2014). Two separate, but interacting, neural systems for familiarity and novelty detection: a dual-route mechanism. *Hippocampus*, 24(5), 516-27. <http://doi.org/10.1002/hipo.22241>

- Kinsbourne, M. (1970). The cerebral basis of lateral asymmetries in attention. *Acta Psychologica*, 33, 193-201. Retrieved from <https://www.ncbi.nlm.nih.gov/pubmed/?term=Kinsbourne+M.+The+cerebral+basis+of+lateral+asymmetries+in+attention>.
- Kinsbourne, M. (1977). Hemi-neglect and hemisphere rivalry. *Advances in Neurology*, 18, 41-9.
- Kwok, S. C., & MacAluso, E. (2015). Exogenous features versus prior experiences modulate different subregions of the right IPL during episodic memory retrieval. *Scientific Reports*, 5(April), 1-12. <http://doi.org/10.1038/srep11248>
- Lane, A. R., Ball, K., & Ellison, A. (2015). Dissociating the neural mechanisms of distance and spatial reference frames. *Neuropsychologia*, 74. <http://doi.org/10.1016/j.neuropsychologia.2014.12.019>
- Learmonth, G., Benwell, C. S. Y., Thut, G., & Harvey, M. (2017). Age-related reduction of hemispheric lateralisation for spatial attention: An EEG study. *NeuroImage*, 153, 139-151. <http://doi.org/10.1016/j.neuroimage.2017.03.050>
- Learmonth, G., Gallagher, A., Gibson, J., Thut, G., & Harvey, M. (2015). Intra- and inter-task reliability of spatial attention measures in pseudoneglect. *PLoS ONE*, 10(9), 1-23. <http://doi.org/10.1371/journal.pone.0138379>
- Leech, R., & Sharp, D. J. (2014). The role of the posterior cingulate cortex in cognition and disease. *Brain*, 137(1), 12-32. <http://doi.org/10.1093/brain/awt162>
- Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). Boundary Vector Cells in the Subiculum of the Hippocampal Formation. *Journal of Neuroscience*, 29(31), 9771-9777. <http://doi.org/10.1523/JNEUROSCI.1319-09.2009>
- Loftus, A. E., & Nicholls, M. E. R. (2012). Testing the activation-orientation account of spatial attentional asymmetries using transcranial direct current stimulation. *Neuropsychologia*, 50(11), 2573-6. <http://doi.org/10.1016/j.neuropsychologia.2012.07.003>
- Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, 44(6), 977-981. <http://doi.org/10.1016/j.neuropsychologia.2005.09.003>
- Longo, M. R., & Lourenco, S. F. (2007). Spatial attention and the mental number line: Evidence for characteristic biases and compression. *Neuropsychologia*, 45(7), 1400-1407. <http://doi.org/10.1016/j.neuropsychologia.2006.11.002>
- Longo, M. R., Trippier, S., Vagnoni, E., & Lourenco, S. F. (2015). Right hemisphere control of visuospatial attention in near space. *Neuropsychologia*, 70, 350-357. <http://doi.org/10.1016/j.neuropsychologia.2014.10.035>
- Lourenco, S. F., & Longo, M. R. (2009). The plasticity of near space: Evidence for contraction. *Cognition*, 112(3), 451-456. <http://doi.org/10.1016/j.cognition.2009.05.011>
- Mandler, G. (1980). UC San Diego UC San Diego Previously Published Works Title Recognizing: The judgment of previous occurrence Recognizing: The Judgment of Previous Occurrence. *Journal Psychological Review Psychological Review*, 87(3), 252-271. Retrieved from <https://cloudfront.escholarship.org/dist/prd/content/qt58b2c2fc/qt58b2c2fc.pdf>
- Marshall, T. R., Bergmann, T. O., & Jensen, O. (2015). Frontoparietal Structural Connectivity Mediates the Top-Down Control of Neuronal Synchronization Associated with Selective Attention. *PLoS Biology*, 13(10), 1-17. <http://doi.org/10.1371/journal.pbio.1002272>

- Mayes, A. R., Montaldi, D., & Migo, E. (2007). Associative memory and the medial temporal lobes. *Trends in Cognitive Sciences*, 11, 126-135. <http://doi.org/10.1016/j.tics.2006.12.003>
- McCourt, M. E., Freeman, P., Tahmahkera-Stevens, C., & Chaussee, M. (2001). The influence of unimanual response on pseudoneglect magnitude. *Brain and Cognition*, 45(1), 52-63. <http://doi.org/10.1006/brcg.2000.1255>
- McCourt, M. E., & Garlinghouse, M. (2000). Asymmetries of visuospatial attention are modulated by viewing distance and visual field elevation: Pseudoneglect in peripersonal and extrapersonal space. *Cortex*, 36(5), 715-731. [http://doi.org/10.1016/S0010-9452\(08\)70548-3](http://doi.org/10.1016/S0010-9452(08)70548-3)
- McCourt, M. E., & Jewell, G. (1999). Visuospatial attention in line bisection: Stimulus modulation of pseudoneglect. *Neuropsychologia*, 37, 843-855. Retrieved from <http://www.sciencedirect.com/science/article/pii/S0028393298001407>
- McGeorge, P., Beschin, N., Colnaghi, A., Rusconi, M. L., & Della Sala, S. (2007). A lateralized bias in mental imagery: evidence for representational pseudoneglect. *Neuroscience Letters*, 421(3), 259-63. <http://doi.org/10.1016/j.neulet.2007.05.050>
- Mesulam, M. (1981). A cortical network for directed attention and unilateral neglect. *Ann Neurol*, 10, 309-25. <http://doi.org/10.1002/ana.410100402>
- Mesulam, M. (1999). Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Phil. Trans R. Soc. Lond. B*, 354, 1325-46. <http://doi.org/10.1098/rstb.1999.1003>
- Montaldi, D., & Mayes, A. R. (2010). The role of recollection and familiarity in the functional differentiation of the medial temporal lobes. *Hippocampus*, 20, 1291-1314. <http://doi.org/10.1002/hipo.20853>
- Montaldi, D., Spencer, T. J., Roberts, N., & Mayes, A. R. (2006). The neural system that mediates familiarity memory. *Hippocampus*, 16(5), 504-520. <http://doi.org/10.1002/hipo.20178>
- Newman, D. P., Lockley, S. W., Loughnane, G. M., Martins, A. C. P., Abe, R., Zoratti, M. T. R., ... Bellgrove, M. A. (2016). Ocular exposure to blue-enriched light has an asymmetric influence on neural activity and spatial attention. *Scientific Reports*, 6(June), 1-10. <http://doi.org/10.1038/srep27754>
- Newman, D. P., O'Connell, R. G., & Bellgrove, M. A. (2013). Linking time-on-task, spatial bias and hemispheric activation asymmetry: a neural correlate of rightward attention drift. *Neuropsychologia*, 51(7), 1215-23. <http://doi.org/10.1016/j.neuropsychologia.2013.03.027>
- Nicholls, M. E. R., Hobson, A., Petty, J., Churches, O., & Thomas, N. A. (2017). The effect of cerebral asymmetries and eye scanning on pseudoneglect for a visual search task. *Brain and Cognition*, 111, 134-143. <http://doi.org/10.1016/j.bandc.2016.11.006>
- Nicholls, M. E. R., & Roberts, G. R. (2002). Can free-viewing perceptual asymmetries be explained by scanning, pre-motor or attentional biases? *Cortex*, 38, 113-136. [http://doi.org/10.1016/S0010-9452\(08\)70645-2](http://doi.org/10.1016/S0010-9452(08)70645-2)
- Nicholls, M. E. R., Thomas, N. A., Loetscher, T., Wignall, S., Yates, M. J., Forte, J. D., & Spence, C. J. (2012). The relationship between vertical stimulation and horizontal attentional asymmetries. *Quarterly Journal of Experimental Psychology*, 65(12), 2384-2396. <http://doi.org/10.1080/17470218.2012.688979>

- Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: a complementary-learning-systems approach. *Psychol Rev*, 110(4), 611-646. <http://doi.org/10.1037/0033-295X.110.4.611>
- O'Keefe, J., Burgess, N., Donnett, J. G., Jeffery, K. J., & Maguire, E. A. (1998). Place cells, navigational accuracy, and the human hippocampus. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 353(1373), 1333-1340. <http://doi.org/10.1098/rstb.1998.0287>
- Orban, G. A. (2016). Functional definitions of parietal areas in human and non-human primates. *Proceedings of the Royal Society B: Biological Sciences*, 283(1828), 20160118. <http://doi.org/10.1098/rspb.2016.0118>
- Parlatini, V., Radua, J., Dell'Acqua, F., Leslie, A., Simmons, A., Murphy, D. G. M., ... Thiebaut de Schotten, M. (2017). Functional segregation and integration within fronto-parietal networks. *NeuroImage*, 146(January 2016), 367-375. <http://doi.org/10.1016/j.neuroimage.2016.08.031>
- Petit, P., Noonan, M. A. P., Bridge, H., O'Reilly, J. X., & O'Shea, J. (2015). Testing the inter-hemispheric competition account of visual extinction with combined TMS/fMRI. *Neuropsychologia*, 74, 63-73. <http://doi.org/10.1016/j.neuropsychologia.2015.04.021>
- Ragland, J. D., Valdez, J. N., Loughhead, J., Gur, R. C., & Gur, R. E. (2006). Functional magnetic resonance imaging of internal source monitoring in schizophrenia: Recognition with and without recollection. *Schizophrenia Research*, 87(1-3), 160-171. <http://doi.org/10.1016/j.schres.2006.05.008>
- Ramsey, L. E., Siegel, J. S., Baldassarre, A., Metcalf, N. V., Zinn, K., Shulman, G. L., & Corbetta, M. (2016). Normalization of network connectivity in hemispatial neglect recovery. *Annals of Neurology*, 80(1), 127-141. <http://doi.org/10.1002/ana.24690>
- Reuter-Lorenz, P. A., Kinsbourne, M., & Moscovitch, M. (1990). Hemispheric control of spatial attention. *Brain and Cognition*, 12, 240-6. [http://doi.org/10.1016/0278-2626\(90\)90018-J](http://doi.org/10.1016/0278-2626(90)90018-J)
- Robertson, I. H., Mattingley, J. B., Rorden, C., & Driver, J. (1998). Phasic alerting of neglect patients overcomes their spatial deficit in visual awareness. *Nature*, 395(6698), 169-172. <http://doi.org/10.1038/25993>
- Robertson, I. H., Tegnér, R., Tham, K., Lo, A., & Nimmo-Smith, I. (1995). Sustained Attention Training for Unilateral Neglect: Theoretical and Rehabilitation Implications. *Journal of Clinical and Experimental Neuropsychology*, 17(3), 416-430. <http://doi.org/10.1080/01688639508405133>
- Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences*, 11(6), 251-257. <http://doi.org/10.1016/j.tics.2007.04.004>
- Rusconi, E., Dervinis, M., Verbruggen, F., & Chambers, C. D. (2013). Critical time course of right frontoparietal involvement in mental number space. *Journal of Cognitive Neuroscience*, 25(3), 465-83. http://doi.org/10.1162/jocn_a_00330
- Schmahmann, J. D., Pandya, D. N., Wang, R., Dai, G., D'Arceuil, H. E., De Crespigny, A. J., & Wedeen, V. J. (2007). Association fibre pathways of the brain: Parallel observations from diffusion spectrum imaging and autoradiography. *Brain*, 130(3), 630-653. <http://doi.org/10.1093/brain/awl359>
- Schmitz, R., & Peigneux, P. (2011). Age-related changes in visual pseudoneglect. *Brain and Cognition*, 76(3), 382-389. <http://doi.org/10.1016/j.bandc.2011.04.002>

- Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, 20(1), 11-21. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/13406589>
- Seghier, M. L. (2013). The angular gyrus: Multiple functions and multiple subdivisions. *Neuroscientist*, 19(1), 43-61. <http://doi.org/10.1177/1073858412440596>
- Sestieri, C., Capotosto, P., Tosoni, A., Luca Romani, G., & Corbetta, M. (2013). Interference with episodic memory retrieval following transcranial stimulation of the inferior but not the superior parietal lobule. *Neuropsychologia*, 51(5), 900-906. <http://doi.org/10.1016/j.neuropsychologia.2013.01.023>
- Sestieri, C., Corbetta, M., Romani, G. L., & Shulman, G. L. (2011). Episodic memory retrieval, parietal cortex, and the default mode network: functional and topographic analyses. *The Journal of Neuroscience*, 31(12), 4407-20. <http://doi.org/10.1523/JNEUROSCI.3335-10.2011>
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2010). Attention to Memory and the Environment: Functional Specialization and Dynamic Competition in Human Posterior Parietal Cortex. *Journal of Neuroscience*, 30(25), 8445-8456. <http://doi.org/10.1523/JNEUROSCI.4719-09.2010>
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2017). The contribution of the human posterior parietal cortex to episodic memory. *Nature Reviews Neuroscience*, 18(3), 183-192. <http://doi.org/10.1038/nrn.2017.6>
- Sharot, T., Delgado, M. R., & Phelps, E. A. (2004). How emotion enhances the feeling of remembering. *Nature Neuroscience*, 7(12), 1376-1380. <http://doi.org/10.1038/nn1353>
- Shimamura, A. P. (2011). Episodic retrieval and the cortical binding of relational activity. *Cognitive, Affective and Behavioral Neuroscience*, 11(3), 277-291. <http://doi.org/10.3758/s13415-011-0031-4>
- Shimamura, A. P., Jurica, P. J., Mangels, J. a., Gershberg, F. B., & Knight, R. T. (1995). Susceptibility to Memory Interference Effects following Frontal Lobe Damage: Findings from Tests of Paired-Associate Learning. *Journal of Cognitive Neuroscience*, 7(2), 144-152. <http://doi.org/10.1162/jocn.1995.7.2.144>
- Shulman, G. L., Astafiev, S. V., Franke, D., Pope, D. L. W., Abraham, Z., Mcavoy, M. P., & Corbetta, M. (2009). Interaction of stimulus-driven reorienting and expectation in ventral and dorsal fronto-parietal and basal ganglia-cortical networks. *Journal of Neuroscience*, 29(14), 4392-4407. <http://doi.org/10.1523/JNEUROSCI.5609-08.2009>.Interaction
- Shulman, G. L., Pope, D. L. W., Astafiev, S. V., Mcavoy, M. P., Snyder, Z., & Corbetta, M. (2010). Right hemisphere dominance during spatial selective attention and target detection occurs outside the dorsal fronto-parietal network. *Journal of Neuroscience*, 30(10), 3640-3651. <http://doi.org/10.1523/JNEUROSCI.4085-09.2010>.Right
- Silvanto, J., Lavie, N., & Walsh, V. (2006). Stimulation of the human frontal eye fields modulates sensitivity of extrastriate visual cortex. *Journal of Neurophysiology*, 96, 941-5. <http://doi.org/10.1152/jn.00015.2006>
- Silver, M. A., & Kastner, S. (2009). Topographic maps in human frontal and parietal cortex. *Trends in Cognitive Sciences*, 13(11), 488-495. <http://doi.org/10.1016/j.tics.2009.08.005>
- Simons, J. S., & Mayes, A. R. (2008). What is the parietal lobe contribution to human memory? *Neuropsychologia*, 46(7), 1739-42. <http://doi.org/10.1016/j.neuropsychologia.2008.05.001>

- Simons, J. S., Peers, P. V., Hwang, D. Y., Ally, B. A., Fletcher, P. C., & Budson, A. E. (2008). Is the parietal lobe necessary for recollection in humans? *Neuropsychologia*, 46(4), 1185-1191. <http://doi.org/10.1016/j.neuropsychologia.2007.07.024>
- Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2010). Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex*, 20(2), 479-85. <http://doi.org/10.1093/cercor/bhp116>
- Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. *Nature Reviews Neuroscience*, 4(8), 637-648. <http://doi.org/10.1038/nrn1178>
- Skinner, E. I., & Fernandes, M. A. (2007). Neural correlates of recollection and familiarity: a review of neuroimaging and patient data. *Neuropsychologia*, 45(10), 2163-79. <http://doi.org/10.1016/j.neuropsychologia.2007.03.007>
- Spinelli, D., Guariglia, C., Massironi, M., Pizzamiglio, L., & Zoccolotti, P. (1990). Contrast sensitivity and low spatial frequency discrimination in hemi-neglect patients. *Neuropsychologia*, 28, 727-32. Retrieved from <http://www.sciencedirect.com/science/article/pii/002839329090127A>
- Squire, L. R. (2004). Memory systems of the brain: A brief history and current perspective. *Neurobiology of Learning and Memory*, 82(3), 171-177. <http://doi.org/10.1016/j.nlm.2004.06.005>
- Squire, L. R., Stark, C. E. L., & Clark, R. E. (2004). The medial temporal lobe. *Annual Review of Neuroscience*, 27(1), 279-306. <http://doi.org/10.1146/annurev.neuro.27.070203.144130>
- Swisher, J. D., Halko, M. A., Merabet, L. B., McMains, S. A., & Somers, D. C. (2007). Visual Topography of Human Intraparietal Sulcus. *Journal of Neuroscience*, 27(20), 5326-5337. <http://doi.org/10.1523/JNEUROSCI.0991-07.2007>
- Szczepanski, S. M., & Kastner, S. (2013). Shifting attentional priorities: Control of spatial attention through hemispheric competition. *Journal of Neuroscience*, 33(12), 5411-21. <http://doi.org/10.1523/JNEUROSCI.4089-12.2013>
- Szczepanski, S. M., & Knight, R. T. (2014). Insights into Human Behavior from Lesions to the Prefrontal Cortex. *Neuron*, 83(5), 1002-1018. <http://doi.org/10.1016/j.neuron.2014.08.011>
- Szczepanski, S. M., Konen, C. S., & Kastner, S. (2010). Mechanisms of spatial attention control in frontal and parietal cortex. *Journal of Neuroscience*, 30, 148-60. <http://doi.org/10.1523/JNEUROSCI.3862-09.2010>
- Thiebaut de Schotten, M., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience*, 14, 1245-6. <http://doi.org/10.1038/nn.2905>
- Thiebaut de Schotten, M., Urbanski, M., Duffau, H., Volle, E., Lévy, R., Dubois, B., & Bartolomeo, P. (2005). Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans. *Science*, pp. 2226-8. <http://doi.org/10.1126/science.1116251>
- Thomas, N. A., Castine, B. R., Loetscher, T., & Nicholls, M. E. R. (2015). Upper visual field distractors preferentially bias attention to the left. *Cortex*, 64, 179-193. <http://doi.org/10.1016/j.cortex.2014.10.018>
- Thomas, N. A., Loetscher, T., & Nicholls, M. E. R. (2014). Asymmetries in attention as revealed by fixations and saccades. *Experimental Brain Research*, 232, 3253-67. <http://doi.org/10.1007/s00221-014-4015-9>

- Todd, T. P., & Bucci, D. J. (2015). Retrosplenial Cortex and Long-Term Memory: Molecules to Behavior. *Neural Plasticity*, 2015. <http://doi.org/10.1155/2015/414173>
- Tulving, E. (1972). Episodic and semantic memory. In E. Tulving & W. Donaldson (Eds.), *Organisation of Memory* (pp. 381-402). New York: Academic.
- Van Hoesen, G. W. (1995). Anatomy of the medial temporal lobe. *Magnetic Resonance Imaging*, 13(8), 1047-1055. [http://doi.org/10.1016/0730-725X\(95\)02012-1](http://doi.org/10.1016/0730-725X(95)02012-1)
- Verdon, V., Schwartz, S., Lovblad, K. O., Hauert, C. A., & Vuilleumier, P. (2010). Neuroanatomy of hemispatial neglect and its functional components: A study using voxel-based lesion-symptom mapping. *Brain*, 133(3), 880-894. <http://doi.org/10.1093/brain/awp305>
- Veronelli, L., Vallar, G., Marinelli, C. V., Primativo, S., & Arduino, L. S. (2014). Line and word bisection in right-brain-damaged patients with left spatial neglect. *Experimental Brain Research*, 232(1), 133-146. <http://doi.org/10.1007/s00221-013-3726-7>
- Vilberg, K. L., & Rugg, M. D. (2007). Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia*, 45(10), 2216-2225. <http://doi.org/10.1016/j.neuropsychologia.2007.02.027>
- Vilberg, K. L., & Rugg, M. D. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*, 46(7), 1787-1799. <http://doi.org/10.1016/j.neuropsychologia.2008.01.004>
- von Economo, C. F., & Koskinas, G. N. (1925). *Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen*. Berlin: Springer.
- Voyer, D., Voyer, S. D., & Tramonte, L. (2012). Free-viewing laterality tasks: A multilevel meta-analysis. *Neuropsychology*. Voyer, Daniel: Department of Psychology, University of New Brunswick, P.O. Box 4400, Fredericton, NB, Canada, E3B 5A3, voyer@unb.ca: American Psychological Association. <http://doi.org/10.1037/a0028631>
- Vuilleumier, P., Schwartz, S., Verdon, V., Maravita, A., Hutton, C., Husain, M., & Driver, J. (2010). Attention-dependent functional abnormality in retinotopic visual cortex for patients with parietal lesions and spatial neglect. *Current Biology*, 18, 1525-9. <http://doi.org/10.1016/j.cub.2008.08.072>.Attention-dependent
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, 9(9), 445-53. <http://doi.org/10.1016/j.tics.2005.07.001>
- Weis, S., Klaver, P., Reul, J., Elger, C. E., & Fernández, G. (2004). Temporal and Cerebellar Brain Regions that Support both Declarative Memory Formation and Retrieval. *Cerebral Cortex*, 14(3), 256-267. <http://doi.org/10.1093/cercor/bhg125>
- Wheeler, M. E., & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *NeuroImage*, 21(4), 1337-1349. <http://doi.org/10.1016/j.neuroimage.2003.11.001>
- Wild, H. M., Heckemann, R. A., Studholme, C., & Hammers, A. (2017). Gyri of the human parietal lobe: Volumes, spatial extents, automatic labelling, and probabilistic atlases. *PLoS ONE*, 12(8), 1-28. <http://doi.org/10.1371/journal.pone.0180866>
- Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, 114(1), 152-176. <http://doi.org/10.1037/0033-295X.114.1.152>

- Yang, N. Y. H., Zhou, D., Chung, R. C. K., Li-Tsang, C. W. P., & Fong, K. N. K. (2013). Rehabilitation Interventions for Unilateral Neglect after Stroke: A Systematic Review from 1997 through 2012. *Frontiers in Human Neuroscience*, 7, 1-11. <http://doi.org/10.3389/fnhum.2013.00187>
- Yazar, Y., Bergström, Z. M., & Simons, J. S. (2014). Continuous theta burst stimulation of angular gyrus reduces subjective recollection. *PloS One*, 9(10), 1-7. <http://doi.org/10.1371/journal.pone.0110414>
- Yazar, Y., Bergström, Z. M., & Simons, J. S. (2017). Reduced multimodal integration of memory features following continuous theta burst stimulation of angular gyrus. *Brain Stimulation*, 10(3), 624-629. <http://doi.org/10.1016/j.brs.2017.02.011>
- Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the Brain Regions Involved in Recollection and Familiarity in Recognition Memory. *The Journal of Neuroscience*, 25(11), 3002-3008. <http://doi.org/10.1523/JNEUROSCI.5295-04.2005>
- Zago, L., Petit, L., Jobard, G., Hay, J., Mazoyer, B., Tzourio-Mazoyer, N., ... Mellet, E. (2017). Pseudoneglect in line bisection judgement is associated with a modulation of right hemispheric spatial attention dominance in right-handers. *Neuropsychologia*, 94(November 2016), 75-83. <http://doi.org/10.1016/j.neuropsychologia.2016.11.024>

Chapter 2: Attention Allocation Systems Selectively Specialised for Spatial or Semantic Processing: A Reversed Pseudoneglect Effect

Abstract

Healthy individuals display systematic inaccuracies when allocating attention to perceptual space. Under many conditions, individuals dedicate more attention to the left side of perceptual space than the right. This is the pseudoneglect effect, and it is driven by the optimised spatial attention processing of the right hemisphere's frontoparietal attention network. Across three experiments, we present evidence that reshapes our fundamental understanding of this neural mechanism. We describe a previously unrecognised reliable attention bias to the right side of perceptual space that is associated with the semantic processing of object recognition. Using an object bisection task, we revealed a significant rightward bias distinct from the leftward bias elicited by the traditional line bisection task. In Experiment 2.2, we found that the extent of rightward bias was associated with bisection of object-like abstract shapes with the greatest challenge to object identification. This result shows that the rightward attention bias is a product of semantic processing lateralised to the left hemisphere. The novel implicit primed attention (IPA) task in Experiment 2.3 demonstrated that engagement of the left hemisphere's FPA network with semantics can prime covert attention to more readily detect right visual field targets. These experiments change our understanding of network specialisation in spatial attention, and we provide novel and crucial insight into the systems supporting intricate and complex attention allocation. Along with revealing a spatial attention system engaged by semantic processing, we provide the impetus for a shift in investigative approach towards studying attention in ways that increasingly reflect our complex environments.

Introduction

The frontoparietal attention (FPA) networks are specialised networks governing the distribution of attention to different areas of perceptual space (Mesulam, 1981). For many years, the right hemisphere FPA network has been considered dominant and optimised for this function (Heilman & Van Den Abell, 1980; Zuanazzi & Cattaneo, 2017). The ‘pseudoneglect’ effect describes the tendency of healthy individuals to allocate more attention to the left side of perceptual space than the right. This behavioural effect has been putatively characterised as the behavioural manifestation of right FPA network optimisation (Benwell, Harvey, et al., 2014; Jewell & McCourt, 2000; Zago et al., 2017).

The line bisection test (Thiebaut de Schotten et al., 2005; Varnava & Halligan, 2007), the landmark task (Benwell, Harvey, et al., 2014; Benwell, Thut, et al., 2014) and greyscale task (Nicholls & Roberts, 2002; Thomas et al., 2014), paradigms used to demonstrate the effect, all require a subject to produce a stimulus centric comparison of the left and right sides of an image. For example, the line bisection task requires the subject to use a straight vertical line to perfectly bisect a straight horizontal line. Upon inspection of a centrally presented line, the horizontal extremities of the stimulus fall into the visual field that is processed by the contralateral hemisphere. Interestingly, healthy individuals show a tendency to allocate more attention towards the left side of visual space on these tasks (Benwell, Thut, et al., 2014; Nicholls & Roberts, 2002; Thiebaut de Schotten et al., 2005; Thomas et al., 2014). Most individuals will consistently place the vertical line to the left of the actual centre of the horizontal line (see *Fig 2.1B* for example). A traditional mechanistic account (Heilman & Van Den Abell, 1980) states that more efficient visuospatial processing of the left visual field by the right hemisphere’s FPA network, increases the perceived size of the left side of the target. This size overestimation of the target of attention, and/or a size underestimation of the non-attended section of the line, results in a shift in the perceived centre away from the midline to the left side (for a review of the pseudoneglect effect with the line bisection task, see (Jewell & McCourt, 2000)).

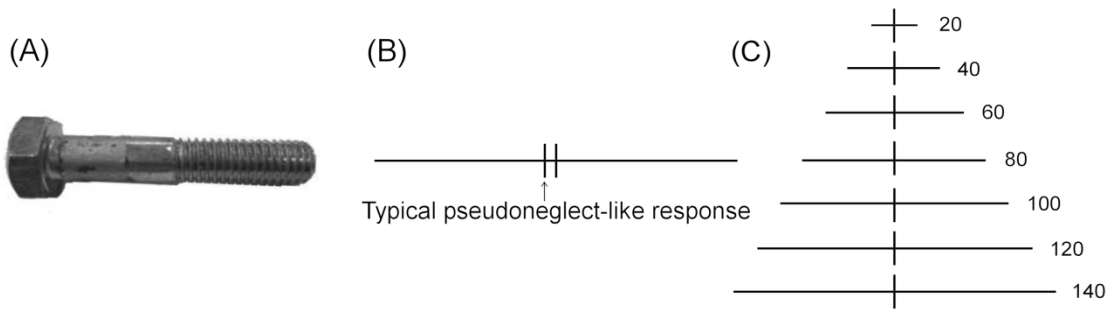


Figure 2.1: **A)** An example object employed in the object bisection task. **B)** A typical pseudoneglect-like response illustrated on a 160 pixel line. **C)** The eight line length types (20, 40, 60, 80, 100, 120, 140, and 160) assessed in the line bisection task with accurate central bisections.

In revealing pseudoneglect, the line bisection, landmark, and greyscale tasks have helped to characterise the functional architecture of the FPA network in healthy individuals (Benwell, Harvey, et al., 2014; Learmonth et al., 2017; Szczepanski & Kastner, 2013; Thiebaut de Schotten et al., 2011) and establish the factors affecting allocation of attention (Jewell & McCourt, 2000; Learmonth et al., 2017). For example, variations in line length have been consistently shown to affect the extent of the bias on the line bisection task. Bisections of small lines is associated with generally more central/accurate judgements than longer lines, which most often elicit the typical leftward ‘pseudoneglect’ response (Benwell, Harvey, et al., 2014; Benwell, Thut, Learmonth, & Harvey, 2013; McCourt & Jewell, 1999).

The line bisection and landmark tasks are used to provide an account of the processing of attention allocation that is unbiased by other cognitive processing (Jewell & McCourt, 2000). However, substantial individual variability in lateralisation bias is common and understanding how asymmetries are manifested with more complex and ecologically natural targets is poorly understood. Allocating attention to judge the length of lines or the darkness of the shading in greyscale bars is very rarely required outside of a controlled scientific testing environment. Understanding how the processing of attention allocation occurs in more ecologically realistic environments would enable better characterisation of naturalistic attention allocation biases. Visual space in daily life almost always contains identifiable information e.g. objects. The identity of objects will, in many circumstances, engage the processes dedicated to item identification, or recognition.

As part of the ventral attention network, activity in the inferior parietal cortex (IPL) drives

engagement of the spatially-specific dorsal attention network (e.g. the intraparietal sulcus contains topographic maps of visual space) (Corbetta & Shulman, 2002, 2011). As a result, the relative activity of each FPA network is closely linked to hemispheric lateralisation of IPL function. Greater attention is attributed to the hemifield that is contralateral to the hemisphere with the most active FPA network and as a result, the locus of attention allocation can, under certain conditions indirectly reflect the lateralisation of the IPL.

Processing within the IPL has been closely linked with semantic judgements (Seghier, 2013; Seghier, Fagan, & Price, 2010) and the potential for interaction between semantic processing and systems that govern the allocation of attention has been suggested but not effectively measured (Lee et al., 2004; Turriziani et al., 2009). Lee et al., (Lee et al., 2004) observed that single, straight lines made up of unfamiliar letters (e.g. $\epsilon \text{L} \text{B} \text{Z} \text{B} \text{B} \text{L} \text{B} \text{B} \text{C} \text{C} \text{B} \text{O} \text{B} \text{r} \text{B} \text{A} \text{B} \text{A}$) or multiple non-letter characters, such as a star (e.g. $\blacktriangle \spadesuit \blacklozenge \star \clubsuit \blacktriangle \# \blacklozenge \star \spadesuit \blacklozenge \blacktriangle \blacklozenge$) produced more central bisections than the traditional solid line bisection task. This suggests that the pseudoneglect effect may be disturbed or modulated by more complex information. Furthermore, it implies that the presence of semantically interesting features within objects may induce interaction between the language processing conducted by specialised regions in the left hemisphere (Josse & Tzourio-Mazoyer, 2004; Lee et al., 2004) and the left hemisphere FPA network. As a result, semantically-driven activity of the FPA network of the left hemisphere has the potential to induce rightward biased bisection errors for objects but not lines.

Another investigation that utilised more complex and ecologically realistic stimuli focused on representational space and semantic concepts (Turriziani et al., 2009). Individuals were asked to make judgements based on the degree of semantic difference between a centrally presented image and images presented in the left and right hemifields. In this study, errors primarily originated from overestimation of semantic difference in the right hemifield (Turriziani et al., 2009). However, a within-subjects contrast with non-semantic spatial judgements was not performed. This makes it difficult to assess the mechanistic distinction between these findings and previously observed pseudoneglect effects in attention. It is also unclear from this study whether semantics can affect perceptual attention allocation, or if the findings of Turriziani et al. (2009) only reflect a bias in internal conceptual judgements.

Development of a paradigm without an intrinsic directional arrangement (e.g. European languages read left to right), improved ecological validity, and comparability with traditional

attention allocation tasks is critical to developing a better understanding of the intricacies of spatial attention allocation. To the authors' knowledge, no study has assessed the effect of object processing on a task assessing lateralisation bias in the allocation of attention until now. We utilised a variant of the traditional line bisection task in which participants moved a vertical line in an attempt to centrally bisect an object (*Fig 2.1A*). The same individuals also performed a traditional line bisection task. Bisections of lines of 8 different lengths were made to compare the well-established line length effect with object bisection data.

In order to better assess the impact of semantic processing on attention allocation, Experiment 2.2 recruited a separate group of participants to complete an abstract shape bisection task. The object-like abstract shapes that were employed varied in their interpretability (*Supplementary Materials 1*) and the same computerised bisection task was adapted to assess errors in their bisection. This approach removed the presence of features that automatically enable object recognition and modulated the engagement of semantic processing (Josse & Tzourio-Mazoyer, 2004).

Materials and Methods - Experiments 2.1 and 2.2

Materials

The experimental session took place in a dedicated testing room at the University of Manchester. All visual tasks were completed on a desktop computer with a 17 inch monitor. Participants sat centrally in front of a desk. Participant's eyes were approximately 72cm from the screen but head position was not fixed. A standard QWERTY keyboard was used for all visual tasks and all responses were made on the number pad.

Procedure

Participants were instructed to move a peripherally presented vertical line (162mm/ $\sim 12.84^\circ$) to bisect the target stimulus as close to its centre as possible. On the number pad of the keyboard, the numbers 4 and 6 moved the vertical line, left and right respectively, across the screen 4.5mm ($\sim 0.36^\circ$) per key press. Numbers 1 and 3 moved the vertical line, left and right respectively, 0.45mm ($\sim 0.036^\circ$) at a time. In order to minimise motor demands, participants were encouraged to press and hold the keys to move the line smoothly. The original position on each side varied randomly within 20mm ($\sim 1.60^\circ$). In addition, the starting laterality of initial line presentation (left or right) was counterbalanced. All target stimuli were presented centrally onscreen. No time limit was set; instead participants were instructed to be as accurate as possible and to move on to the next example as soon as they believed the bisection to be accurate. On average, subjects required 5-10 seconds to perform the bisection of each stimulus. In order to minimise task-switching effects, participants completed the line and object bisection tasks in separate blocks. Block order was counterbalanced across the subjects in Experiment 2.1.

Experiment 2.1 - Object and Line Bisection Tasks

Participants

A total of 26 (1 male, 18-35 years, mean = 19.73) participants with normal or corrected-to-normal vision, and no history of neurological disorder completed the object and line bisection variants of the task. Sample size was based on that of similar investigations (Benwell, Harvey, et al., 2014; Benwell, Thut, et al., 2013). All participants read the participant information sheet and provided written informed consent at the start of the experimental session. All procedures

were approved by the University of Manchester Research Ethics Committee.

Images

A total of 144 images were presented in the present study. Straight black horizontal lines (72) measuring a width of 9mm (approximately (approximation is due small variability in participant seating posture) 0.72° visual angle), 18mm ($\sim 1.43^\circ$), 27mm ($\sim 2.15^\circ$), 36mm ($\sim 2.86^\circ$), 45mm ($\sim 3.58^\circ$), 54mm ($\sim 4.30^\circ$), 63mm ($\sim 5.01^\circ$), and 72mm ($\sim 5.73^\circ$) were presented in the line bisection task. Greyscale images of everyday objects (72) (Digital greyscale photographs of everyday objects developed by Migo, Montaldi, & Mayes, 2013) were presented in this experiment. All object images measured 76mm ($\sim 6.042^\circ$) from left to right. Vertical image size varied between 9mm ($\sim 0.72^\circ$) and 122mm ($\sim 10^\circ$). Participants also bisected the mirror image of all objects to control for the inherent horizontal asymmetry of many objects. Stimuli were presented and responses recorded through E-Prime (Psychology Software Tools, Inc.).

Experiment 2.2 - Abstract Shape Bisection Tasks

Participants

A further 33 (5 male, 18-22, mean = 19.58) participants with normal or corrected-to-normal vision and no history of neurological disorder completed the bisections of abstract shapes. We expected that the scope for individuals to interpret the shapes differently may increase the noise in the data resulting from this experiment compared to experiment 2.1. The increase in the sample size reflects an attempt to counteract this potential increase. All participants read the participant information sheet and provided written, informed consent at the start of the experimental session. All procedures were approved by the University of Manchester Research Ethics Committee.

Images

Abstract shapes (72) were developed by using the object images developed by Migo et al., (2013) as a template. The object images were filled completely grey (RGB = 102) to remove all internal image features. Edges that clearly revealed the original identity of the shape were then removed by the addition of a small filled grey rectangle. This procedure resulted in a set of stimuli that were not easily recognisable but retained most of the spatial characteristics of the original image (Fig 2.2). The ease/difficulty with which one could interpret the object identity of an

abstract shape was assessed in a separate group of participants. Subjects in this shape interpretation rating experiment were shown all object-like abstract shapes and asked to provide a rating of how easy/difficult it was to interpret the object identity of the image. The procedure and distribution of results is presented in Supplementary Materials 1. As in Experiment 2.1, the mirror image of all abstract shapes was also presented in Experiment 2.2 to control for the inherent horizontally asymmetrical features of the shape.

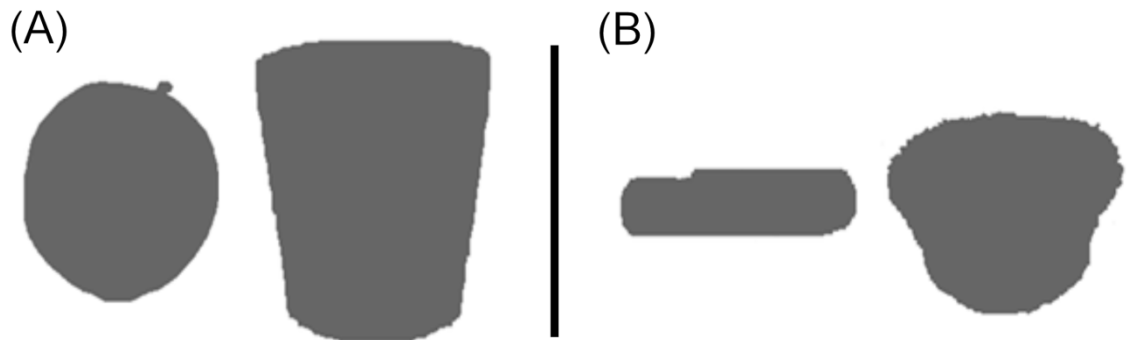


Figure 2.2: Four examples of shapes employed in the abstract shape bisection task. **A)** Shapes were rated as ‘2 - challenging’ to interpret (on a 1 (easy) - 5 (impossible) scale of difficulty) during the standardisation procedure. **B)** Shapes rated as ‘4 - very difficult’ to interpret during the standardisation procedure.

Results

Experiment 2.1 - Object and Line Bisection

Data on the object and line bisection tasks were collected for 26 participants (Fig 2.3). A one-way, repeated measure ANOVA assessed the difference between average subject bisection errors to the eight line lengths (9mm, 18mm, 27mm, 36mm, 45mm, 54mm, 63mm, 72mm) assessed in the line bisection task. There was no main effect of line length ($F(2.87, 71.76) = 2.15, p = 0.104$ (sphericity not assumed), $\eta_p^2 = 0.079$). A one-sample t -test found that the average leftward bisection errors observed in our sample on the line bisection task (collapsed across all line lengths; Mean = -0.126mm^2 , SD = 0.59mm^2 , CI = $[-0.37 - 0.10\text{mm}^2]$) were not significantly different from zero ($t(25) = 1.14, p = 0.264, d = 0.215$). We observed a tendency for lines of increasing length to correlate with greater leftward bisection errors that did not reach statistical significance ($r = -0.121, p = 0.081$). This tendency highlights that the absence of a significant bias in line bisection here is a function of our assessment of small as well as long lines. The importance of this factor is explored in the discussion.

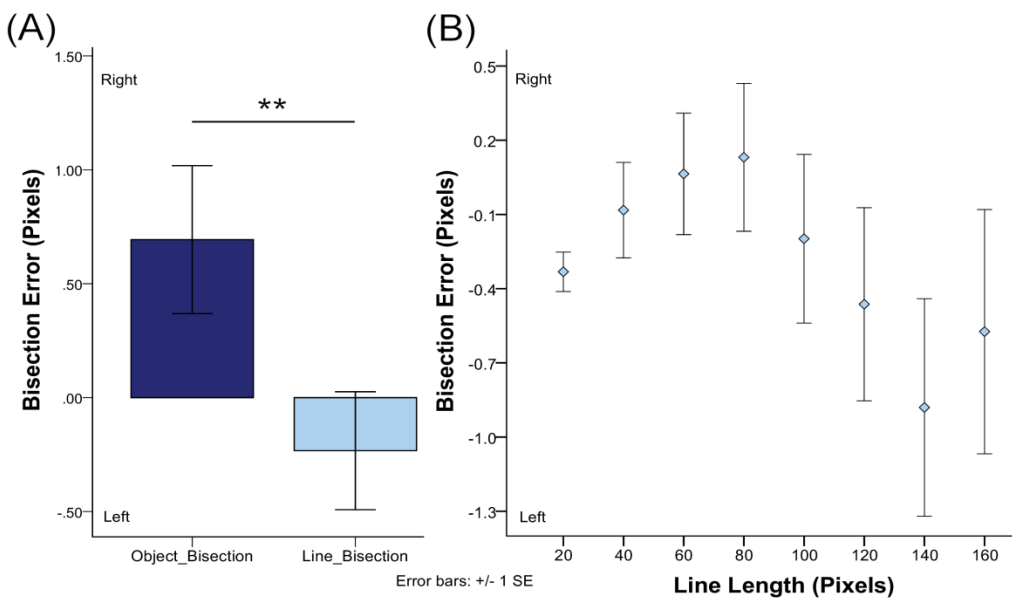


Figure 2.3: A summary of data from the object and line bisection tasks in Experiment 2.1. **A)** An illustration of the mean bisection errors of the line and object bisection tasks. We observed a significant difference between the direction of mean bisection errors of line and object bisections ($p = 0.005$). **B)** An illustration of the individual bisection errors across each line length type. **Note** - Negative bisection errors depict leftward bisection errors, and positive bisection errors depict rightward bisection errors. ** signifies a p value <0.01 .

A one-sample *t*-test compared average subject object bisection errors against zero (100% accuracy/unbiased responding). Interestingly, we observed errors in the bisection of objects (Mean = 0.29mm, SD = 0.72mm, CI = [0.010 - 0.59mm]) with a strong, but non-significant, trend towards the right side of centre (0mm; $t(25) = 2.05$, $p = 0.051$, Cohen's $d (d) = 0.427$). Critically, a paired samples *t*-test showed that errors in the bisection of objects, was significantly different ($t(25) = 3.08$, $p = 0.005$, $d = 0.176$) to the errors in bisecting lines (collapsed across all lines). Small lines have previously been shown to produce the most rightward bisection errors (Benwell, Harvey, et al., 2014; McCourt & Jewell, 1999). Interestingly, we observed significantly ($t(25) = 3.58$, $p = 0.001$ and $t(25) = 2.49$, $p = 0.02$ respectively) more rightward bisections of objects than the smallest lines (9mm and 18mm - very similar to the line lengths used by Benwell et al., (Benwell, Harvey, et al., 2014)).

Experiment 2.2 - Abstract Shape Bisection

Data from one subject were removed prior to condition of interest analysis because the subject's mean bisection error was >2.5 times larger than the SD. Data from 32 individuals were eligible for analysis.

A one-sample *t*-test assessed the difference between average subject bisection errors in the abstract shapes bisection task (Mean = 0.23mm, SD = 0.60mm, CI = [0.012 - 0.45mm]) against zero (*Fig 2.4A*). Errors in the bisection of abstract shapes were significantly ($t(31) = 2.17$, $p = 0.038$, $d = 0.388$) rightward of centre (>0). We assessed whether the average lateralisation bias of an image was related to the ease with which it could be interpreted as an object. Interestingly, we observed a significant correlation ($r = 0.337$, $p = 0.048$) indicating that more rightward biased bisection errors were associated with the increasingly difficult interpretation of abstract shapes (*Fig 2.4B*).

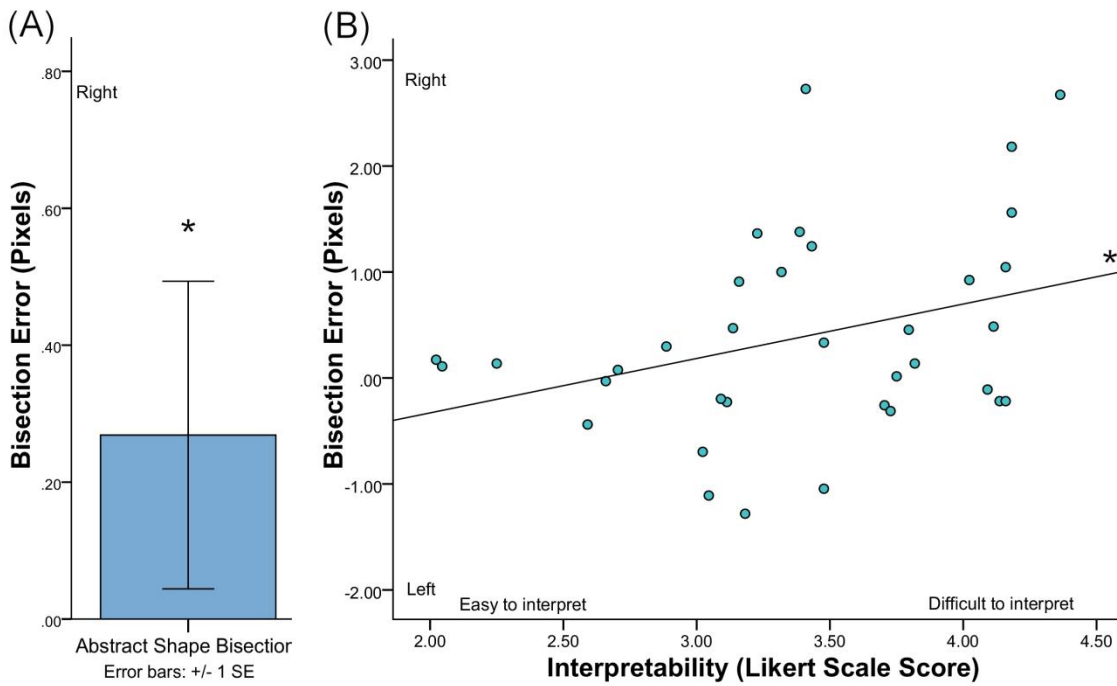


Figure 2.4: A summary of data from the abstract shape bisection task in Experiment 2.2. **A)** We observed significantly rightward abstract shape bisection errors ($p = 0.038$). **B)** Bisection errors became significantly ($r = 0.337$, $p = 0.048$) more rightward with abstract shapes that were more difficult to interpret. * signifies a p value < 0.05 .

Interim Discussion

As it is well established that the bisection of simple lines readily generates leftward bisection errors (Jewell & McCourt, 2000), this experiment aimed to assess the effect of increased target complexity on bisection errors in healthy individuals. In this experiment, line bisection errors (collapsed across line lengths) were not found to be significantly leftward of centre, however, our results replicated the well-established line length effect, whereby increases in line length are accompanied by greater leftward bisection errors (*Fig 2.3B*), [e.g. 8, 31]. Though the trend of rightward bias in object bisections that we observed was not statistically significant ($p = 0.051$), object targets were bisected with significantly more rightward errors than lines (*Fig 2.3A*). Additionally, we observed a significant difference between the bisection errors of very small lines (associated with the most rightward line bisections) and the bisection errors of objects. Importantly, our results show a rightward bias in the bisection of objects that is distinct and more pronounced than the line length effect observed with line bisections.

Experiment 2.2 more directly assessed the contribution of the semantic aspect of object processing to the right visual field bias observed in Experiment 2.1. Interestingly, we observed that our object-like abstract shapes were also associated with bisection errors with a significant rightward bias (*Fig 2.4A*). This is in stark contrast to previous findings using non-object-like abstract shapes (Churches, Loetscher, Thomas, & Nicholls, 2017). This previous work employed bisection of simple, semantically neutral shapes (circle, rectangle, triangle), and revealed a consistent and significant leftward bias. In the current study, objects were not mentioned by the experimenter prior to or during the abstract shape bisection session. Despite this, some silhouettes were inherently more interpretable as objects than others (*established in a separate shape interpretation rating experiment detailed in Supplementary Materials 1*) and all participants reported interpreting some of the silhouettes as objects. Despite image identity being task-irrelevant, recognition of one shape as an object may have triggered participants to (intentionally/unintentionally) attempt to identify all other subsequent silhouettes. Interestingly, we found a significant relationship between the difficulty of shape interpretation and the direction of bisection error. Shapes that were more difficult to interpret (*Fig 2.2B*) produced greater rightward bisection errors (*Fig 2.4B*).

A large and consistent rightward bisection bias is indicative of greater activation of the left

hemisphere FPA network (Loftus & Nicholls, 2012). To summarise, we have observed rightward bisection errors that are specific to objects and object-like stimuli and a relationship between increasingly rightward bisection errors with abstract shapes that were more difficult to interpret. These findings provide strong, novel evidence that semantic processing associated with object recognition can induce a rightward bias in attention allocation. Furthermore, it suggests a balance of processing that is more complex than the traditional account that the right hemisphere's FPA network is uniquely specialised for attention allocation. Rather it highlights, for the first time, the specialisation of the left hemisphere's FPA network for the processing of semantically engaging stimuli in visual space. The IPL represents one brain region that may be critical to this specialisation. In the right hemisphere, the IPL has been closely linked with highly perceptual and spatial processing and is one driver of the pseudoneglect effect (Corbetta & Shulman, 2002, 2011). In contrast, the same region in the left hemisphere has been closely linked with semantic judgements (Davey et al., 2015; Seghier et al., 2010).

Pseudoneglect has also been observed in challenges that draw on covert attention allocation. The traditional line, object, and abstract shape bisection tasks, and the previous investigations that hinted at a semantic-attention interaction (Cristescu, Devlin, & Nobre, 2006; Turriziani et al., 2009) all allow time for overt shifts in attention and deliberate comparisons across the two hemifields. As a result, the manner in which semantic processing areas interact with covert attention allocation is currently unknown. Though overlap between the systems processing covert and overt is considerable, some substantial differences have been observed (Heyman, Montemayor, & Grisanzio, 2017; Hunt & Kingstone, 2003). It is possible that only overt attention allocation displays a semantic-related attention bias. This case would impact predictions of which brain regions supported the effect and the future questions to be investigated. In addition, semantic object recognition represents an additional stage of processing that is absent during spatial attention allocation to line stimuli. As a result, the behavioural manifestations of semantic processing may occur later in the perceptual experience. This delay may reduce or prevent overlap of these manifestations with the fast processing of covert attention allocation. More simply, an individual may covertly attend before additional semantic processing can exert a measurable influence. A rightward bias of attention allocation on a speeded measure of covert attention allocation would demonstrate, for the first time, an interaction between the systems processing covert attention allocation and semantic processing.

Experiments 2.1 and 2.2 have revealed clear evidence of an interaction between the systems governing the allocation of attention and the processing of semantic information. This striking distinction illustrates the narrow focus of the traditional line bisection task on visuospatial processing. In light of the discovery of the impact of semantics on attention allocation, the ecological relevance of the pseudoneglect effect should be considered carefully. The way each FPA network contributes to the allocation of attention to encounters that are more complex than observing straight lines or greyscales requires substantial further investigation. In Experiment 2.3, we investigated the impact of the semantic-attention interaction observed in Experiments 2.1 and 2.2, on a multifaceted attention allocation task.

Experiment 2.3 - Implicit Primed Attention (IPA) Task

We developed a novel implicit primed attention (IPA) task (*Fig 2.5*) to investigate whether the attention-semantic interaction identified in Experiments 2.1 and 2.2 is also observable in covert attention allocation. The pseudoneglect effect has previously been demonstrated using a speeded lateral target identification task with central fixation (Nicholls et al., 2017; Petit et al., 2015). This illustrated that with semantically null targets, the right FPA network is optimised for the covert detection of lateralised visual information. Before asking participants to indicate the side on which an X-Target was presented, we showed subjects either an object or an abstract shape in either the lower or upper visual field (LoVF/UpVF). We hypothesised that object recognition systems would be recruited upon object perception or abstract shape, and that semantic processing, specialised in the left hemisphere would prime the left hemispheres FPA network. This priming would induce faster detection of subsequent X-Targets in the right visual field.

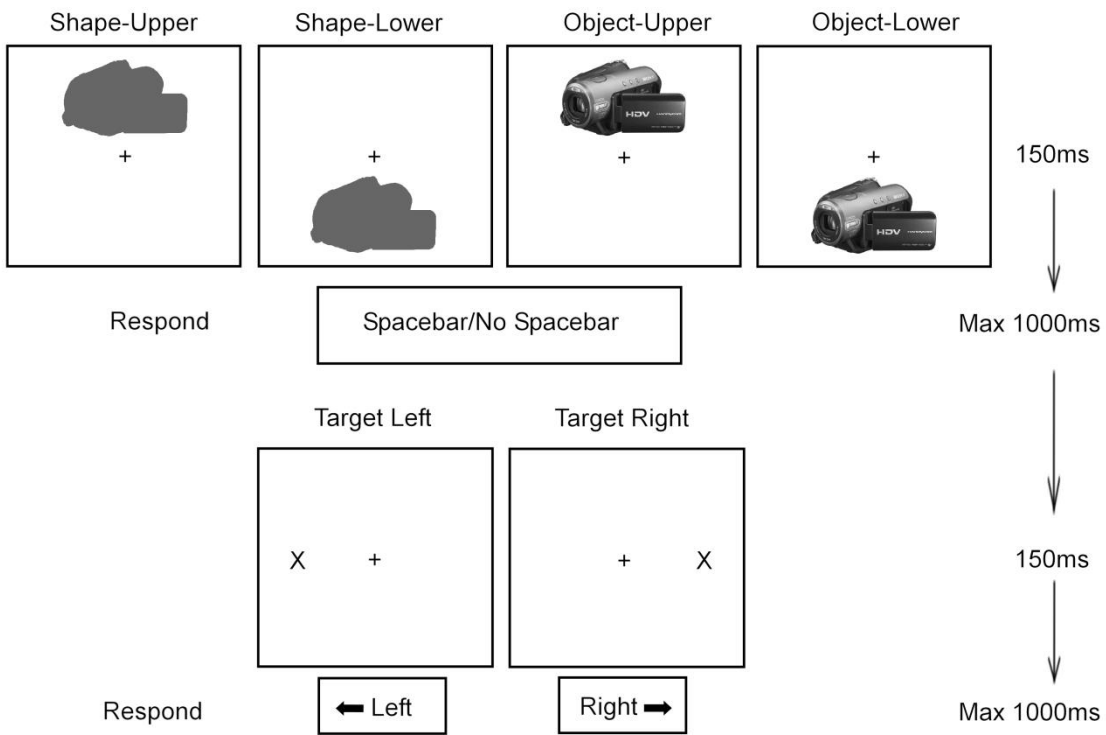


Figure 2.5: A schematic representation of the IPA paradigm. Subjects were instructed to centrally fixate throughout the trial and to respond twice. Following the first object/shape presentation, the first response choice indicated whether the image was an object or an abstract shape. The second response required identification of the location of a laterally presented X-target.

Experiment 2.3 - Materials and Methods

Participants

A further 22 (8 male, 18-35, mean = 22.64) participants with normal or corrected-to-normal vision and no history of neurological disorder completed the IPA paradigm. This approximate sample size has been used previously in experiments of this nature (Chambers et al., 2006; Shulman et al., 2010). All participants read the participant information sheet and provided written, informed consent at the start of the experimental session. All procedures were approved by the University of Manchester Research Ethics Committee.

Materials

The equipment used in Experiment 2.1 and 2.2 was also utilised in Experiment 2.3. Eye movements were recorded throughout the IPA paradigm using an ASL infrared eye tracking system (Applied Science Laboratories, Model Eye-Trac 6000, sampling rate 60 Hz).

Images

We utilised a black fixation cross measuring 21mm x 21mm with 4mm thick lines to centrally fixate participants. The same objects and shapes developed for Experiments 2.1 and 2.2 were presented in Experiment 2.3. Shapes and objects measured 44mm (3.5°) horizontally. Vertical height of shapes and objects varied between 5mm (0.40°) and 66mm (5.25°).

An "X" was presented as a target 86mm (6.84°) from the centre of the fixation cross. The X-Target measured 15mm (1.19°) x 16mm (1.27°) and its lines were 2mm (0.16°) thick.

Procedure

Participants were instructed to keep their eyes focused on a centrally presented fixation cross and to utilise their peripheral vision to observe the images presented to them. An object or shape was then presented either above or below the fixation cross for 150ms (fast enough to prevent observation through reactive eye movements (Szczepanski & Kastner, 2013)). Participants were instructed to indicate whether the image was an object or shape as quickly as possible (limit 1000ms) by pressing the spacebar with the thumb on their right hand. Half of participants pressed the spacebar if the image was an object and did not respond if the image was a shape. The other half of participants pressed the spacebar for a shape but not an object.

1000ms post image presentation (850ms post image clearance), a single X-Target was presented on either the left or right of the fixation cross for 150ms. Irrespective of their response to the image, participants were asked to indicate the side on which the cross appeared. Responses were made on the g (left) and j (right) keys of the keyboard using the index (g) and forth (j) fingers on the right hand. Participants were instructed to respond as quickly and as accurately as possible (limit 1000ms).

Results

Data from one participant were removed entirely from the analysis because of technical difficulties in data collection. Data from 21 participants were entered into the analysis. A repeated measures 2x2x2 ANOVA assessed differences in reaction times for responding to the laterally presented X-Targets between Image Type (Abstract Shape/Object) x Image Vertical Position (LoVF/UpVF) x X-Target Horizontal Position (Right/Left). Interestingly, reaction times to the right visual field X-Targets were significantly shorter than to X-Targets in the left visual field ($F(1,20) = 35.46$, $p < 0.001$, $\eta^2 = 0.639$; Fig 2.6A). There was no effect of image type (abstract shape or object) or image vertical position (LoVF/UpVF) on subsequent X-Target reaction times ($F(1,20) = 1.20$, $p = 0.663$, $\eta^2 = 0.01$, and $F(1,20) = 1.11$, $p = 0.305$, $\eta^2 = 0.052$ respectively). There were also no two-way interactions between image type and image vertical position ($F(1,20) = 1.40$, $p = 0.25$, $\eta^2 = 0.066$), image type and X-Target position ($F(1,20) = 2.01$, $p = 0.172$, $\eta^2 = 0.091$), image vertical position and X-Target position ($F(1,20) = 0.085$, $p = 0.774$, $\eta^2 = 0.004$), nor a three-way interaction between image type, image vertical position and X-Target position ($F(1,20) = 0.132$, $p = 0.72$, $\eta^2 = 0.007$).

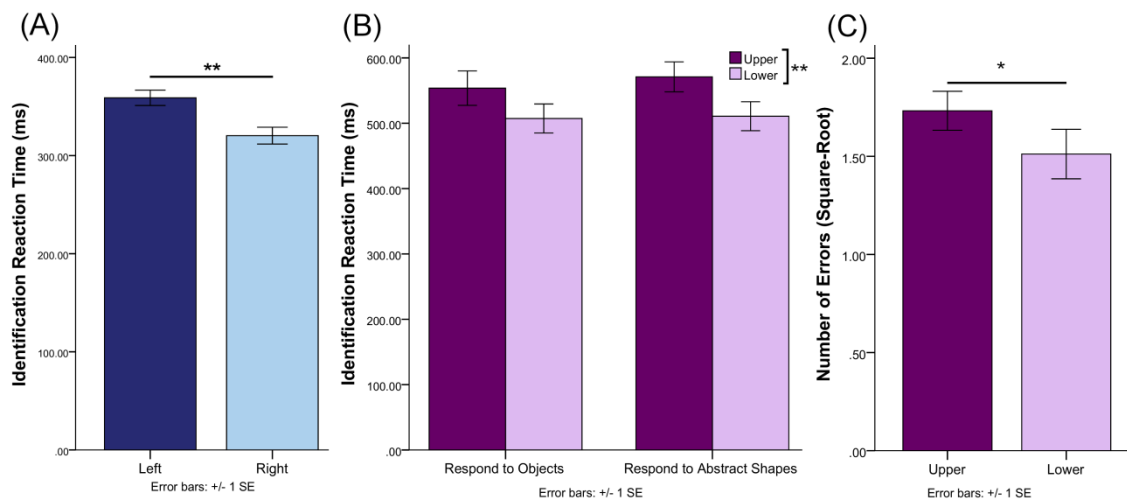


Figure 2.6: A summary of data from the novel IPA task in Experiment 2.3. **A)** Reaction times for responding to an X-Target presented in the right visual field were significantly shorter than for responding to an X-Target in the left visual field ($p < 0.001$). **B)** We observed significantly ($p < 0.001$) faster reaction times when images (for both objects and abstract shapes) were presented in the LoVF than the UpVF. **C)** We observed significantly ($p = 0.015$) fewer errors in the identification of object/abstract images presented in the LoVF than the UpVF. ** signifies a p value < 0.01 .

We conducted an exploration of the effects of space on the speed of object or abstract shape decision with a 2x2 ANOVA (Image Type (Object/Abstract Shape) x Image Vertical Position (LoVF/UpVF)). We observed reaction times that were significantly ($p < 0.001$) faster for images presented in the LoVF than the UpVF (*Fig 2.6B*). This effect did not vary by image type. We utilised the same 2x2 ANOVA with the number of errant decisions as the dependent variable. Significantly ($p = 0.015$) fewer errors were observed when subjects identified object/abstract images that were presented in the LoVF than the UpVF (*Fig 2.6C*).

To confirm that we were assessing covert attention allocation and ensure that erroneous fixations or saccades did not influence our observations, we performed a separate analysis that included only trials where a central fixation was recorded during both the object/abstract shape image presentation and the subsequent lateral X-Target presentation. When a separate analysis was conducted using only eye tracking restricted data, we observed the same reaction time effects described here. The details of the analysis of this subset of the data are available in Supplementary Materials 2.

Discussion

The IPA paradigm has provided additional evidence for distinct hemispheric specialisations that characterise the left and right hemisphere FPA networks. The requirement to rapidly (200ms) allocate covert attention from a central fixation point to detect a lateral target has previously elicited faster reaction times and fewer errors in the left visual field (Nicholls et al., 2017; Petit et al., 2015). However, we show here that implicit priming of object identification (the semantic system) by a prior object/abstract shape decision produces reaction times that are faster when the subsequent X-Target is in the right visual field. Faster reaction times to subsequently presented lateral X-Targets in the right visual field represent a complete reversal of the pseudoneglect effect observed previously on this type of task (Nicholls et al., 2017; Petit et al., 2015). Like Experiment 2.1 and 2.2, this right visual field processing advantage reflects greater task related engagement of the left hemisphere FPA network. Critically, we have demonstrated that the semantic specialisation of the left hemisphere FPA network is pertinent in the processing of fast, covert attention allocation in addition to the overt attentional biases observed in Experiment 2.1 and 2.2.

More research investigating the characteristics of the left hemisphere's FPA network is required to provide insight into the temporal dynamics of the semantic attention allocation system. Fortunately, the new IPA paradigm employed here contains a variable delay between the presentation of object/shape images and subsequent lateral target identifications. This will allow for a within-subjects assessment of multiple attentional dynamics (e.g. the relationship between semantic-attention interactions and spatial position effects). This flexible paradigm will allow for a detailed assessment of the means (spatial and temporal dynamics) by which other factors that influence the FPA networks and attention allocation exert an effect (see (Jewell & McCourt, 2000) for details of other factors).

In addition to our observation of faster reaction times in the right visual field in the IPA paradigm, we also observed a difference in both the speed and accuracy of identification of the object/shape primes. Errors (including identification of object images as abstract shapes and vice versa, incorrect subsequent X-Target response, and missed trials) occurred more often on trials where the priming image was presented in the UpVF. Likewise, participants were significantly slower at making the object/abstract shape decision when the image appeared in

the UpVF than for targets in the LoVF on correct trials (i.e., object image identified as object, shape identified as abstract shape).

Previous work has investigated differences in attention allocation at different vertical positions and a tendency for healthy individuals to allocate greater attention to the UpVF has been observed (Churches et al., 2017; Nicholls, Mattingley, Berberovic, Smith, & Bradshaw, 2004). This tendency is in great contrast to the LoVF object identification advantage described for the first time in the current study. As described earlier, others have proposed that peripersonal attention allocation is optimised in the LoVF, whereas UpVF processing prioritises allocation of attention to more distant items (Previc & Blume, 1993). Items in peripersonal space can be directly interacted with, and may represent immediately accessible reward or danger. It is logical for the brain to allocate greater resources to fast and accurate item classification in peripersonal space. The LoVF advantage observed here is consistent with the enhanced processing often required in peripersonal space. Our observations show a reversal of the traditional UpVF bias to the LoVF, and the classic pseudoneglect (leftward) bias to a rightward bias. These findings further illustrate that attention allocation priorities should be investigated with stimuli that increasingly reflect the complexity of our environments.

Conclusions and Implications

In this series of experiments, we have demonstrated the hemispheric asymmetries of attention allocation systems specialised for semantic and spatial processing for the first time. Our novel variant of the manual line bisection task has revealed a previously unrecognised perceptual effect, whereby the attention allocation system specialised for semantic processing, optimised in the left hemisphere, is recruited by semantically engaging stimuli. This recruitment results in a perceptual bias characterised by greater engagement of attention with the right side of visual space. In addition, the novel IPA paradigm has revealed that covert attention allocation is also characterised by distinct semantically dependent processes. This finding represents a critical step in enabling future work to investigate the mechanism of the semantic-attention interaction. Further work should utilise the adaptability of the IPA paradigm to investigate the temporal and spatial dynamics of the semantic-attention interaction. These investigations should aim to reveal the commonalities and differences between the processing of overt and covert attention and establish the factors that result in the recruitment of one system over another.

The work presented here has provided a vital step forward in our understanding of the mechanisms that underlie everyday allocation of attention and how to investigate them. We have recognised and demonstrated that tasks typically used to investigate pseudoneglect in the past, have failed to fully encapsulate ecologically relevant variables. To address this, we developed paradigms that could accurately reveal the mechanisms supporting the allocation of attention in more complex encounters. For instance, the IPA paradigm represents a novel investigative tool and a template that can be utilized to better our understanding of the numerous factors affecting the allocation of attention. This is critical if we are to achieve a complete understanding of how attention is prioritised and guided by external and internal influences. In turn, this underpins the exploration of the neural bases of attention and attention allocation, and informs more complete diagnostic techniques for patients with brain damage or disease.

References

- Benwell, C. S. Y., Harvey, M., Gardner, S., & Thut, G. (2013). Stimulus- and state-dependence of systematic bias in spatial attention: additive effects of stimulus-size and time-on-task. *Cortex*, 49, 827-36. <http://doi.org/10.1016/j.cortex.2011.12.007>
- Benwell, C. S. Y., Harvey, M., & Thut, G. (2014). On the neural origin of pseudoneglect: EEG-correlates of shifts in line bisection performance with manipulation of line length. *NeuroImage*, 86, 370-80. <http://doi.org/10.1016/j.neuroimage.2013.10.014>
- Benwell, C. S. Y., Thut, G., Grant, A., & Harvey, M. (2014). A rightward shift in the visuospatial attention vector with healthy aging. *Frontiers in Aging Neuroscience*, 6, 113-124. <http://doi.org/10.3389/fnagi.2014.00113>
- Benwell, C. S. Y., Thut, G., Learmonth, G., & Harvey, M. (2013). Spatial attention: differential shifts in pseudoneglect direction with time-on-task and initial bias support the idea of observer subtypes. *Neuropsychologia*, 51(13), 2747-56. <http://doi.org/10.1016/j.neuropsychologia.2013.09.030>
- Churches, O., Loetscher, T., Thomas, N. A., & Nicholls, M. E. R. (2017). Perceptual biases in the horizontal and vertical dimensions are driven by separate cognitive mechanisms. *Quarterly Journal of Experimental Psychology*, 70(3), 444-460. <http://doi.org/10.1080/17470218.2015.1131841>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201-15. <http://doi.org/10.1038/nrn755>
- Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. *Annual Reviews Neuroscience*, 34, 569-99. <http://doi.org/10.1146/annurev-neuro-061010-113731>
- Cristescu, T. C., Devlin, J. T., & Nobre, A. C. (2006). Orienting attention to semantic categories. *NeuroImage*, 33(4), 1178-1187. <http://doi.org/10.1016/j.neuroimage.2006.08.017>
- Davey, J., Cornelissen, P. L., Thompson, H. E., Sonkusare, S., Hallam, G., Smallwood, J., & Jefferies, E. (2015). Automatic and Controlled Semantic Retrieval: TMS Reveals Distinct Contributions of Posterior Middle Temporal Gyrus and Angular Gyrus. *Journal of Neuroscience*, 35(46), 15230-15239. <http://doi.org/10.1523/JNEUROSCI.4705-14.2015>
- Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, 30, 327-330. <http://doi.org/10.1212/WNL.30.3.327>
- Heyman, G. M., Montemayor, J., & Grisanzio, K. A. (2017). Dissociating attention and eye movements in a quantitative analysis of attention allocation. *Frontiers in Psychology*, 8(MAY), 1-11. <http://doi.org/10.3389/fpsyg.2017.00715>
- Hunt, A. R., & Kingstone, A. (2003). Covert and overt voluntary attention: Linked or independent? *Cognitive Brain Research*, 18(1), 102-105. <http://doi.org/10.1016/j.cogbrainres.2003.08.006>
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, 38(1), 93-110. [http://doi.org/10.1016/S0028-3932\(99\)00045-7](http://doi.org/10.1016/S0028-3932(99)00045-7)
- Josse, G., & Tzourio-Mazoyer, N. (2004). Hemispheric specialization for language. *Brain Research Reviews*, 44(1), 1-12. <http://doi.org/10.1016/j.brainresrev.2003.10.001>

- Learmonth, G., Benwell, C. S. Y., Thut, G., & Harvey, M. (2017). Age-related reduction of hemispheric lateralisation for spatial attention: An EEG study. *NeuroImage*, 153, 139-151. <http://doi.org/10.1016/j.neuroimage.2017.03.050>
- Lee, B. H., Kim, M., Kang, S. J., Park, K. C., Kim, E.-J., Adair, J. C., & Na, D. L. (2004). Pseudoneglect in solid-line versus character-line bisection tasks: a test for attention dominance theory. *Cognitive and Behavioral Neurology*, 17(3), 174-178. <http://doi.org/10.1097/01.wnn.0000175227.22343.9b>
- Loftus, A. E., & Nicholls, M. E. R. (2012). Testing the activation-orientation account of spatial attentional asymmetries using transcranial direct current stimulation. *Neuropsychologia*, 50(11), 2573-6. <http://doi.org/10.1016/j.neuropsychologia.2012.07.003>
- McCourt, M. E., & Jewell, G. (1999). Visuospatial attention in line bisection: Stimulus modulation of pseudoneglect. *Neuropsychologia*, 37, 843-855. Retrieved from <http://www.sciencedirect.com/science/article/pii/S0028393298001407>
- Mesulam, M. (1981). A cortical network for directed attention and unilateral neglect. *Ann Neurol*, 10, 309-25. <http://doi.org/10.1002/ana.410100402>
- Migo, E., Montaldi, D., & Mayes, A. R. (2013). A visual object stimulus database with standardized similarity information. *Behavior Research Methods*, 45(2), 344-54. <http://doi.org/10.3758/s13428-012-0255-4>
- Nicholls, M. E. R., Hobson, A., Petty, J., Churches, O., & Thomas, N. A. (2017). The effect of cerebral asymmetries and eye scanning on pseudoneglect for a visual search task. *Brain and Cognition*, 111, 134-143. <http://doi.org/10.1016/j.bandc.2016.11.006>
- Nicholls, M. E. R., Mattingley, J. B., Berberovic, N., Smith, A., & Bradshaw, J. L. (2004). An investigation of the relationship between free-viewing perceptual asymmetries for vertical and horizontal stimuli. *Cognitive Brain Research*, 19(3), 289-301. <http://doi.org/10.1016/j.cogbrainres.2003.12.008>
- Nicholls, M. E. R., & Roberts, G. R. (2002). Can free-viewing perceptual asymmetries be explained by scanning, pre-motor or attentional biases? *Cortex*, 38, 113-136. [http://doi.org/10.1016/S0010-9452\(08\)70645-2](http://doi.org/10.1016/S0010-9452(08)70645-2)
- Petitot, P., Noonan, M. A. P., Bridge, H., O'Reilly, J. X., & O'Shea, J. (2015). Testing the inter-hemispheric competition account of visual extinction with combined TMS/fMRI. *Neuropsychologia*, 74, 63-73. <http://doi.org/10.1016/j.neuropsychologia.2015.04.021>
- Previc, F. H., & Blume, J. L. (1993). Visual search asymmetries in three-dimensional space. *Vision Research*, 33(18), 2697-2704. [http://doi.org/10.1016/0042-6989\(93\)90229-P](http://doi.org/10.1016/0042-6989(93)90229-P)
- Reuter-Lorenz, P. A., Kinsbourne, M., & Moscovitch, M. (1990). Hemispheric control of spatial attention. *Brain and Cognition*, 12, 240-6. [http://doi.org/10.1016/0278-2626\(90\)90018-J](http://doi.org/10.1016/0278-2626(90)90018-J)
- Schneider, W., Eschmann, A., & Zuccolotto, A. (2012). *E-Prime User's Guide*. Pittsburgh: Psychology Software Tool, Inc. Retrieved from https://www.researchgate.net/publication/260296789_E-prime_User%27s_Guide
- Seghier, M. L. (2013). The angular gyrus: Multiple functions and multiple subdivisions. *Neuroscientist*, 19(1), 43-61. <http://doi.org/10.1177/1073858412440596>
- Seghier, M. L., Fagan, E., & Price, C. J. (2010). Functional Subdivisions in the Left Angular Gyrus Where the Semantic System Meets and Diverges from the Default Network. *Journal of Neuroscience*, 30(50), 16809-16817. <http://doi.org/10.1523/JNEUROSCI.3377-10.2010>

- Szczepanski, S. M., & Kastner, S. (2013). Shifting attentional priorities: Control of spatial attention through hemispheric competition. *Journal of Neuroscience*, 33(12), 5411-21. <http://doi.org/10.1523/JNEUROSCI.4089-12.2013>
- Thiebaut de Schotten, M., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience*, 14, 1245-6. <http://doi.org/10.1038/nn.2905>
- Thiebaut de Schotten, M., Urbanski, M., Duffau, H., Volle, E., Lévy, R., Dubois, B., & Bartolomeo, P. (2005). Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans. *Science*, pp. 2226-8. <http://doi.org/10.1126/science.1116251>
- Thomas, N. A., Loetscher, T., & Nicholls, M. E. R. (2014). Asymmetries in attention as revealed by fixations and saccades. *Experimental Brain Research*, 232, 3253-67. <http://doi.org/10.1007/s00221-014-4015-9>
- Turriziani, P., Oliveri, M., Bonni, S., Koch, G., Smirni, D., & Cipolotti, L. (2009). Exploring the relationship between semantics and space. *PLoS ONE*, 4(4). <http://doi.org/10.1371/journal.pone.0005319>
- Zago, L., Petit, L., Jobard, G., Hay, J., Mazoyer, B., Tzourio-Mazoyer, N., ... Mellet, E. (2017). Pseudoneglect in line bisection judgement is associated with a modulation of right hemispheric spatial attention dominance in right-handers. *Neuropsychologia*, 94(November 2016), 75-83. <http://doi.org/10.1016/j.neuropsychologia.2016.11.024>
- Zuanazzi, A., & Cattaneo, L. (2017). The right hemisphere is independent from the left hemisphere in allocating visuospatial attention. *Neuropsychologia*, 102, 197-205. <http://doi.org/10.1016/j.neuropsychologia.2017.06.005>

Chapter 3: These Ones are Small, but the Ones Out There are Far Away: Spatial Attention, Forced Perspective, and the Line Length Effect

Abstract

Healthy individuals make systematic errors in allocating attention to perceptual space. The majority of the population display a bias in favour of attention allocation to the left side of perceptual space. Most agree that this effect is a behavioural manifestation of a specialisation of spatial attention processing in the frontoparietal attention (FPA) network of the right hemisphere. Many factors modulate the extent and direction of this attention bias. For example, increasing the length of straight horizontal lines that are the subject of line centre judgements has been associated with an increasingly leftward attention lateralisation (the line length effect). Despite 20 years of study, the neural mechanisms that underpin the line length effect remain poorly understood. A separate, large body of work has observed stronger leftward attention biases with smaller distances between the stimuli and observer (the target-observer proximity effect). In this set of experiments, we reconcile these two idiosyncratic characteristics of attention processing that, until now, have been thought to rely on independent mechanistic foundations. We hypothesised that forced perspective ambiguity causes the misattribution of line length as indicative of item distance. In other words, long lines recruit peripersonal object processing, whereas short lines induce distant object processing. First, we conducted a within-subject comparison of the lateralised attention allocation biases associated with different sizes of objects and horizontal lines. We observed a previously unrecognised association between taller object images and increasingly leftward biases. Line specific shape processing (the distance-independent interpretation of the line length effect) could not explain this effect. In experiment 2.2, we utilised a functional magnetic resonance imaging conjunction analysis to illustrate significant overlap of activation in the fusiform gyrus during a line centre judgement (the landmark task), and an object attention allocation task. This suggests that the visual system could feasibly interpret lines of different lengths as objects at different distances. Our observations strongly support a proximity-dependent mechanism wherein larger lines and objects are misperceived as closer than their smaller equivalents.

Introduction

Precise and accurate interactions with our environments form a central component of daily life. We seamlessly integrate information pertaining to an object's identity and spatial location into a single comprehensible percept. Despite the fundamental importance of this function, error and bias in healthy perception is measurable under many conditions. 'Pseudoneglect' is a term frequently used to describe the tendency of the majority of healthy individuals to preferentially allocate slightly more attention to the left than the right side of visual space. Variability in the strength and direction of the idiosyncrasies of perception has helped us to better understand the mechanisms supporting perception and attention. For example, investigations of the pseudoneglect effect has helped reveal the natural specialisation of the right frontoparietal attention (FPA) network in the processing of highly perceptual and spatial attention allocation (Benwell, Harvey, et al., 2014; Mesulam, 1981; Szczepanski & Kastner, 2013).

The line bisection test (Hughes et al., 2004; Reuter-Lorenz et al., 1990; Thiebaut de Schotten et al., 2005), the landmark task (Benwell, Harvey, et al., 2014; Benwell, Thut, et al., 2014; Fink et al., 2002) and greyscale task (Loftus & Nicholls, 2012; Nicholls & Roberts, 2002; Thomas et al., 2014) all require the participant to produce a stimulus centric comparison of the left and right sides of an image. For example, the line bisection task requires the subject to attempt to perfectly bisect a straight horizontal line using a smaller vertical line (*Fig 3.1A*). Upon inspection of a centrally presented line, the horizontal extremities of the line fall into the visual field processed by the contralateral hemisphere. During completion of these tasks, the right FPA network generally shows more robust activity than the left (Benwell, Harvey, et al., 2014; Szczepanski & Kastner, 2013). This hemispheric imbalance results in greater attention allocated to the left visual field, an increase in the perceived size of the left side of a centrally presented stimulus (like a horizontal line), and leftward bisection errors (*Fig 3.1A*; for a review of the pseudoneglect effect on the line bisection task, see 12). As a result of this close relationship between bisection errors and attention allocation, these tasks can function as an accurate index of FPA network balance.

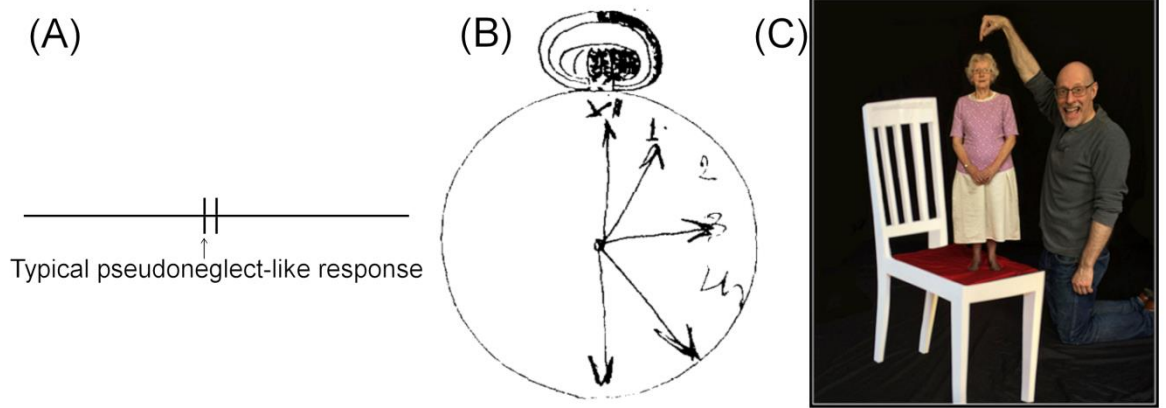


Figure 3.1: *A) A typical pseudoneglect-like response illustrated on a 160 pixel line with an accurate central bisection for reference. B) A typical right hemisphere damaged unilateral hemispatial neglect patient drawing of a clock. Note the inability to report features of contralesional space. C) The forced perspective effect is demonstrated here by Richard Wiseman and his new version of the Beuchet Chair illusion (Wiseman, 2016).*

Variability in the Pseudoneglect Effect

The line bisection, landmark, and greyscale tasks provide an excellent account of attention allocation in the absence of potentially confounding variables. The association between performing highly perceptual and spatial tasks (such as the line bisection task) and the pseudoneglect effect reflects a response that is averaged across the population. In addition, the stimuli used in these tasks are generally very simple and lack the complexity and diversity of environmentally realistic encounters. The translation of research into spatial attention allocation and the pseudoneglect effect has resulted in some uncertain and unclear findings when more complex and naturalistic scenarios are tested (Hatin, Sykes Tottenham, & Oriet, 2012; J. S. Robertson, Forte, & Nicholls, 2015). Many factors have been associated with the modulation of attention allocation (Jewell & McCourt, 2000). Importantly, these factors have been used to better characterise the idiosyncrasies of attention allocation mechanisms. However, it is possible that more complex stimuli recruit additional or different mechanisms that remain untapped by these tasks. This unaccounted variance may contribute to the mixed findings of investigations that utilise complex and naturalistic stimuli. As a result, it is important that further work builds towards using more complex and ecologically realistic stimuli to characterise these systems.

In this study, we aimed to establish whether common mechanisms underpin the effect of two well-known factors that modulate attention allocation. Unilateral hemispatial neglect (UHN) patients display consistent, pronounced and disabling impairment of attention allocation when presented with either objects or non-objects (such as lines in a line-bisection task) (Kinsbourne, 1977; Mesulam, 1981). Caused by brain damage to the FPA networks (particularly in the right hemisphere), UHN is characterised by consistent inattention to contralesional space and an inability to withdraw attention from ipsilesional space (see *Fig 3.1B*) (Beschlin et al., 1997; Heilman & Van Den Abell, 1980; Mesulam, 1999; Shelton, Bowers, & Heilman, 1990; Verdon et al., 2010). The lack of a difference between the response to objects and non-objects has led to a lack of focus on the distinctions between the attentional processing of these stimuli. Recent evidence from healthy individuals suggests that aspects of attention processing may differ between objects and non-objects (Gray and Montaldi, submitted). This work has provided strong evidence that the processing of the semantic aspect of objects can produce a left hemisphere lateralisation of FPA network activity and a rightward bias in spatial attention allocation.

Here, we focus on another aspect of stimulus processing that varies between objects and lines and investigate its effect on the lateralisation of attention allocation. As well as differences in features, the size of objects and lines are often very dissimilar. Interestingly, the size/length of lines (shorter/longer) substantially affects attention lateralisation. Though line centre judgements are biased to the left with long lines, these become increasingly rightward with decreasing line lengths (Benwell, Harvey, et al., 2014). A reduction in the engagement of the right FPA network has been associated with this rightward shift (Benwell, Harvey, et al., 2014). In spite of this finding, the critical features that produce the line length effect are poorly understood. More specifically, why is the right FPA network more interested in long, than short lines? Moreover, the line length effect has not been linked with characteristics of attention in more complex and environmentally realistic conditions. So what behaviourally relevant mechanism does it really index?

The target-observer proximity effect is another example of an idiosyncratic modulation of attention allocation. This modulation describes the shift of attention lateralisation from the left to the right side that accompanies an increase in the distance between stimulus and observer. As with the line length effect, engagement of the right FPA network has been shown to decrease as the target-observer distance increases (reflecting a decrease in the angle subtended by the

stimulus on the retina). The demands of attention allocation in peripersonal and extrapersonal space vary. Important features in peripersonal space frequently occur in very different areas of the visual field. In contrast, more distant information is characterised by smaller changes in visual angle between important features. The target-observer proximity effect potentially reflects the processing of these different demands on attention.

Forced perspective is an optical illusion where small and distant items, and large and proximal items are perceptually equivalent. The title of this article references the attempt and failure of Father Ted Crilly to explain forced perspective to Father Dougal McGuire in the classic Channel 4 sitcom *Father Ted* (Matthews & Linehan, 1997). The classic Beuchet chair illusion (Wiseman, 2016) provides another engaging example of this perceptual effect (*Fig 3.1C*). As a result of forced perspective ambiguity, long lines may be misperceived as items that are closer than short lines. This difference in interpretation of the lines may therefore recruit the same mechanism that underpins the target-observer proximity effect. Until now, the potential relationship between the line length, and target-observer proximity effects had not been considered or empirically investigated.

Forced perspective misperception was discovered and is frequently demonstrated using object stimuli (Wiseman, 2016). Importantly, we understand that forced perspective misperception frequently occurs in the absence of informative distance cues. The line length effect is observed under these same conditions. As a result, we propose that forced perspective misperception, along with the target-observer proximity effect, provides a plausible and empirically assessable explanation of the line length effect.

Performing a line centre (landmark) judgement from a large viewing distance is associated with central or rightward bisection biases rather than the pseudoneglect effect. However, when tools that extend a subject's reach are used, peripersonal processing is engaged and the pseudoneglect bias is observable (Gamberini, Seraglia, & Priftis, 2008). This work provides strong evidence that the brain's interpretation of the distance to the bisection target can have a substantial impact upon the recruitment of peripersonal rather than extrapersonal attention processing. Moreover, it demonstrates that this difference in the system that is engaged can subsequently influence the lateralisation of attention allocation (Longo & Lourenco, 2006). The brain errantly views image size (e.g. line length) as indicative of the distance between the target and the observer (forced perspective). As a result, long lines should (in the absence of

informative distance cues) lead to interpretation-based recruitment of peripersonal over extrapersonal processing. In contrast, the opposite interpretation (smaller image = further away) should induce extrapersonal processing for short lines.

Despite the apparent similarities between the features of the line length, and target-observer proximity, effects, a shared cause has, to the authors' best knowledge, not been previously identified or tested. To investigate this, we utilised a variant of the traditional line bisection task in which participants moved a vertical line to attempt to centrally bisect an object (Fig 3.2A). The data regarding the differences in bisection of lines and objects are presented in Gray and Montaldi (submitted; Chapter 2). Here, we performed additional analysis of this dataset to explore the hypothesis that changes in the size and shape of objects would manipulate the engagement of the FPA networks, and relate closely to the lateralisation of attention allocation bias. Large objects, like long lines, would engage peripersonal processing mechanisms, recruit the right FPA more strongly, and produce more substantial leftward bisection errors. In this experiment, the same individuals also performed a traditional line bisection task. Bisections of lines of 8 different lengths allowed for comparison of the well-established line length effect with novel object bisection data (Fig 3.2B).

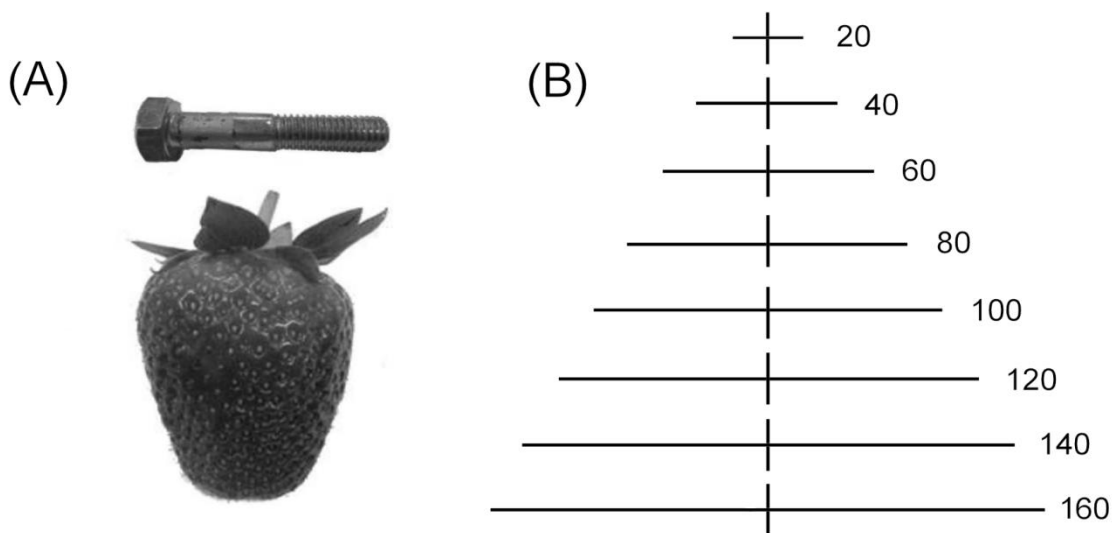


Figure 3.2: **A)** Two example objects used in the object bisection task. **B)** The eight line lengths (20, 40, 60, 80, 100, 120, 140, and 160) assessed in the line bisection task with accurate central bisections.

Materials and Methods - Experiment 3.1 - Object and Line Bisection Tasks

The collection of the data for this experiment was originally described in Experiment 2.1 of Gray and Montaldi (submitted; Chapter 2). Here, these data are discussed further and additional analyses are presented.

This experiment presented participants ($N = 26$) with an image of either an everyday object or a straight horizontal black line. Participants were instructed to move a peripherally presented vertical line ($162\text{mm}/\sim 12.84^\circ$) to bisect the target stimulus as close to its centre as possible.

Straight black horizontal lines measured a width of $9\text{mm}/\sim 0.72^\circ$ visual angle, 18mm ($\sim 1.43^\circ$), 27mm ($\sim 2.15^\circ$), 36mm ($\sim 2.86^\circ$), 45mm ($\sim 3.58^\circ$), 54mm ($\sim 4.30^\circ$), 63mm ($\sim 5.01^\circ$), and 72mm ($\sim 5.73^\circ$). Greyscale images of everyday objects (Digital greyscale photographs of everyday objects developed by Migo, Montaldi, & Mayes, 2013) were presented in the object bisection task. All object images measured 76mm ($\sim 6.042^\circ$) from left to right. Vertical image size varied between 9mm ($\sim 0.72^\circ$) and 122mm ($\sim 10^\circ$). This difference in vertical size was crucial to the subsequent analyses in this article.

Results

Data on the object and line bisection tasks are presented in Fig 3.3. For full details of the results, see Gray and Montaldi (submitted; Chapter 2). In summary, we observed a tendency for longer lines to be bisected to the left of centre and shorter lines to be bisected more centrally (though this was not a significant effect; Fig 3.3A). Bisection of everyday objects revealed errors that were significantly rightward of the bisection of line stimuli ($t(25) = 3.08$, $p = 0.005$, $d = 0.176$; Fig 3.3B). We also observed a strong tendency for individuals to display a rightward bias ($t(25) = 2.05$, $p = 0.051$, $d = 0.427$) when bisecting objects, though this tendency did not reach statistical significance.

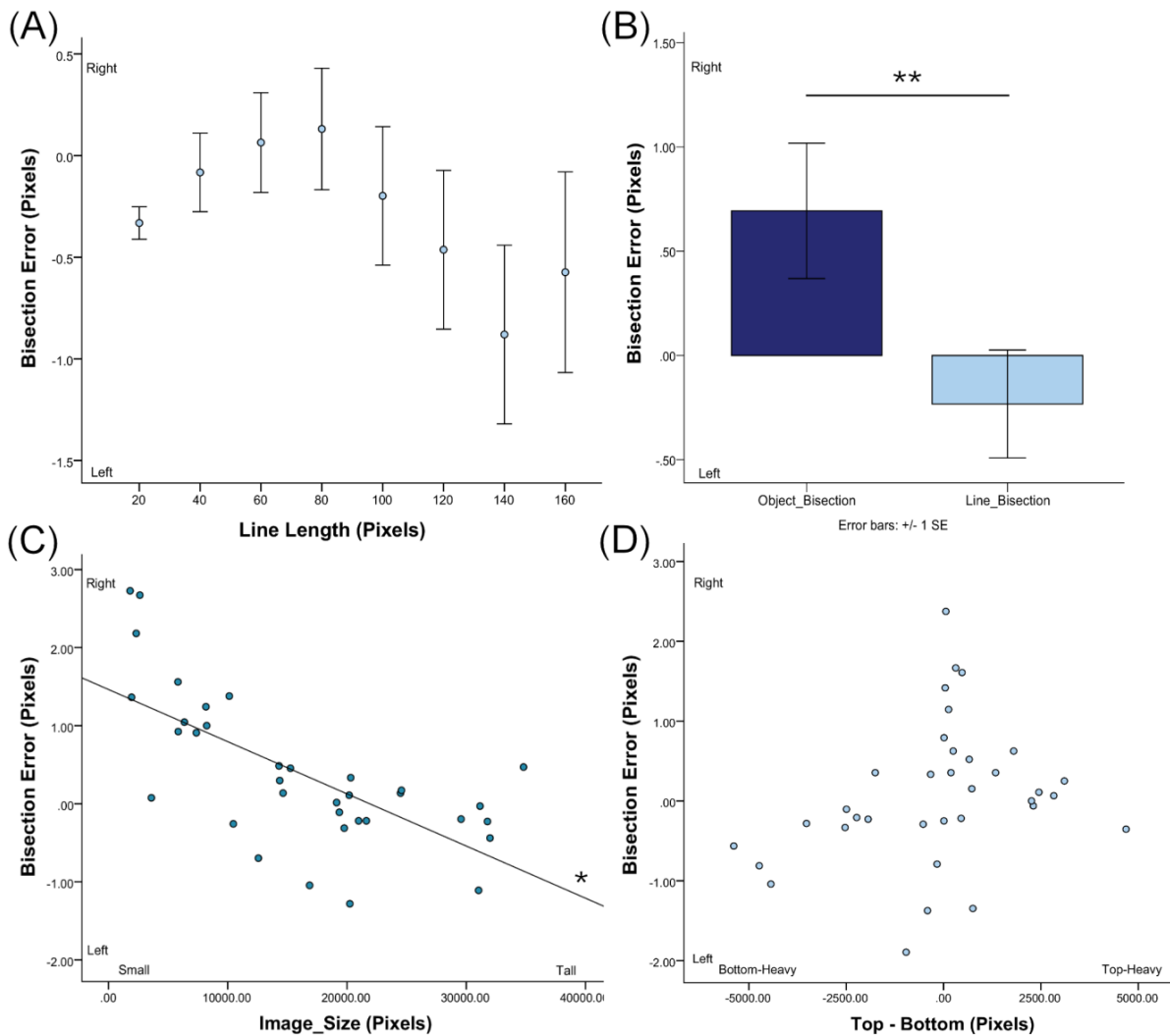


Figure 3.3: A summary of data from the object and line bisection tasks in experiment 3.1. **A)** An illustration of the individual bisection errors across each line length type. **B)** An illustration of the mean bisection errors of the line and object bisection tasks. We observed a significant difference between the direction of mean bisection errors of line and object bisections ($p = 0.005$). **C)** As image height (image width is constant across all images) increases, bisection errors become increasingly biased to the left ($r = -0.513$, $p = 0.002$). **D)** The balance of image information in the upper (UpVF) or lower visual field (LoVF) does not relate to the direction of bisection errors ($r = 0.282$, $p = 0.101$). **Note** - Negative bisection errors depict leftward bisection errors, and positive bisection errors depict rightward bisection errors. ** signifies a p value < 0.01 .

Additional Analyses: Image Size and Shape Analysis

Interestingly, more detailed analysis of object bisection errors revealed that increasing image height (Mean = 6819.15mm², SD = 4341.91mm², CI = [5327.65 - 8310.64mm²]) was significantly correlated with smaller rightward bisection errors ($r = -0.513$, $p = 0.002$) (Fig 3.3C). In contrast, the balance of image information in the upper visual field (UpVF) and lower visual field (LoVF) (UpVF - LoVF (number of image pixels), Mean = -93.26mm², SD = 1016.34mm², CI = [-339.26 - 152.75mm²]) was not correlated with object bisection errors ($r = 0.282$, $p = 0.101$). In other words, presentations predominantly in the UpVF (top-heavy images) produce the same bisection errors as presentations in the LoVF (bottom-heavy images) (Fig 3.3D).

Finally, we performed a Pearson's correlation analysis to assess the relationship between the line length, and image size effect. This post-hoc test was performed to test the proposal by Gray and Montaldi (submitted) that a perceptual attention allocation system is dominant during the line bisection task, whereas a semantic attention allocation system is dominant during the object bisection task. An index of the size and direction of the line length effect was calculated for each participant by subtracting their mean bisection for the two longest lines (25%) from their mean bisection error for the two shortest line lengths (25% of total bisections). In this way, a larger line length effect would be represented by a large positive value. A smaller line length effect would result in a small positive value and the inverse of the traditional line length effect would be represented by negative values. The same process was conducted for the object stimuli. Bisection errors produced with the largest 25% of objects were subtracted from the errors associated with the smallest 25% of objects. We observed no significant relationship between the line length, and the object image size effects ($r = -0.104$, $p = 0.620$).

Interim Discussion

The line bisection task has been developed as a reliable tool to investigate the natural tendency of healthy individuals to allocate more attention to the left side of perceptual space than the right. This extent of this pseudoneglect effect is consistently and predictably modulated by the length of the horizontal line being bisected. The mechanism underpinning the line length effect and spatial attention allocation has been considered for more than two decades (Anderson, 1996; Benwell, Harvey, et al., 2013, 2014; McCourt & Jewell, 1999; Monaghan & Shillcock, 1998). However, the relationship we observe between increases in image height and the greater extent of leftward bisection errors does not follow a logical extrapolation from the line length effect described earlier. A theoretical extrapolation of the line length effect (without consideration of item-observer proximity) would expect targets with equal proportions of information in the left, right, upper and lower visual fields (circular shapes, most similar in relative proportions to very small lines) to be bisected centrally or with a small rightward bias. Similarly, one would expect shapes with a comparable structure to lines (short, wide shapes) to be bisected with the greatest leftward attentional bias. The relationship we have observed is, however, in the opposite direction to this prediction.

As introduced earlier, target-observer proximity, the distance between the target of a line bisection or landmark task and the subject completing the task, also modulates the lateralisation bias of spatial attention allocation (Gamberini et al., 2008; Longo & Lourenco, 2006; Longo et al., 2015; Lourenco & Longo, 2009). Earlier, we described a forced perspective, proximity-dependent mechanism by which common processing could support both the line length and target-observer proximity effects. Forced perspective illusions are a product of the ambiguity between viewing distance and item size in the absence of informative distance cues. In this experiment, we have provided the first evidence that, with regard to attention allocation, long lines and larger shapes are interpreted as closer than short lines and small shapes. These 'closer' stimuli preferentially recruit peripersonal attention allocation processing and elicit greater leftward attention biases. In contrast, a shift in attention allocation bias to the right was observed with smaller stimuli that produced responses in accordance with processing in extrapersonal (out of reach) space. Until now, this common forced-perspective, proximity-dependent mechanism explaining the line length and proximity effect has remained unrecognised and lacked convergent evidence.

In the current experiment, bisection of long lines (63mm/ $\sim 5.01^\circ$ and 72mm/ $\sim 5.73^\circ$) produced leftward group-average bisection errors consistent with the traditional mechanistic account of the line length effect (described in the introduction). The absence of statistical significance in the comparison of these line types may have been a function of the limited number of times each line type was bisected, thus reducing the power to detect a significant difference, and additionally, the requirement for a more stringent F contrast in the one-way ANOVA (due to unequal variance). The data in *Fig 3.3A* illustrate this characteristic shape of the line length effect despite the limited number of times that each line variant was bisected.

We also performed a within-subjects analysis of the relationship between the line length effect and image size effect. No correlation between the two effects was observed in this study. This is unsurprising as the two effects are produced by the different systems that are engaged by object and line stimuli. As described in Gray and Montaldi (submitted) and illustrated in *Fig 3.3B*, we observed a rightward attention bias with the presentation of objects. This is indicative of a dominance of the left hemisphere FPA network over the right for semantically engaging stimuli (e.g. objects), which varies with image size in this study. In contrast, the line length effect is a product of variable dominance of right FPA network activity. As a result, it is not surprising that no correlation is observed between the line length effect and image size effect.

Experiment 3.1 has provided convergent evidence with previous work from our lab (experiment 2.3 from Gray and Montaldi, submitted) that lateralisation of the attention allocation bias is more dependent on perceived image size and semantic engagement content than vertical position. In experiment 1, we observed no difference between the bisection errors associated with ‘top-heavy’ objects (more information in the UpVF) and ‘bottom-heavy’ objects (more information in the LoVF). Similarly, experiment 2.3 of Gray and Montaldi (submitted) showed that the vertical position of an image presentation has no subsequent effect on lateralisation bias of attention. These findings are not consistent with the observations of Nicholls et al. (Nicholls et al., 2012) and Thomas et al., (Thomas et al., 2015). These previous studies both identified a stronger leftward bias with presentations exclusively in the UpVF. As a result, one could predict that attention allocation within the LoVF would lead to a greater right visual field processing advantage than when attention is manipulated within the UpVF.

The recruitment of discrete processing systems and the observation of distinct mechanistic idiosyncrasies provide an interesting explanation of the difference between findings of this

collection of work and the previous similar investigations mentioned above (Nicholls et al., 2012; Thomas et al., 2015). It is possible that the left hemisphere FPA, unlike the right hemisphere FPA network, is either not modulated by vertical position, or is changed in an, as yet unrecognised way. These interpretations are compatible with the previous observation that vertical and horizontal asymmetries occur independently and are supported by distinct neural processes (Churches et al., 2017). Additionally, these perspectives suggest that meaningful and measurable idiosyncrasies characterise the semantic attention system that is observed in this study and by Gray and Montaldi (submitted).

Neuroimaging and the Plausibility of a Forced Perspective Explanation of the Line Length Effect - Experiment 3.2

The FPA network introduced earlier has been characterised in detail and a mechanistic model that includes the dorsal attention network (DAN) and ventral attention network (VAN), can now describe the pseudoneglect effect as a result (Corbetta & Shulman, 2002, 2011; Duecker & Sack, 2015). This model proposes that the DAN governs the allocation of attention to specific areas of visual space. The DAN consists of the intraparietal sulcus, which contains topographic maps of visual space, superior parietal lobule, precuneus, frontal eye fields, supplementary eye field, and dorsolateral prefrontal cortex. No hemispheric lateralisation has been shown in the parietal regions of the DAN (Duecker & Sack, 2015). Instead, strong right hemisphere lateralisation of VAN activity in highly perceptual and spatial attention paradigms has been observed (Corbetta & Shulman, 2011). This well-evidenced model suggests that the lateralisation of the VAN, particularly within parietal regions, drives the DAN to allocate attention to the left side of space and produce the pseudoneglect effect.

Variable VAN engagement has been closely linked with many factors that affect attention lateralisation (e.g. detection of, and orientation to salient perceptual information (Chambers et al., 2007), arousal (Benwell, Thut, et al., 2013), semantic processing (Brown, Rissman, Chow, Uncapher, & Wagner, 2018; Seghier, 2013)). Interestingly, the modulation of attention allocation by the line length (Benwell, Harvey, et al., 2014), and target-observer proximity effects (Longo et al., 2015; Rinaldi et al., 2018) have been closely linked with the variable engagement of the VAN (particularly in parietal regions). It is reasonable to hypothesise that modulation of the same neural mechanism in the parietal aspects of the VAN support both of the line length, and

target-observer proximity effects.

The plausibility of one mechanistic explanation that accounts for both the line length and target-observer proximity effects is reliant on the commonality of line and object processing. If lines and objects share some common processing mechanisms, then it is feasible that a mechanistic explanation of the line length effect also accounts for non-line dependent lateralisation effects. Such a mechanism would offer a wider, more ecologically realistic mechanism with which to explain the line length effect. Alternatively, if the allocation of attention to lines and objects recruits distinct networks of cortical processing, then mechanisms that are unique to lines could plausibly explain the line length effect. The left spatial pseudoneglect bias decreases as stimuli become shorter and potentially less akin to a prototypical horizontal line. As a result, line-specific mechanisms could include a unique relationship between the similarity between a stimulus and a prototypical horizontal line, and the recruitment of the FPA networks.

In experiment 3.2, we utilised functional Magnetic Resonance Imaging (fMRI) in order to better understand the common and distinct processing that supports attention allocation to objects and non-object lines. This comparison aimed to assess whether the line length effect should be accounted for using an explanation that is unique to line stimuli, or whether the mechanistic explanation should also be applicable to object processing. We asked participants to complete a line centre judgement (landmark) task and an object perception task whilst undergoing an fMRI scan. This aimed to establish whether the brain areas that support attention and perception in the landmark task are also recruited when allocating attention to object stimuli.

Materials and Methods - Experiment 3.2

Participants

Data were collected from 19 individuals (13 males, 19-31 years, mean = 22.3). All participants were right-handed with normal or corrected-to-normal vision and no history of neurological disorder. All participants read the participant information sheet, and provided written, informed consent at the start of the experimental session. Volunteers received £20 in exchange for 90 minutes of participation in the fMRI study. All procedures were approved by the University of Manchester Research Ethics Committee. Data from one subject were removed due to issues with data acquisition.

Materials

The preparation and practice elements of the fMRI study were conducted in a dedicated testing room at the University of Manchester. MRI scanning was performed at the NIHR/Wellcome Trust Manchester Clinical Research Facility on a 3T MRI scanner (Philips, Achieva). Participants viewed all stimuli in the scanner through MRI compatible goggles (VisualSystem, NordicNeuroLab). Stimuli were presented and responses recorded through E-Prime (Psychology Software Tools, Inc.). Stimulus responses were recorded in the scanner using an eight-button, bimanual response pad (Current Designs, HHSC-2X4-C).

Stimuli

Individuals were presented with a small vertical line, length 6% of total screen height, in the centre (horizontal and vertical centre) of the screen. A straight, horizontal line, spanning 35% of total screen width, centrally bisected the vertical line (see *Fig 3.4A*). The position of the vertical line was always central and perfectly aligned with the vertical arms of a fixation cross. The fixation cross was also used as the null event for the fMRI analysis. In contrast, on each presentation (i.e., for each event) the position of the horizontal line varied along the X axis. Eleven horizontal line positions with different degrees of displacement from centre were presented. -5%, -4%, -3%, -2%, -1%, 0% (central), 1%, 2%, 3%, 4%, 5% of total horizontal line length away from central presentation. *Fig 3.4A* illustrates landmark bisections at -5%, 5%, and 0% divergence from centre.

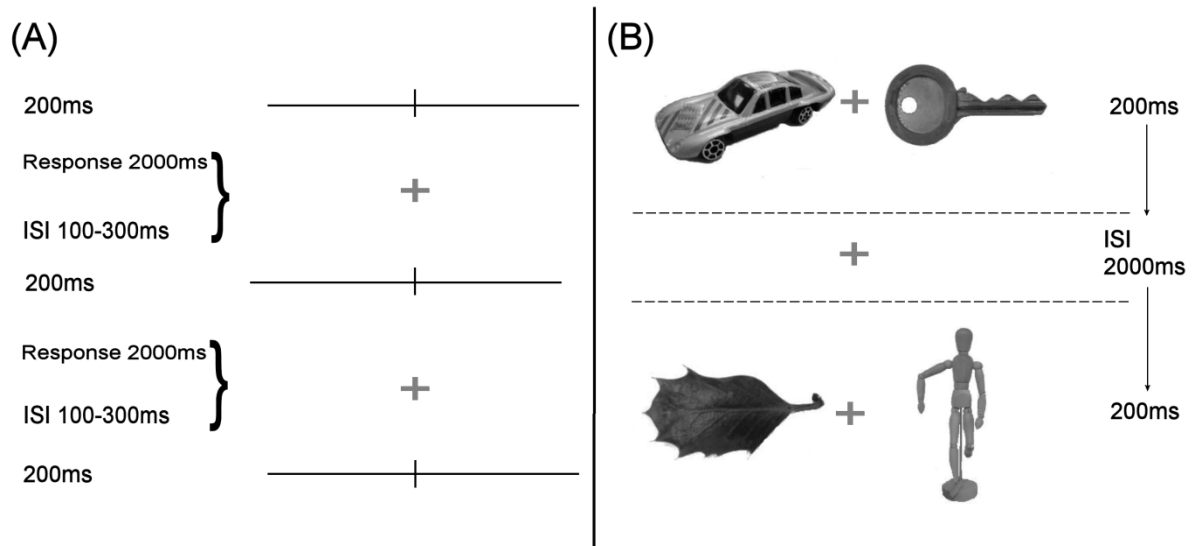


Figure 3.4: A schematic representation of the landmark task (A) and object perception task (B). From top to bottom, the landmark task images represent stimuli with (1) -5%, (2) 5%, and (3) 0% divergence from centre.

All images used in the object perception task were digital photographs of everyday objects (see Fig 3.4B). Stimuli were selected from a database of images Migo *et al.*, (2013) consisting of 48 object sets (for example, scissors, keys, apple), each set containing between 16 and 25 variants of the object (e.g., 16 different apples). A further 72 object sets (each containing 17 object variants) were selected from a similar database (Konkle, Brady, Alvarez, & Oliva, 2010).

The width of each object image was 25% of TSW. Object image height was variable but never exceeded 25% of TSW. Object images were presented on the left (centre of image at 35% TSW), and right (65% TSW) side of visual space. The screen was the same size for all participants. However, due to technical limitations of MRI compatible goggles, it is not possible to quantify the exact size of the screen or the precise visual angle required to view images. Prior to beginning the experiment, participants all reported that they could see the text on the preparatory screen clearly (this text occupied the majority of positions that were later taken by the object images) and no participants indicated difficulty viewing the images when questioned after the session.

Procedure

Participants completed four blocks of object perception, landmark task, and a memory test in the current experiment. Only fMRI data from the object perception and landmark task are presented here. In each object perception block, two different object images were presented

simultaneously either side of a central fixation cross for 200ms. Participants were instructed to maintain fixation on the central fixation cross and use their peripheral vision to take in as much information as they could about both images. The inter-stimulus interval, during which a fixation cross was visible (to ensure implicit null events), was jittered between 1500ms and 2500ms (average = 2000ms). Each object perception block consisted of 45 events; 30 two-object presentations, and 15 null events of the same duration consisting of only the central fixation cross. 120 pairs of images (240 images) were shown across all four object perception blocks. The order of presentation of image pairs was pseudo-randomised for each participant with the condition that null trials should be non-consecutive.

The location of each image during study was fully counterbalanced across participants (participant 1 encountered apple_1 on the left, participant 2 encountered apple_1 on the right). Two objects from the same object set (e.g. two apples) were never shown in the same pair. During the object perception task, participants were not required to respond but were strongly encouraged to try to encode as much detail about the objects as they could.

Following the observation of all image pairs in the object perception phase of each block, participants completed 36 judgements of the landmark task intermixed with 18 null events. On average, each event lasted 2400ms. Lines were presented for 200ms, and participants were asked to indicate as soon as possible whether the left or right end of the horizontal line was closest to centre (response time was limited to 2000ms). The intertrial interval was between 100ms and 300ms (average = 200ms). Null events consisted of an unchanging fixation cross throughout this time. Participants were instructed to indicate which end of the horizontal line was closest to the vertical line. Participants responded using their index and middle fingers of their right hand for a left and right response respectively.

Subjects' memory for objects they observed in the object perception was then tested. At test, two images, one that had been presented previously (target) and one similar unseen item (similar lure) were presented centrally one after the other. Participants were asked to indicate which of the two images had been seen before. Images from each study location (left and right) were equally and randomly distributed between the first and second presentations at test. Trial order was also randomised.

A practice session was conducted prior to entering the scanner. 16 pairs of object images and 8 null events were shown in the practice object perception phase. 16 pairs that were sourced from the practise object perception list were shown as part of the practice test phase. Subjects also completed 16 practise landmark task trials.

fMRI Acquisition and Analyses

Prior to engaging in the behavioural fMRI procedure, participants acclimatised and rested in the scanner whilst T1-weighted images (matrix size: 256 x 256, 180 slices, voxel size: 1mm isotropic) were obtained. Functional images assessing the blood oxygenation level dependent (BOLD) signal were then collected using a SENSE spiral-in sequence. Across four sessions, we acquired 920 (230 per session) volumes (TR = 2.5s; TE = 35ms). Each volume consisted of 40 slices (matrix size: 96 x 96; voxel size: 2.5 x 2.5 x 3.5 mm³). The participant's head was stabilized using foam wedges and soft pads. This minimised motion during scanning. Earplugs were provided to minimize MRI scanner related noise.

SPM12 (Statistical Parametric Mapping, Wellcome Department of Cognitive Neurology, University College London, London, UK; Available at: <http://www.fil.ion.ucl.ac.uk/spm/>) was used to pre-process and analyse the MRI data. Data were realigned within and between each session and then co-registered to the individual's anatomical scan. Anatomical images were segmented into white matter, grey matter, and CSF and the normalisation parameters were then applied to the participants' functional scans. Following normalisation, functional images were smoothed with a 5 x 5 x 7mm FWHM Gaussian kernel. The Art Repair toolbox revealed that there was minimal motion in all participants' volumes which did not exceed 2mm and 2 degrees.

Functional data were analysed using the general linear model (GLM) framework within an event-related design modelling the canonical hemodynamic response function. Landmark task trials were grouped into conditions based on the response of the subject. This resulted in two landmark task conditions that represented trials where participants had perceived the left (1) or right (2) side of the horizontal line as closer to the centre. Null events in the landmark task (3) were classified as a separate condition. We classified the object perception task based on subsequent memory performance. Trials were grouped into conditions according to whether both items from study were not later recognised (4), the left item was recognised and the right was missed (5), the right item was recognised and the left was missed (6), or both items were

recognised (7). Null events were classified as a separate condition (8). Conditions of no interest and time periods relating to the test phase were also modelled as separate conditions but are not reported here. The time series was high-pass filtered to remove low-frequency noise (<128s). First-level linear contrasts were calculated to produce effect estimates for each participant. Each subject's mean contrast estimate was then entered into a second-level one sample *t*-test analysis.

Results - Experiment 3.2

Behaviour

Measure	Condition	Mean	Standard Deviation	95% Confidence Interval
Side Preference	Shorter Left Side	81.74%	8.22%	77.94 - 85.54%
	Shorter Right Side	83.70%	10.99%	78.63 - 88.79%
Reaction Times	Shorter Left Side	442.97ms	97.38ms	394.55 - 491.39ms
	Shorter Right Side	461.78ms	116.27ms	403.97 - 519.60ms
Subsequent Memory	Both Missed	20.67%	5.21%	18.15 - 23.17%
	Left Hit, Right Missed	26.39%	5.94%	23.52 - 29.24%
	Right Hit, Left Missed	23.04%	6.93%	19.69 - 26.36%
	Both Hit	29.55%	2.61%	28.28 - 30.80%

Table 3.1: A table of descriptive statistics for behavioural measures in Experiment 3.2.

One-sample *t*-tests assessed the difference between the frequency of “shorter left side” (henceforth referred to as a left response) and “shorter right side” (right) responses on the landmark task. Reaction times of left and right-sided line centre judgements were also analysed. *Table 3.1* provides descriptive statistics for these conditions. Subjects were very accurate at identifying the shortest side of each line judgement (mean accuracy = 88.70%). Interestingly, reaction times in line centre judgements that produced a left response were significantly faster ($t(17) = 2.29$, $p = 0.035$, $d = 0.54$) than right responses (*Fig 3.5A*). We did not observe a difference between accuracy for left or right line centre judgements ($t(17) = 0.67$, $p = 0.51$).

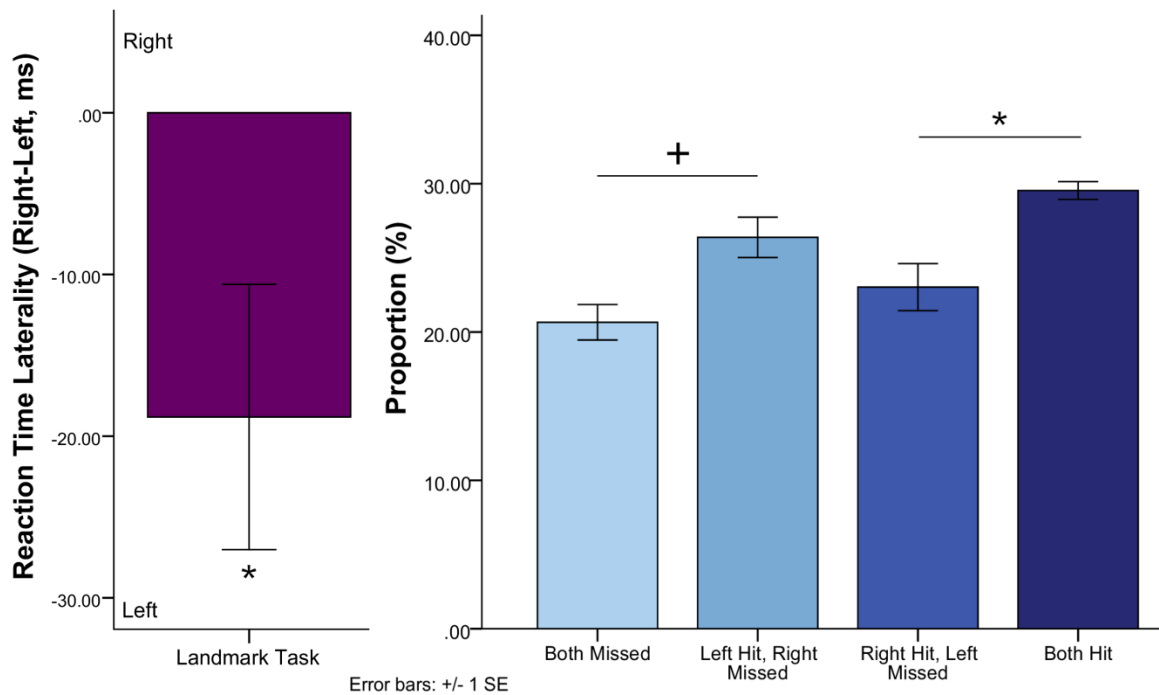


Figure 3.5: **A)** An illustration of the significantly faster reaction times observed with left than right judgements ($p = 0.035$). **B)** The proportion of responses in the Both Hit category was greater than in the Both Missed and Right Hit, Left Missed subsequent memory types. The proportion of Left Hit, Right Missed responses was also greater than the proportion of Both Missed responses. *** signifies a p value < 0.001 , * signifies a p value = 0.025, + signifies a p value < 0.05 uncorrected for Bonferroni multiple comparisons.

The following analyses are presented to contextualise the use of encoding trials that were classified as both hit; right hit, left missed; left hit, right missed; both missed in our subsequent comparison with the landmark task. The potential for a difference in the proportion of subsequent memory types (Both Missed (1); Left Hit, Right Missed (2); Right Hit, Left Missed (3); Both Hit (4)) was assessed with a one-way ANOVA with repeated measures. We observed a significant main effect of subsequent memory type in the proportions of trial classifications ($F(2.19, 37.20) = 6.73$, $p = 0.003$, $\eta_p^2 = 0.28$, sphericity not assumed). Subsequent pairwise comparisons revealed that the proportion of responses in the Both Hits category was greater than in the Both Missed and Right Hits, Left Missed categories (BH/BM - $p < 0.001$; BH/RHLM - $p = 0.030$). We also observed a greater proportion of responses in the Left Hit, Right Missed category than in the Both Missed category ($p = 0.023$, uncorrected for Bonferroni multiple comparisons). All other comparisons in the analysis produced p values > 0.05 (uncorrected). These proportions

are displayed in *Fig 3.5B*. These comparisons allow for the theoretical comparison of lateralisation biases between the object and landmark tasks in our discussion.

Neuroimaging

We investigated the brain activity that accompanied the object perception task that produced the different subsequent memory effects. This analysis is focussed on the Both Hit subsequent memory condition. The Both Hit and landmark task conditions both require the fast allocation of attention and perceptual processing to both sides of visual space. For completeness, the same analysis was conducted with data from the other subsequent memory conditions and no notable differences were observed. Contrast maps for these conditions versus the null events are provided in *Supplementary Fig 3.1*.

When Both Hit trials were compared with the null condition, the substantial differences in the quantity of visual information produced notable differences in activity in visual processing regions (*Fig 3.6A*). We observed a significant cluster of activity across visual regions ($k = 2793$) (*Supplementary Table 3.2*). Peak activation ($F(1,14) = 133.83$, $p_{\text{FDR}} = 0.019$) occurred in the temporal aspect of the right fusiform gyrus (BA 37, $x = 33$, $y = -44.5$, $z = -14$).

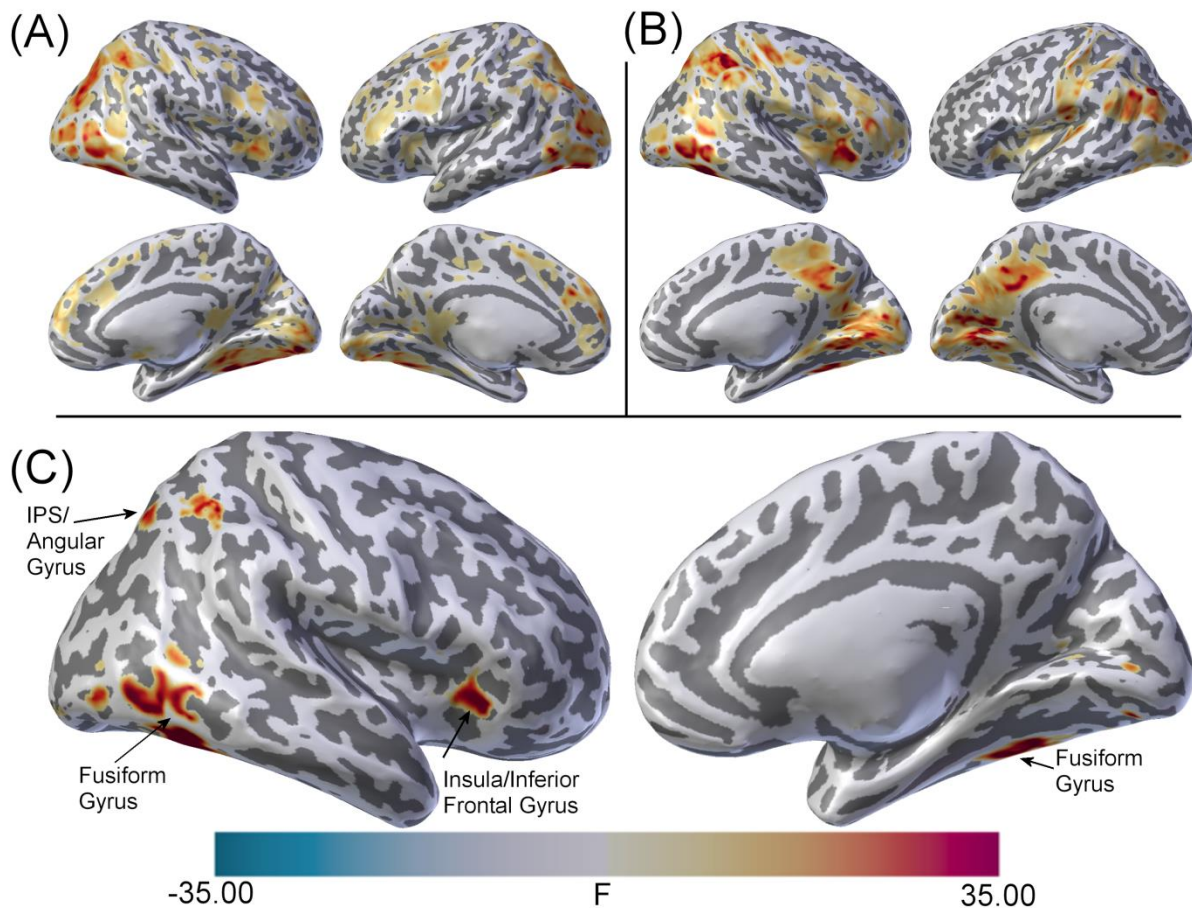


Figure 3.6: **A)** Successful object perception produced greater activity than null events (presentation of fixation cross) in the dorsal and ventral visual streams. **B)** Contrasting activity that was associated with the landmark task with null events revealed activity in the right fusiform gyrus and bilateral parietal cortices. **C)** Inclusive masking of images B and C allowed for identification of voxels that exhibited greater activation during both object perception, and landmark task trials. Colour intensity reflects the F statistic of the contrast. All images display only voxels that survived cluster based FDR correction for multiple comparisons.

Completion of the landmark task was associated with a more limited range of areas than the object perception task. These included substantial activations in the bilateral parietal cortices (left - $k_E = 322$, right - $k_E = 316$), and right fusiform gyrus ($k_E = 132$). Fig 3.6A displays the voxels that showed activity associated with all landmark task judgements. Regions that showed activation in the landmark task are listed in *Supplementary Table 3.1*. Landmark task trials associated with left and right line-centre judgements were also analysed separately (*Supplementary Fig 3.2A & B*).

A conjunction analysis identified brain regions that were active both in the landmark task and the object perception task. In line with the hypotheses of this study, we observed co-activation

of the right fusiform gyrus in the landmark task and object perception/study task ($x = 41, y = -50, z = -18$). All brain regions that demonstrated activations in the two tasks are listed in *Table 3.2* and displayed in *Fig 3.6C*. Separate conjunction analyses were also conducted using the response-dependent landmark task conditions (left or right judgements). These revealed highly similar results to the conjunction between object perception and all landmark trials.

Cluster	Location (aal)	BA	Voxels	MNI $x y z$	Z-value
$k_E = 536$ $q < 0.001$	Cerebellum 4-5 (R)	NA	66	18 -50 -21	6.01
	Inferior Occipital Cortex (R)	37	73	43 -62 -14	5.58
	Fusiform Gyrus (R)	37	132	41 -50 -18	5.11
	Inferior Temporal Cortex (R)	37	172	53 -57 -7	5.11
	Middle Occipital Cortex (R)	18	42	38 -82 0	3.87
$k_E = 56$ $q = 0.011$	Intraparietal Sulcus/Angular Gyrus (R)	7/39	37	36 -47 42	4.56
	Superior Parietal Cortex (R)	7	49	23 -65 49	3.92
$k_E = 47$ $q = 0.011$	Inferior Frontal Gyrus/Insula Cortex (R)	13	42	38 26 -4	4.46

Table 3.2: Brain region activations in the landmark task are listed that were also active in the object perception/study task. Only regions with activity that survived a FDR corrected cluster extent threshold of 35 voxels are listed.

Finally, we performed a Pearson's correlation analysis to assess whether the activity in the right fusiform gyrus, right parietal cortex, or inferior frontal gyrus (data extracted from a 6mm sphere surrounding the peak activation in the region) related to the left/right response bias or reaction time of individual subjects to left and right line-centre judgements on the landmark task. We observed a significant (uncorrected for multiple comparisons) association between the difference in the percentage of left and right line-centre judgements and the BOLD signal in the fusiform gyrus during these judgements ($r = 0.477, p = 0.045, Fig 3.7A$). This showed that subjects displaying more BOLD activity in the fusiform gyrus also produced more judgement errors on the right line-centre judgements (from overestimating the size of the right side of the line) and/or fewer errors on the left line-centre judgements (a reduction in the overestimation

of the left side of the line). This brain-behaviour relationship was not evident in the right parietal cortex or inferior frontal gyrus ($r = 0.176$, $p = 0.485$; $r = 0.067$, $p = 0.79$ respectively, Fig 3.7B & C). We did not observe significant associations between the BOLD signal and reaction times on the landmark task (fusiform gyrus - $r = 0.366$, $p = 0.122$, parietal cortex - $r = -0.252$, $p = 0.31$, inferior frontal gyrus - $r = -0.192$, $p = 0.44$).

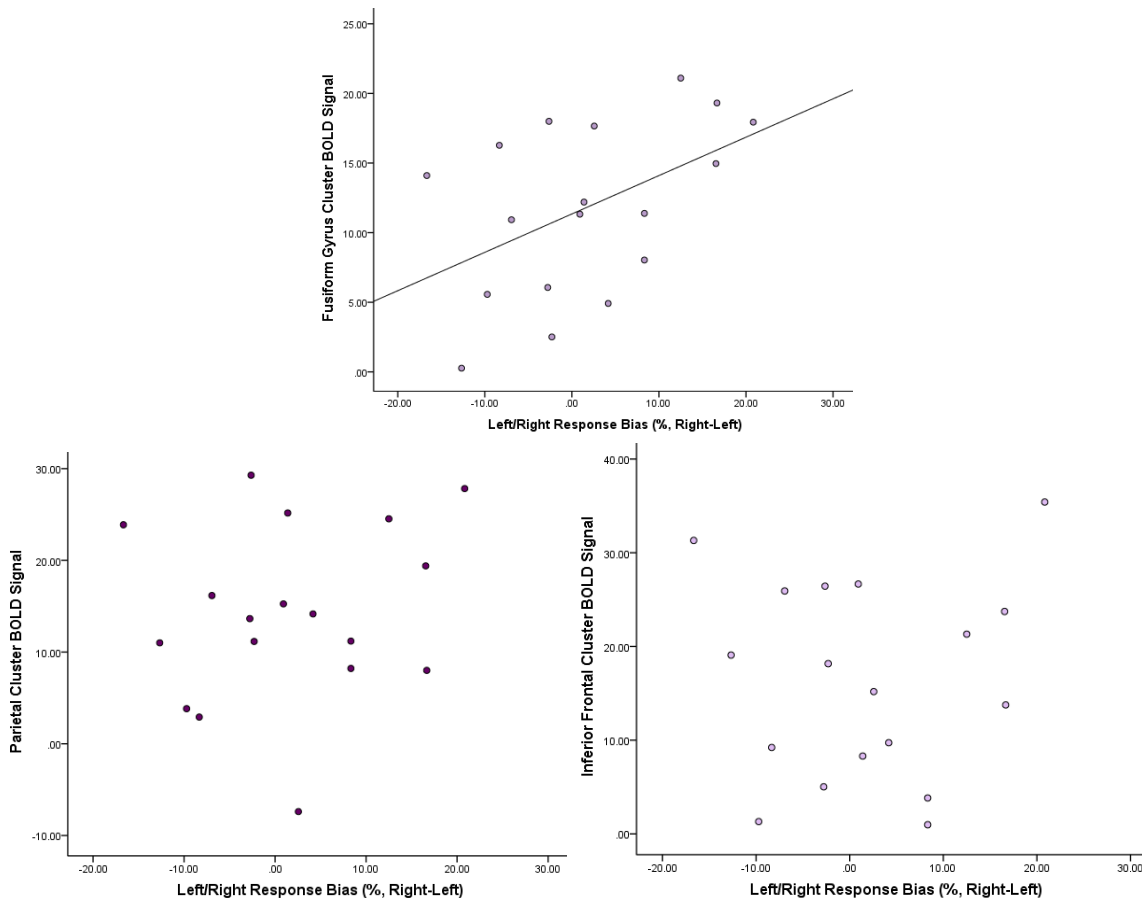


Figure 3.7: The difference in the BOLD signal between the landmark task and null trials was extracted from each of the clusters showing common activation in the landmark and object perception tasks. **A)** Greater BOLD signal in the fusiform gyrus was significantly (uncorrected) associated ($r = 0.477$, $p = 0.045$) with an increasingly rightward attention bias. **B)** No significant association was observed between the BOLD signal in the right parietal cortex cluster and the bias of attention ($r = 0.176$, $p = 0.485$). **C)** No significant association was observed between the BOLD signal in the inferior frontal gyrus cluster and the bias of attention ($r = 0.067$, $p = 0.79$).

Discussion

In experiment 3.2, we aimed to establish the feasibility of a common forced perspective, proximity-dependent mechanism to explain the line length effect and the target-observer proximity effect. Experiment 3.1 utilised a novel object bisection task (an adaptation of the traditional line bisection task) that revealed a significant relationship between taller object images (image width was matched across trials and the vertical centre of the image was always presented centrally) and increasingly leftward bisection errors (*Fig 3.3C*). The forced perspective, proximity-dependent mechanism proposes that, in the absence of informative distance cues, both long lines and large objects are misperceived as more proximal to the observer than short lines and small objects. This mechanism is predicated on the similarity of perceptual and attention processing of lines and objects. Identification of the brain regions engaged during the landmark, and object perception tasks, employed in experiment 3.2, provided an excellent opportunity for this comparison.

Here, we demonstrated activation that was common to both the landmark, and object perception tasks in regions (*Table 3.2*) traditionally associated with the allocation of attention (intraparietal sulcus/angular gyrus, superior parietal cortex, and insular cortex/inferior frontal gyrus) (Corbetta & Shulman, 2002, 2011). Both tasks were associated with activation in the VAN (IPL; *Fig 3.6C and Supplementary Table 3.1*). Covert orienting of attention has been closely linked to the processing of the IPL (Chambers, Payne, Stokes, & Mattingley, 2004). As a result, the IPL activation observed in both tasks was expected due to the common requirement for covert attention allocation. The inferior frontal gyrus activation that we also observe in both tasks has also previously been linked to the allocation of attention to a number of stimulus types. These regions are described within the ventral attention network and their damage frequently leads to unilateral hemispatial neglect of contralesional space (Corbetta & Shulman, 2011).

Interestingly, we also revealed extensive activation of the right fusiform gyrus in both tasks. The fusiform gyrus has been closely associated with the processing of objects and object recognition (neurosynth Z-score = 8.03). The neurosynth neuroimaging database (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) suggests that 74% of studies using objects report activation in the same location as the peak fusiform gyrus voxel observed here in the landmark task. The voxel

where we observed peak activation in the fusiform gyrus was not included in a mask of either the occipital or fusiform face area (Julian, Fedorenko, Webster, & Kanwisher, 2012). Instead, the location and extent of the conjunctive activation in the current study overlapped well with a lateral occipital object-selective processing mask (mask provided by 26). This provides some support to the proposal that this activation is a function of the object-like processing of lines.

Though we did not observe any significant differences in the number of left/right responses in the landmark task, we identified a correlation between the difference in the number of left and right responses and the extent of landmark task-related activity in the fusiform gyrus in a post-hoc Pearson's correlation analysis. This effect did not survive correction for multiple comparisons and should be interpreted with some caution. However, in the landmark task, an increase in the number of left/decrease in the number of right responses is reflective of greater allocation of attention to the right side of space (Reuter-Lorenz et al., 1990). In this case, more rightward attention allocation increases the overestimation of the size of the right side of a line and decreases the overestimation of the size of the left side of a line. This results in more “left shorter” responses and fewer “right shorter” responses. We suggest that the increasingly rightward response bias associated with greater activity in the fusiform gyrus reflects a similar bias to the more rightward biases associated with the bisection of objects that was observed in Gray and Montaldi (submitted, Chapter 1). If a line is considered as an object, rather than an abstract line, some attempt to classify the identity that object may recruit more processing in left hemisphere language centres. We do not suggest that this left FPA network processing would be equal to the recognition of semantically interesting objects (as in Gray and Montaldi (submitted, Chapter 1), but instead, that it may mitigate the right hemisphere bias associated with highly perceptual abstract processing.

Here, we utilised a task in which the participant was firmly directed towards the perceptual features of the objects while also allocating attention to both sides of space in a short period of time. This experiment has demonstrated the feasibility of the forced perspective, proximity-dependent account of the line length, and item-observer proximity effects. A conjunction analysis revealed activation during an object perception, and a landmark task in the IPL, IPS, and a region of the fusiform gyrus that has been closely linked with object processing. The activation, in both tasks, of regions of the brain associated with object processing and attention allocation also suggests that mechanistic explanations of line-based modulations of attention

(such as the line length effect) should also be explored and integrated with theories of object processing.

The absence of a behaviourally diagnostic measure of forced perspective, either through assessment of different line lengths in the landmark task, or objects of markedly different sizes in the object perception task, represents a limitation of the findings of experiment 3.2. Though regions engaged by the processing of line perception overlap considerably with object perception processing, we did not vary the engagement of line or object processing and therefore enable assessment of the functional significance of this overlap. Future research should produce a variant of the object bisection task (used in experiment 3.1 of this study) which utilises pre-bisected objects of different sizes. The natural variability in the size and shape of objects will enable a more detailed investigation of the neural underpinnings of the forced perspective, proximity-dependent account of the line length, and target-observer proximity effects.

We did not observe a rightward bias in subsequent memory in the object perception task in experiment 3.2. This object perception task was highly perceptually focused and was therefore unlike the object bisection task in experiment 3.1 (also presented in Gray and Montaldi (submitted)). Unlike experiment 3.2, participants in experiment 3.1 were unhurried in the object bisection task and could fully engage with the semantic and associative characteristics of the target. This additional opportunity afforded by the object bisection task to recruit semantic, non-perceptual processing produced a right visual field bias in spatial attention allocation. A previous study provided a similar direct comparison between a tightly time-limited and an unhurried attention allocation paradigm also showed a difference in attention allocation lateralisation. A pronounced pseudoneglect attention bias was associated with brief (500ms), but not lengthier (10s), presentations of semantically engaging naturalistic scenes (Dickinson & Intraub, 2009). Previous work has also shown a pseudoneglect effect with naturalistic environments (Dickinson & Intraub, 2009; McGeorge et al., 2007), and experiment 1 of this study helps to integrate the findings of Gray and Montaldi (submitted) with these previous observations.

Summary

The two experiments presented in this article provide a direct empirical assessment of our novel interpretation of the line length effect (leftward bias with long lines, increasingly rightward with shorter lines). Forced perspective is an illusion that results from the perceptual ambiguity between object size and object distance. We hypothesised that forced perspective would induce processing associated with different distances with lines of different lengths. The target-observer proximity effect describes the shift in the lateralisation of attention allocation from left to right with increasing distances between the target and the observer. We hypothesised that forced perspective interpretation of long lines as closer than short lines leads to the line length effect.

For the first time, experiment 3.1 showed that, like small lines, smaller objects elicit more rightward bisection errors. In contrast, larger objects, like long lines, produce stronger leftward attention allocation biases. A logical extrapolation based on the line length effect would predict the inverse relationship and as a result, cannot explain these observations. Instead, our forced perspective and target-observer proximity interpretation of the line length effect provides an excellent account of these results.

In experiment 3.2, we utilised fMRI to illustrate that object processing and attention allocation brain mechanisms are recruited during both the landmark task and a bilateral object perception task. Critically, the object-like processing of lines observed in experiment 3.2 suggests that small lines could easily be interpreted by the brain as small or distant objects, and that critically, they could feasibly be subject to the same forced perspective misperception as objects.

Using forced perspective, we have provided a novel mechanistic bridge between the line length and target-observer proximity effect. We have clearly demonstrated in this study that consideration of ecologically relevant variables can bring together apparently disparate strands of research to better characterise cognitive processes. With our forced perspective, proximity-dependent interpretation of the line length, and target-observer proximity effects, future work can utilise the methods that were uniquely developed by both streams of work. In addition, these experiments provide the cornerstone on which the characterisation of attention allocation

processing in increasingly ecologically realistic environments can be built. This progression is critical to attaining an absolute understanding of the distribution and prioritisation of attention in health and states of brain damage or disease.

References

- Anderson, B. (1996). A mathematical model of line bisection behaviour in neglect. *Brain*, 119(3), 841-50. <http://doi.org/10.1093/brain/119.3.841>
- Benwell, C. S. Y., Harvey, M., Gardner, S., & Thut, G. (2013). Stimulus- and state-dependence of systematic bias in spatial attention: additive effects of stimulus-size and time-on-task. *Cortex*, 49, 827-36. <http://doi.org/10.1016/j.cortex.2011.12.007>
- Benwell, C. S. Y., Harvey, M., & Thut, G. (2014). On the neural origin of pseudoneglect: EEG-correlates of shifts in line bisection performance with manipulation of line length. *NeuroImage*, 86, 370-80. <http://doi.org/10.1016/j.neuroimage.2013.10.014>
- Benwell, C. S. Y., Thut, G., Grant, A., & Harvey, M. (2014). A rightward shift in the visuospatial attention vector with healthy aging. *Frontiers in Aging Neuroscience*, 6, 113-124. <http://doi.org/10.3389/fnagi.2014.00113>
- Benwell, C. S. Y., Thut, G., Learmonth, G., & Harvey, M. (2013). Spatial attention: differential shifts in pseudoneglect direction with time-on-task and initial bias support the idea of observer subtypes. *Neuropsychologia*, 51(13), 2747-56. <http://doi.org/10.1016/j.neuropsychologia.2013.09.030>
- Beschin, N., Cocchini, G., Della Sala, S., & Logie, R. H. (1997). What the Eyes Perceive, The Brain Ignores: A Case of Pure Unilateral Representational Neglect. *Cortex*, 33, 3-26. [http://doi.org/10.1016/S0010-9452\(97\)80002-0](http://doi.org/10.1016/S0010-9452(97)80002-0)
- Brown, T. I., Rissman, J., Chow, T. E., Uncapher, M. R., & Wagner, A. D. (2018). Differential Medial Temporal Lobe and Parietal Cortical Contributions to Real-world Autobiographical Episodic and Autobiographical Semantic Memory. *Scientific Reports*, (April), 1-14. <http://doi.org/10.1038/s41598-018-24549-y>
- Chambers, C. D., Payne, J. M., & Mattingley, J. B. (2007). Parietal disruption impairs reflexive spatial attention within and between sensory modalities. *Neuropsychologia*, 45(8), 1715-1724. <http://doi.org/10.1016/j.neuropsychologia.2007.01.001>
- Churches, O., Loetscher, T., Thomas, N. A., & Nicholls, M. E. R. (2017). Perceptual biases in the horizontal and vertical dimensions are driven by separate cognitive mechanisms. *Quarterly Journal of Experimental Psychology*, 70(3), 444-460. <http://doi.org/10.1080/17470218.2015.1131841>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201-15. <http://doi.org/10.1038/nrn755>
- Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. *Annual Reviews Neuroscience*, 34, 569-99. <http://doi.org/10.1146/annurev-neuro-061010-113731>
- Dickinson, C. A., & Intraub, H. (2009). Spatial Asymmetries in Viewing and Remembering Scenes: Consequences of an Attentional Bias? *Attention Perception and Psychophysics*, 71(6), 1251-1262. <http://doi.org/10.3758/APP.71.6.1251>
- Duecker, F., & Sack, A. T. (2015). The hybrid model of attentional control: New insights into hemispheric asymmetries inferred from TMS research. *Neuropsychologia*, 74, 21-29. <http://doi.org/10.1016/j.neuropsychologia.2014.11.023>
- Fink, G. R., Marshall, J. C., Weiss, P. H., Toni, I., & Zilles, K. (2002). Task instructions influence the cognitive strategies involved in line bisection judgements - evidence from modulated

- neural mechanisms revealed by fMRI. *Neuropsychologia*, 40, 119-30.
[http://doi.org/10.1016/S0028-3932\(01\)00087-2](http://doi.org/10.1016/S0028-3932(01)00087-2)
- Gamberini, L., Seraglia, B., & Priftis, K. (2008). Processing of peripersonal and extrapersonal space using tools: Evidence from visual line bisection in real and virtual environments. *Neuropsychologia*, 46(5), 1298-1304. <http://doi.org/10.1016/j.neuropsychologia.2007.12.016>
- Gray, O.J., & Montaldi, D. (submitted). Attention Allocation Systems Selectively Specialised for Spatial or Semantic Processing: A Reversed Pseudoneglect Effect.
- Hatin, B., Sykes Tottenham, L., & Oriet, C. (2012). The relationship between collisions and pseudoneglect: Is it right? *Cortex*, 48(8), 997-1008.
<http://doi.org/10.1016/j.cortex.2011.05.015>
- Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, 30, 327-330. <http://doi.org/10.1212/WNL.30.3.327>
- Hughes, L. E., Bates, T. C., & Aimola Davies, A. (2004). Grasping at sticks: pseudoneglect for perception but not action. *Experimental Brain Research*, 157(3), 397-402.
<http://doi.org/10.1007/s00221-004-1958-2>
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, 38(1), 93-110.
[http://doi.org/10.1016/S0028-3932\(99\)00045-7](http://doi.org/10.1016/S0028-3932(99)00045-7)
- Julian, J. B., Fedorenko, E., Webster, J., & Kanwisher, N. (2012). An algorithmic method for functionally defining regions of interest in the ventral visual pathway. *NeuroImage*, 60(4), 2357-2364. <http://doi.org/10.1016/j.neuroimage.2012.02.055>
- Kinsbourne, M. (1977). Hemi-neglect and hemisphere rivalry. *Advances in Neurology*, 18, 41-9.
- Konkle, T., Brady, T. F., Alvarez, G. A., & Oliva, A. (2010). Conceptual distinctiveness supports detailed visual long-term memory for real-world objects. *Journal of Experimental Psychology: General*, 139(3), 558-578. <http://doi.org/10.1037/a0019165>
- Loftus, A. E., & Nicholls, M. E. R. (2012). Testing the activation-orientation account of spatial attentional asymmetries using transcranial direct current stimulation. *Neuropsychologia*, 50(11), 2573-6. <http://doi.org/10.1016/j.neuropsychologia.2012.07.003>
- Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, 44(6), 977-981.
<http://doi.org/10.1016/j.neuropsychologia.2005.09.003>
- Longo, M. R., Trippier, S., Vagnoni, E., & Lourenco, S. F. (2015). Right hemisphere control of visuospatial attention in near space. *Neuropsychologia*, 70, 350-357.
<http://doi.org/10.1016/j.neuropsychologia.2014.10.035>
- Lourenco, S. F., & Longo, M. R. (2009). The plasticity of near space: Evidence for contraction. *Cognition*, 112(3), 451-456. <http://doi.org/10.1016/j.cognition.2009.05.011>
- Matthews, A., & Linehan, G. (1997). Father Ted. Channel 4.
- McCourt, M. E., & Jewell, G. (1999). Visuospatial attention in line bisection: Stimulus modulation of pseudoneglect. *Neuropsychologia*, 37, 843-855. Retrieved from
<http://www.sciencedirect.com/science/article/pii/S0028393298001407>

- McGeorge, P., Beschin, N., Colnaghi, A., Rusconi, M. L., & Della Sala, S. (2007). A lateralized bias in mental imagery: evidence for representational pseudoneglect. *Neuroscience Letters*, 421(3), 259-63. <http://doi.org/10.1016/j.neulet.2007.05.050>
- Mesulam, M. (1981). A cortical network for directed attention and unilateral neglect. *Ann Neurol*, 10, 309-25. <http://doi.org/10.1002/ana.410100402>
- Mesulam, M. (1999). Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Phil. Trans R. Soc. Lond. B*, 354, 1325-46. <http://doi.org/10.1098/rstb.1999.1003>
- Migo, E., Montaldi, D., & Mayes, A. R. (2013). A visual object stimulus database with standardized similarity information. *Behavior Research Methods*, 45(2), 344-54. <http://doi.org/10.3758/s13428-012-0255-4>
- Monaghan, P., & Shillcock, R. (1998). The cross-over effect in unilateral neglect: Modelling detailed data in the line-bisection task. *Brain*, 121, 907-21. Retrieved from <https://www.ncbi.nlm.nih.gov/pubmed/?term=Monaghan++The+cross-over+effect+in+unilateral+neglect>
- Nicholls, M. E. R., & Roberts, G. R. (2002). Can free-viewing perceptual asymmetries be explained by scanning, pre-motor or attentional biases? *Cortex*, 38, 113-136. [http://doi.org/10.1016/S0010-9452\(08\)70645-2](http://doi.org/10.1016/S0010-9452(08)70645-2)
- Nicholls, M. E. R., Thomas, N. A., Loetscher, T., Wignall, S., Yates, M. J., Forte, J. D., & Spence, C. J. (2012). The relationship between vertical stimulation and horizontal attentional asymmetries. *Quarterly Journal of Experimental Psychology*, 65(12), 2384-2396. <http://doi.org/10.1080/17470218.2012.688979>
- Reuter-Lorenz, P. A., Kinsbourne, M., & Moscovitch, M. (1990). Hemispheric control of spatial attention. *Brain and Cognition*, 12, 240-6. [http://doi.org/10.1016/0278-2626\(90\)90018-J](http://doi.org/10.1016/0278-2626(90)90018-J)
- Rinaldi, L., Bertolini, G., Bockisch, C. J., Maravita, A., Girelli, L., & Brugger, P. (2018). More far is more right: Manual and ocular line bisections, but not the Judd illusion, depend on radial space. *Brain and Cognition*, 122, 34-44. <http://doi.org/10.1016/j.bandc.2018.01.009>
- Robertson, J. S., Forte, J. D., & Nicholls, M. E. R. (2015). Deviating to the right: Using eyetracking to study the role of attention in navigation asymmetries. *Attention, Perception, and Psychophysics*, 77(3), 830-843. <http://doi.org/10.3758/s13414-014-0813-1>
- Schneider, W., Eschmann, A., & Zuccolotto, A. (2012). *E-Prime User's Guide*. Pittsburgh: Psychology Software Tool, Inc. Retrieved from https://www.researchgate.net/publication/260296789_E-prime_User%27s_Guide
- Seghier, M. L. (2013). The angular gyrus: Multiple functions and multiple subdivisions. *Neuroscientist*, 19(1), 43-61. <http://doi.org/10.1177/1073858412440596>
- Shelton, P. A., Bowers, D., & Heilman, K. M. (1990). Peripersonal and vertical neglect. *Brain*, 113(1), 191-205. <http://doi.org/10.1093/brain/113.1.191>
- Slagter, H. A., Davidson, R. J., & Tomer, R. (2010). Eye-blink rate predicts individual differences in pseudoneglect. *Neuropsychologia*, 48, 1265-1268. <http://doi.org/10.1016/j.neuropsychologia.2009.12.027>
- Szczepanski, S. M., & Kastner, S. (2013). Shifting attentional priorities: Control of spatial attention through hemispheric competition. *Journal of Neuroscience*, 33(12), 5411-21. <http://doi.org/10.1523/JNEUROSCI.4089-12.2013>

- Thiebaut de Schotten, M., Urbanski, M., Duffau, H., Volle, E., Lévy, R., Dubois, B., & Bartolomeo, P. (2005). Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans. *Science*, pp. 2226-8. <http://doi.org/10.1126/science.1116251>
- Thomas, N. A., Castine, B. R., Loetscher, T., & Nicholls, M. E. R. (2015). Upper visual field distractors preferentially bias attention to the left. *Cortex*, 64, 179-193. <http://doi.org/10.1016/j.cortex.2014.10.018>
- Thomas, N. A., Loetscher, T., & Nicholls, M. E. R. (2014). Asymmetries in attention as revealed by fixations and saccades. *Experimental Brain Research*, 232, 3253-67. <http://doi.org/10.1007/s00221-014-4015-9>
- Verdon, V., Schwartz, S., Lovblad, K. O., Hauert, C. A., & Vuilleumier, P. (2010). Neuroanatomy of hemispatial neglect and its functional components: A study using voxel-based lesion-symptom mapping. *Brain*, 133(3), 880-894. <http://doi.org/10.1093/brain/awp305>
- Wiseman, R. (2016). A new version of the beuchet chair illusion. *I-Perception*, 7(6), 0-4. <http://doi.org/10.1177/2041669516679168>
- Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C., & Wager, T. D. (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nature Methods*, 8(8), 665-670. <http://doi.org/10.1038/nmeth.1635>

Chapter 4: Convergent Evidence for Hemispheric Specialisation of Memory Retrieval Mechanisms in the Inferior Parietal Lobule

Abstract

A diverse range of functions reportedly involve the inferior parietal lobule (IPL; angular gyrus and supramarginal gyrus). However, these have proven difficult to fully characterise and in many cases, the processing that is performed by the IPL remains poorly understood. IPL processing has been implicated in episodic memory retrieval, as well as attention allocation, and semantic conceptual judgements. The right hemisphere IPL has been closely linked with the specialised processing of spatial attention, whereas the left hemisphere IPL has been more closely associated with episodic memory retrieval. As a function of this apparent specialisation, causal investigations of the IPL and memory have focused solely on left hemisphere IPL function. However, no studies have directly investigated this apparent distinction in hemispheric specialisation until now. Here, we propose, and provide novel and compelling evidence, that the recruitment of the IPL of each hemisphere is highly dependent on the informational content of a retrieved episode. First, we classify previous fMRI reports of IPL activity arising from episodic memory retrieval (111 contrasts, 73 studies) according to our proposed perspective on IPL hemispheric specialisation. We demonstrate that across the literature, activity in the right IPL is consistently associated with retrieval of the perceptual/experiential aspects of memory (96% right/80% left). In contrast, activation of the left IPL is consistently associated with retrieval of the semantic/conceptual aspects of memory (95.1% left/45.9% right). Second, using fMRI, we describe, with a focus on the IPL, the neural bases of retrieval, when accurate memory is dependent on perceptual, and not semantic, information (an object forced-choice recognition paradigm with highly similar lures). In this task, we show that, whereas the activity of the left angular gyrus decreases relative to baseline, the right angular gyrus increases its activity. This highly consistent and divergent pattern, not observed in other core recollection or default mode network areas, supports our novel perspective of IPL hemispheric specialisation in memory retrieval. Our evidence redefines IPL functional specialisation, refines our understanding of both left and right IPL processing, and should guide future investigations exploring the role of the right IPL and connected structures, in memory retrieval.

Introduction

Our understanding of the brain systems, rather than isolated structures, that enable the encoding, storage and retrieval of the what, where, and when of life events, otherwise known as episodic memories, has vastly improved with the advent of neuroimaging techniques. For the last 15 years, the functional role played by the inferior parietal lobule (IPL) (angular gyrus and supramarginal gyrus) in the retrieval of episodic memory has been a contentious frontier in cognitive neuroscience (Davidson et al., 2010; Hutchinson et al., 2009; Simons & Mayes, 2008; Wagner et al., 2005; Yazar et al., 2014, 2017). Successful retrieval of episodic memories has been strongly associated with neuroimaging activations of the IPL (Yazar, Bergström, & Simons, 2012). Despite the consistency of this association, an interesting disconnect exists between the seemingly minimal effects of damage to the IPL on memory and the IPL activity consistently observed during memory retrieval (Berryhill et al., 2007; Davidson et al., 2010; Simons et al., 2008).

A number of hypotheses have been presented by memory researchers to account for the theoretical discord between human lesion and neuroimaging observations (Ciaramelli et al., 2008; Simons et al., 2010; Vilberg & Rugg, 2008; Wagner et al., 2005). Amongst these hypotheses, the attention to memory (AToM) model of parietal cortex function has divided scientific opinion, and both support and criticism has been provided by highly variable investigative methods (Cabeza et al., 2011, 2008; Ciaramelli et al., 2008; Hutchinson et al., 2009).

The role of the IPL in the allocation of attention is relatively clear and has been thoroughly and causally investigated (Chambers & Heinen, 2010; Corbetta & Shulman, 2011; Gitelman et al., 1999; Szczepanski & Kastner, 2013). Aspects of the IPL have been shown to regulate the reflexive allocation of attention to salient information (Chambers et al., 2007; Corbetta & Shulman, 2011). The voluntary, goal-directed distribution of attention to the environment is processed by the intraparietal sulcus and the superior parietal cortex (Corbetta & Shulman, 2002, 2011). The AToM model proposes that the IPL performs conceptually similar functions in memory retrieval (Cabeza et al., 2011; Ciaramelli et al., 2008). Specifically, it suggests that the IPL reflects bottom-up attention allocation to the salient contents of medial temporal lobe output, and the superior lateral parietal cortex processes top-down exploration in memory

search (Cabeza et al., 2011, 2008; Ciaramelli et al., 2008; Hutchinson et al., 2009). Recent evidence has identified temporal and spatial distinctions between the areas in the IPL associated with the allocation of attention and memory retrieval (Capotosto et al., 2017; Hutchinson et al., 2009; Sestieri et al., 2010). These works have shown that the AToM model is likely to be an overly simplistic explanation of IPL function and that the particular nature of the relationship between these closely associated areas of cortex requires further investigation. Despite the evidence contravening the AToM model, the presence of multiple functional areas in the IPL does not preclude shared functional characteristics across these areas for attention and memory (Sestieri et al., 2017). We propose that hemispheric lateralisation in cortical processing may represent one functional characteristic that is very similar across these areas of cognition.

Pseudoneglect is a term used to describe the tendency of healthy individuals to implicitly and preferentially allocate more attention to the left visual field than the right. A large body of research attributes this effect to the specialisation of attention allocation processing by the right ventral attention network, including the IPL (e.g. Darling, Logie, & Della Sala, 2012; Jewell & McCourt, 2000; Nicholls, Hobson, Petty, Churches, & Thomas, 2017; Slagter, Davidson, & Tomer, 2010; Zago et al., 2017). Pseudoneglect represents an example of a behavioural manifestation of IPL hemispheric specialisation in attention that might also be observed in memory. The IPL, namely the angular gyrus and supramarginal gyrus, and the temporo-parietal junction in the right hemisphere clearly show specialisation for the processing of perceptual spatial attention allocation (e.g. Darling, Logie, & Della Sala, 2012; Jewell & McCourt, 2000; Nicholls, Hobson, Petty, Churches, & Thomas, 2017; Slagter, Davidson, & Tomer, 2010; Zago et al., 2017). In contrast, the left hemisphere shows an obvious specialisation in language and semantic processing (Cai, Van der Haegen, & Brysbaert, 2013; Josse & Tzourio-Mazoyer, 2004; Knecht, 2000). Interestingly, the lateralisation of spatial attention allocation shifts away from the leftward pseudoneglect bias, when the semantic processing is engaged. Gray and Montaldi (submitted) observed a right visual field attention bias (a reversal of the pseudoneglect effect) when allocating attention to semantically engaging stimuli. This probably reflects hemispheric specialisation of the the left hemisphere IPL for the processing of the allocation of attention to semantic/conceptual stimuli (Davey et al., 2015; Neyens et al., 2017; Price, Pelle, Bonner, Grossman, & Hamilton, 2016).

Here, we first present an investigation of whether the distinction in hemispheric specialisation of the IPL previously observed in attention allocation and semantic processing is also evident for episodic memory processing. We performed a systematic review of previous fMRI investigations of episodic memory retrieval that observed IPL activations. These highly variable previous studies were classified according to whether they assessed the retrieval of either perceptual/experiential or semantic/conceptual aspects of memories. Memory assessments were classified according to both the content of the memory that had been encoded and the requirements of the retrieval challenge at test. A perceptually defined memory experience was characterised by two features: 1) detailed sensory information, most often in the visual domain, and 2) memory tests in which accurate performance was highly dependent on re-experiencing sensory information. For example, the detailed perceptual features of the encoded item (e.g. a semi-consumed lager beer) are crucial to distinguishing between two similar variants of the same item (e.g. distinguishing between your beer and the beer belonging to a second party). Two different criteria were used to classify a semantic and conceptually defined memory experience: 1) information stored in memory with limited perceptual detail, and 2) memory tests in which accurate performance could be effectively achieved through memory for a semantic or conceptual label for the information. For example, without needing to draw on the raw percept that led to that memory, one may recognise they had encountered the concept 'wine' earlier.

We hypothesised that attempting to retrieve perceptual information from memory would reveal activations that were more closely related to spatial attention allocation processing. In contrast, tasks or contrasts that targeted semantic or conceptual information in memory would better reflect semantic processing systems. As a result, paradigms in which performance was dependent on remembering perceptual details of the original encounter, rather than semantic features/concepts, were expected to be most likely to engage the right hemisphere IPL. Conversely, we expected left hemisphere IPL activations to be more prevalent during semantic/conceptual memory.

Systematic Review of IPL Episodic Retrieval Memory Effects - Experiment 4.1

The process of identification, screening, and classification of eligible studies is illustrated in the PRISMA 2009 flow diagram *Supplementary Fig 4.1*. A brief summary of the encoding and retrieval methods, specific contrasts, and the resulting IPL activations of each study included in the review are provided in *Supplementary Tables 4.1* and *4.2*.

Studies were identified through <https://www.ncbi.nlm.nih.gov/pubmed> searches. We identified studies written in the English language for assessment of eligibility using the terms: episodic, memory, retrieval, and fMRI. Studies included in the analysis contained at least one memory contrast with an activation reported (in a table of activations) in the angular gyrus and/or supramarginal gyrus of the left and/or right hemisphere. The exact locations within the IPL that showed activity in these contrasts was not recorded. These were not required to assess the hemispheric lateralisation of the IPL that was associated with each memory type. In *Supplementary Tables 4.1* and *4.2*, we provide details of the contrast of interest, as well as the encoding and retrieval procedures that were performed by participants.

We distinguished between memory contrasts that probed semantic/conceptual information at retrieval and those that required the retrieval of perceptual details (see criteria on the previous page). The consistency with which IPL activations were observed in these two classes of studies was classified as a dependent variable.

Results and Discussion

Imaging contrasts of memory paradigms that require retrieval of perceptual information show activation of the right IPL in 96% of cases (48/50). The same contrasts elicit left IPL activations in 80% (40/50) of cases. Instead, the left IPL is active far more consistently, 95.1% (58/61), than the same cortical area in the right hemisphere, during the retrieval of semantic or conceptual information, 45.9% (28/61). These studies collectively highlight a relationship between hemispheric specialisation of IPL engagement and perceptual versus semantic processing in episodic memory.

This review has therefore identified a clear relationship between the hemispheric lateralisation of IPL activations in fMRI investigations of episodic retrieval and the informational nature of the target memory. Some specific examples of these fMRI studies offer a particularly clear insight into this hemispheric specialisation. For example, Dobbins & Wagner, (2005) provided a comparison of the retrieval mechanisms associated with semantic and perceptual source memories. A recognition contrast in which subjects recollected items that were encoded with a semantic judgement revealed left hemisphere lateralised activations of the IPL and other nodes of the core recollection network. In contrast, recollection of perceptual memory features was associated with comparable areas exclusively in the right hemisphere. Similarly, right, but not left hemisphere IPL was active during recall of perceptually rich visually observed video clips compared to perceptually impoverished narrative descriptions of the clips (St-Laurent, Moscovitch, & McAndrews, 2016). In contrast to these observations with perceptual/experiential memory studies, source recognition of noun words that were encoded with one of two semantic judgements activated a highly left hemisphere lateralised network of cortical regions that included the left IPL (Frithsen & Miller, 2014). These lateralisation distinctions are typical of those observed throughout the review. A large number of contrasts (63/111) showed bilateral activations of the IPL. The bilateral activations in these contrasts most likely reflects the presence of both perceptual and semantic information in the retrieved episode.

The angular gyrus is a subdivision of the IPL and a node of the default mode network (DMN). It exhibits changes in activity with a wide variety of tasks. Interestingly, Seghier, Fagan, & Price, (2010) observed three functional subdivisions within the left angular gyrus. Two subregions were implicated in a default mode network role, where their activity changed in all tasks relative to

fixation (increase in dorsomedial angular gyrus, and decrease in middle angular gyrus). In the ventrolateral angular gyrus, activity changed according to a semantic matching task. Interestingly, a recent study of functional connectivity during retrieval revealed substantial connectivity of the left angular gyrus with other non-medial temporal cortex nodes of the default mode network. In contrast, the right angular gyrus exhibited strong retrieval-related functional connectivity with the medial temporal lobe (Bellana et al., 2016). These highlighted works, along with the collective assessment of IPL activations in episodic memory contrasts in this study, strongly suggest that the right IPL performs an important, and underappreciated functional role in memory retrieval.

Many recognition tasks require very little retrieval of the perceptual features of an encoding experience (i.e., if we have conceptual memory that an apple was encoded, remembering what the apple looked like is not critical to recognition when the apple is presented alongside other fruits). Instead, retrieval of semantic concepts is often sufficient for accurate recognition memory. In many of the studies that observe IPL episodic memory retrieval effects, semantic/conceptual memory alone could support accurate performance. For example, the traditional Yes/No memory task does not utilise similar lures at test. As a result, the representations of encoded items and new items are very different and can be successfully distinguished by a simple semantic label for each encoded target. The hippocampus plays a key role in supporting associative memory (Mayes et al., 2007; Montaldi & Mayes, 2010). Therefore, the hippocampus is likely to support the accurate associative retrieval of semantic labels and concepts without drawing on the IPL. This may explain why IPL patients do not appear amnesic when assessed with many traditional memory techniques.

Causal studies, utilising patients and neurostimulatory techniques, have shown evidence of a functional role of the IPL in the retrieval of perceptual experiences (Berryhill et al., 2007; Bonnici, Richter, Yazar, & Simons, 2016; Davidson et al., 2010; Nilakantan, Bridge, Gagnon, VanHaerents, & Voss, 2017). In contrast to memory for semantic/conceptual labels, these studies require retrieval and integration of multiple perceptual features. Davidson et al., (2010) observed that memory retrieval was impaired in patients with lateral parietal cortex lesions. In particular, details of autobiographical recall were reduced despite preserved descriptions of non-specific semantic details. In addition, the patients produced fewer remember responses during a remember/know recognition task. Simons, Peers, Mazuz, Berryhill, & Olson, (2010)

observed that during a recognition memory task, only *confidence* in recollections, not accuracy, was reduced in patients with IPL damage. Although this suggests an impairment of subjective memory in these patients, a reduction in their objective memory for the perceptual details of these recollections may also explain this effect. Interestingly, Yazar, Bergström, & Simons, (2017) recently demonstrated an impairment of the multimodal integration of perceptual features following transcranial magnetic stimulation of the left angular gyrus (the right hemisphere was not assessed). These studies all suggest that perceptual feature memory, but not semantic, conceptual memory, is impaired when IPL function is compromised. This was recently corroborated by a rare example of augmented perceptual memory precision following up-regulation of left angular gyrus activity (the right hemisphere was not assessed) with TMS (Nilakantan et al., 2017).

Left hemisphere IPL activations associated with episodic memory retrieval are observed with greater frequency than right IPL activations. We suggest that this difference in lateralisation is associated with the contents of memory retrieval. In addition, it appears that the DMN connectivity of the IPL is potentially distinct from its functional role in memory (Bellana et al., 2016). The consistent left hemisphere activity (strongly associated with semantic/DMN processing) has led many recent investigations into IPL function that focus solely on the left IPL (N.-F. Chen, Lo, Liu, & Cheng, 2016; Hutchinson et al., 2009; Nilakantan et al., 2017; Thakral, Madore, & Schacter, 2017; Yazar et al., 2014, 2017). The semantic processing that accompanies many memory tasks is likely to have important implications for retrieval processing. The lack of recognition for this idea has potentially misled the focus of investigations of episodic retrieval and inhibited targeted assessment of the functional role of the IPL.

In contrast to those memory paradigms that can be successfully completed through retrieving the semantic or conceptual details of an episode, some memory tasks can only be completed through the retrieval of perceptual information from memory. Recognition tasks using a target and highly similar lures (e.g., four apples) offer this opportunity (Migo, Montaldi, Norman, Quamme, & Mayes, 2009). In these tasks, retrieving the label of an object (e.g., apple) does not aid the participant in distinguishing the target from other similar variants of the same object. Right hemisphere IPL activations have been observed with this type of task (Dennis et al., 2012; Wais, Jahanikia, Steiner, Stark, & Gazzaley, 2017). Dennis *et al.*, (2012) used related lures (items within a semantic category, e.g. different cats) and showed greater activity in the right

angular gyrus for remember false alarms, than know false alarms. In another study utilising similar lures, the right angular gyrus showed a large cluster of activation that was greater in correct rejection (high fidelity: retrieval to reject/novelty detection) than false alarm (low fidelity: retrieval to reject/novelty detection) responses (Wais et al., 2017). Although these contrasts provide interesting insight into the neural bases of memory of differing fidelity, they have fallen short of what is needed to understand hemispheric differences in IPL function as they have not contrasted activity for hits and correct rejections (strongly associated with the parietal old/new effect (Hutchinson et al., 2009)). The impact of non-invasive neuromodulation with TMS on the frequency of false alarms and correct rejections has also never been assessed. If targets were discernible from lures through their distinguishable perceptual details then a difference in activity in the right hemisphere IPL would be predicted when contrasting hits and correct rejections.

Neural Mechanisms Supporting Highly Perceptual Memory Retrieval - Experiment 4.2

Here, we employed a novel variant of the forced choice corresponding recognition paradigm in which the perceptual details of the encoded target was the only critical information to be retrieved at test. This recognition memory test corresponds with the encoding/object perception phase presented in Gray and Montaldi (in preparation, Chapter 3). Using similar lures in a test of object recognition allowed for targeted assessment of perceptual detail retrieval in the absence of the engagement of semantic or conceptual retrieval. In addition to a traditional Old/New recognition test format, the current study critically employed a novel Old/Old format in which individuals were required to make a choice between two similar objects (e.g. two apples) that were *both* shown previously. The requirement to make an Old/New decision in the Old/Old format, between two items that are very similar in memory strength, was expected to provide a highly sensitive measure allowing for identification of potentially subtle, but robust, lateralisation biases in memory for perceptual detail.

Our review of previous IPL activations that were associated with episodic memory demonstrated similarities between the hemispheric specialisation of the attention and memory systems. Experiment 3.2 assessed the relationship between the spatial position (left/right) in which an item was encountered at encoding and the subsequent accuracy of memory. In an earlier study, Cansino, Maquet, Dolan, & Rugg, (2002) presented single objects to each side of visual space to

produce a perceptual encoding experience that could later be used to tap source memory (on which side of visual space did you encounter this object?). This did not show any effect of spatial position, however, the duration of exposure was long enough for participants to fully orient to the object. It is unclear with these extended presentations whether the distribution of visual input remains substantially biased to one hemisphere. The absence of such a clearly unihemispheric input may have mitigated the observation of any lateralisation effects. We utilised a novel variant of this encoding approach in the present study.

As described in Gray and Montaldi (in preparation, Chapter 3), we simultaneously presented object images to each side of visual space (object A | object B) for a very short time (200ms). This prevented eye-movements and ensured that processing of each item was performed overwhelmingly by the contralateral hemisphere. As mentioned, pseudoneglect results from the functional specialisation of attention allocation mechanisms in the right hemisphere (Capotosto, Babiloni, Romani, & Corbetta, 2012; Heilman & VanDen Abell, 1980; Mesulam, 1981; Roy, Sparing, Fink, & Hesse, 2014; Szczepanski & Kastner, 2013). We therefore hypothesised that the affinity of the right IPL for the processing of perceptually demanding information (in attention or memory) may convey a memory advantage for the left side of visual space.

We employed fMRI to identify the regions of the brain engaged by perceptually specific and accurate memory retrieval. Reliance on semantic processing was fundamentally unhelpful to accurate task performance. Instead, the contrasts used here specifically assess the variable engagement of perceptual episodic retrieval by different memory-related processes.

Methods - Experiment 4.2

The collection of the data for this experiment was originally described in Experiment 3.2 of Gray and Montaldi (in preparation; Chapter 3). Here, the test phase of this paradigm is presented and analysed for the first time.

This experiment consisted of three phases, an encoding, a landmark task, and a test phase. On each trial of the encoding phase, participants (N = 19) were presented with two images (digital photographs) of everyday objects. Stimuli were selected from the Similar Object and Lure Image Database (SOLID - Frank, Gray and Montaldi (submitted); Fig 4.1A). As mentioned, we utilised an Old/New condition (20 trials per block, 80 trials total) in which an item that was previously shown at encoding (old) was presented alongside an unseen item (new). We also employed a novel Old/Old format requiring a choice between two similar objects that were both shown at encoding (10 trials per block, 40 trials total).

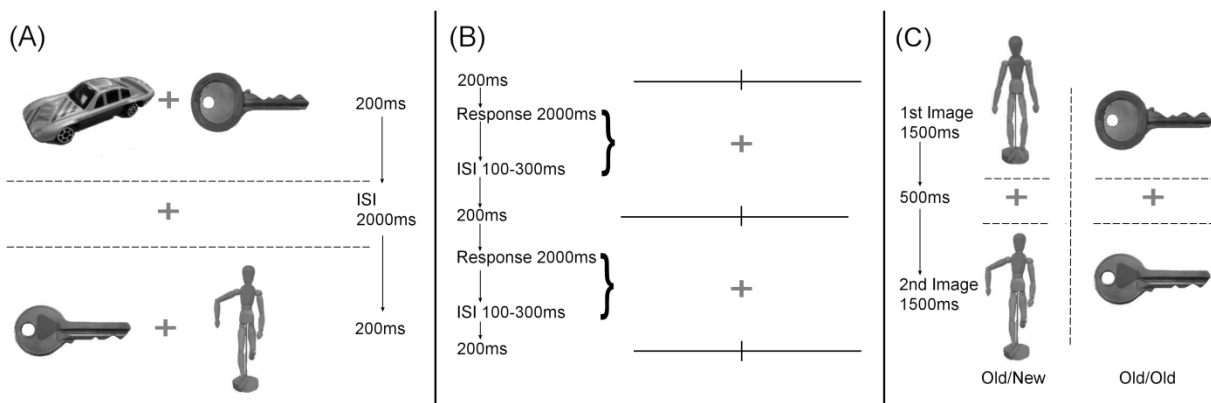


Figure 4.1: A schematic representation of the (A) study, (B) landmark task, and (C) test phases of the fMRI experiment. Note the presence of two similar items both having been seen at study in the Old/Old test format, in contrast to the presence of a similar lure, not seen at study, in the Old/New test format.

Participants completed four blocks of study (Fig 4.1A), landmark task (Fig 4.1B), and test (Fig 4.1C), in the current experiment. In each study phase, two object images were presented simultaneously either side of a central fixation cross for 200ms (45 events/block; 30 two-object presentations, and 15 null events; inter-stimulus interval jittered between 1500ms-2500ms). Participants were instructed to maintain fixation on the central fixation cross and use their peripheral vision to take in as much information as they could about both images.

Following the presentation of all object pairs in the study phase of each block, participants completed 36 judgements of the landmark task intermixed with 18 null events. In the landmark task, individuals were presented with a small vertical line in the centre of the screen that was bisected by a horizontal line (see *Fig 4.1B*). On each trial, the position of the horizontal line varied along the X axis (11 horizontal line positions with different degrees of displacement from centre were presented; -5% - +5%). Lines were presented for 200ms and participants had up to 2000ms to respond indicating which edge of the horizontal line was closest to the vertical line.

Methods - Test Phase

The test phase for the objects presented in each study block was then conducted. At test, two images were presented centrally one after the other. Images were the same size as presented in the study phase. The first image was 1500ms and then immediately replaced by a fixation cross for 500ms. The second image was then presented for 1500ms and then immediately replaced by the word “Decide” in the centre of the screen. At this stage participants were required to indicate which of the two images had been seen before. Participants used their index finger of each hand to indicate which of the first or second image they had seen in the study phase. The index finger associated with each option was counterbalanced across participants.

Images from each study location (left and right) were equally and randomly distributed between the first and second presentations at test. Two different test formats were used: an Old/New format (Target versus Similar Foil - 24 tests) and an Old/Old format (Target versus Target - 24 tests). The Old/New condition consisted of a previously presented target and a similar foil. The Old/Old condition comprised two similar images of the same object type that had both been shown separately in the study condition. The order of presentation of the image pairs and the order of presentation of each test format were randomised.

Two test formats were adopted; a traditional Old/New format (target versus similar foil - 20 tests per block) and a novel Old/Old format (see *Fig 4.1C* for an illustration of these test formats). Each object type in the Old/Old test format (target versus target - 10 tests per block) had two equally similar encoded targets; no foils were required in the Old/Old format. This allowed for comparison of the relative memory strength of each item without the contribution of novelty detection.

A practice session was conducted prior to entering the scanner. 16 study pairs and 8 null events were shown in the practice study phase. 16 pairs sourced from the practise study list were shown as part of the practice test phase.

fMRI Acquisition and Analyses

Participants acclimatised and rested in the scanner whilst T1-weighted images (3T MRI scanner (Philips, Achieva), matrix size: 256 x 256, 180 slices, voxel size: 1mm isotropic) were obtained prior to the behavioural procedure. Functional images assessing the blood oxygenation level dependent (BOLD) signal were collected using a SENSE spiral-in sequence (four sessions; 920 volumes; 230 volumes/session; TR = 2.5s; TE = 35ms; each volume: 40 slices, matrix size: 96 x 96; voxel size: 2.5 x 2.5 x 3.5 mm³).

Details of the pre-processing procedures employed within SPM12 (Statistical Parametric Mapping, Wellcome Department of Cognitive Neurology, University College London, London, UK; Available at: <http://www.fil.ion.ucl.ac.uk/spm/>) have previously been described in Gray and Montaldi (in preparation, Chapter 3).

Functional data were analysed using the general linear model (GLM) framework within an event-related design modelling the canonical hemodynamic response function. Trials were grouped into conditions based on the response of the subject. This resulted in separate conditions representing the 1500ms item presentations that resulted in hits, misses, false alarms, and correct rejections for items originally presented to the left and right side of visual space in the Old/New test format. The Old/Old test format produced conditions relating to 'item chosen' and 'item not chosen' trials, classified according to position of original presentation in visual space. Null events were classified as a separate condition. The time series was high-pass filtered to remove low-frequency noise (<128s). First-level linear contrasts were calculated to produce effect estimates for each participant. Each subject's mean contrast estimates were then entered into a second-level one sample *t*-test analysis.

A priori regions-of-interest (ROIs) were derived from the automated anatomical labelling (AAL) atlas within the Wake Forest University PickAtlas SPM toolbox (Maldjian, Laurienti, Kraft, & Burdette, 2003; Tzourio-Mazoyer et al., 2002) and consisted of bilateral angular gyri. Subsequent to our angular gyrus analysis, ROIs were created of other default mode network regions to

investigate the potential for common patterns of activation across this network. ROIs of the hippocampus, dorsomedial prefrontal cortex, ventromedial prefrontal cortex, posterior cingulate cortex, and lateral temporal cortex were created. All ROIs are displayed in *Supplementary Fig 4.2* overlaid on the canonical MNI brain. A 4x2x2 repeated measures ANOVA and subsequent paired sample t-tests assessed the difference between left and right hemisphere angular gyrus activations associated with items encoded on each side of visual space and with each type of recognition memory decision (hits/misses/correct rejections/false alarms). Analysis of linear correlations between activity in these ROIs and behavioural measures of accuracy and reaction times further investigated the behavioural relevance of the ROI.

Results

Behavioural

Fig 4.2 displays the mean difference in rates of successful identification for targets originally encountered on the left and right sides of visual space in the Old/New format and the Old/Old format. Statistical analyses were conducted on data from 19 participants. Collapsed across location of target at study, the mean accuracy of the sample in the Old/New condition was 57.3% (SD = 7.7%, 95% CI = [53.7% - 68.2%]). In subsequent analyses of the Old/New condition, we included only trials with a large difference in similarity between the target and lure (>1218 similarity difference - as indexed by the SOLID dissimilarity score (Frank, Gray, and Montaldi (submitted))). This ensured we assessed differences in memory rather than unconfident guesses. Memory accuracy for these items was 64.7% (SD = 7.98%, 95% CI = [61.14% - 68.33%]). On average, this produced conditions made up of 13 trials for accurate memory judgements (hits and correct rejections) and 8 trials for incorrect memory judgements (misses and false alarms) in the Old/New memory conditions. Each Old/Old condition was made up of 20 trials. When asked to provide an estimation of the percentage of trials that were Old/Old, on average, participants judged 8% of trials were Old/Old (SD = 8%).

One-sample t-tests assessed whether accuracy was significantly biased to one side of visual space in the Old/New and Old/Old test format. We did not observe a significant difference in subsequent memory accuracy for objects originally encountered on the left and right side of visual space in the Old/New ($t(18) = -0.883$, $p = 0.416$) or Old/Old ($t(18) = 1.05$, $p = 0.307$) test format.

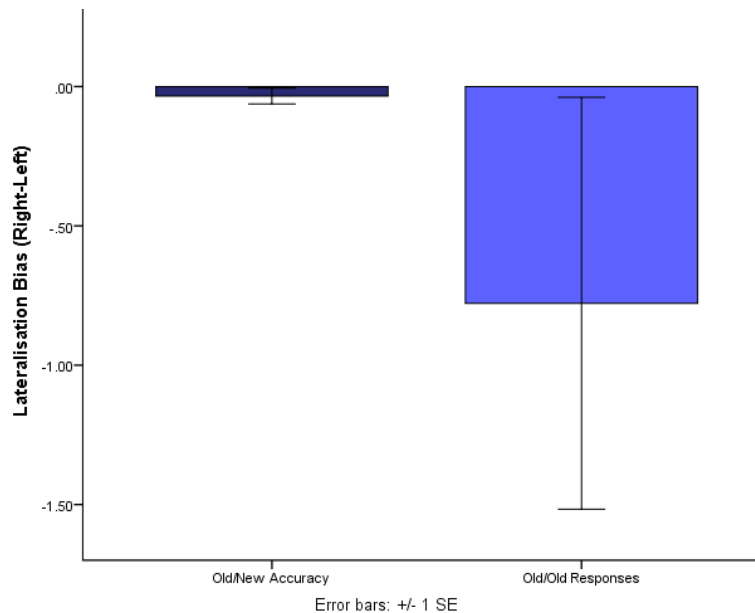


Figure 4.2: The difference between memory accuracy for stimuli originally presented on the right and left side of visual space. In both test formats, items encoded on the left and right side of perceptual space were identified equally well.

Voxel-wise Image Analysis

Data from one subject were excluded because of technical issues with data collection and pre-processing. Direct contrasts between conditions of interest were produced for the remaining 18 subjects. We observed no significant differences in activity in direct contrasts between hits, misses, false alarms and correct rejections that did not vary according to the side of object presentation at encoding. We also did not observe test phase activity that was significantly different between items presented on the left and right side of space that did not vary according to the subject's memory response. Assessing memory on each side of space was planned in the design of the experiment. We report *uncorrected* clusters of activity in the IPL in direct univariate contrasts reflecting memory for items originally presented on the right side of visual space. These results should be interpreted with considerable caution.

Successful Perceptual Memory of Items from the Right Associated with Right IPL Activation (uncorrected) in the Old/New task

A cluster in the right supramarginal gyrus showed greater activity for correct rejections than for either successful target identification (hits) (MNI = 53, -20, 25; $k = 18$; $p = 0.016_{\text{uncorrected}}$), or false alarms (MNI = 58, -20, 28; $k = 14$, $p = 0.022_{\text{uncorrected}}$). This activation is displayed on an inflated brain in Fig 4.3A.

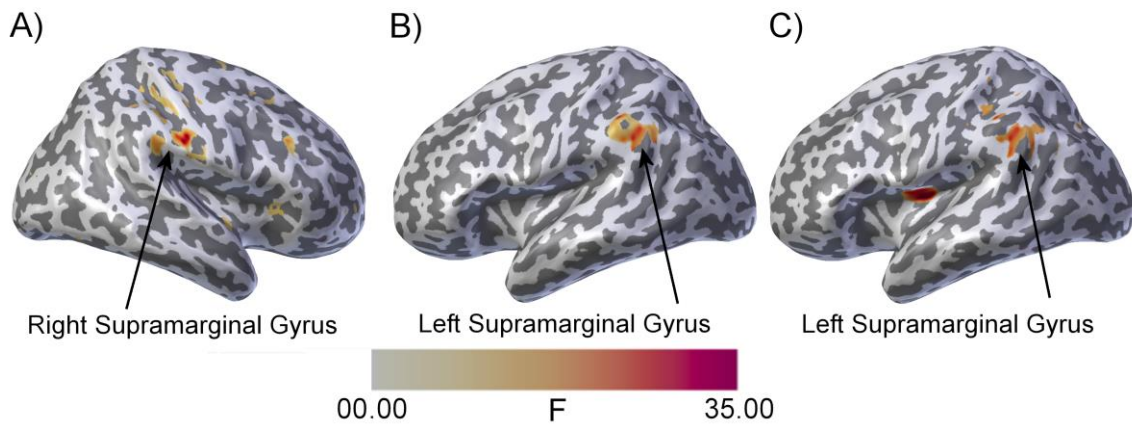


Figure 4.3: **A)** Successful perceptually-based memory retrieval of items from the right side of space was associated with an uncorrected cluster of activity within the supramarginal gyrus ($p = 0.016_{\text{uncorrected}}$). **B)** Unsuccessful recognition attempts of items from the right side of space were associated with a significant cluster of activity in the left supramarginal gyrus ($p = 0.042_{\text{uncorrected}}$). **C)** Successful recognition of items originally presented on the left side of visual space produced significantly more left supramarginal gyrus activity than those originally presented on the right side ($p = 0.002_{\text{FWE corrected}}$).

Unsuccessful Recognition Attempts of Items from the Right Associated with Left IPL Activation (uncorrected) in the Old/New task

Processing of previously encountered items that were not recognised in the test phase was associated with greater activity in the left supramarginal gyrus (MNI = -60, -30, 35; $k = 11$, $p = 0.042_{\text{uncorrected}}$) than that found for successfully recognised items (hits). Activation is displayed in Fig 4.3B.

Items Originally Encountered on the Left Additionally Recruit the Left IPL during Correct Recognition

A cluster in the left supramarginal gyrus was significantly (MNI = -62, -52, 28; $k = 61$, $p = 0.002_{\text{FWE corrected}}$) more active during correct recognition of items that were encoded on the left side of visual space than those encoded on the right (Fig 4.3C).

Region of Interest Analysis

A 4x2x2 repeated measures ANOVA with memory type (hit/false alarm/correct rejection/miss), side of original presentation (left/right), and hemisphere (left/right) assessed mean angular gyrus activity in this task. We observed a significant main effect of hemisphere on angular gyrus activity ($F(1,17) = 98.05$, $p < 0.001$, $\eta_p^2 = 0.852$). We did not observe a main effect of memory type ($F(3,51) = 0.64$, $p = 0.594$, $\eta_p^2 = 0.036$) or original side of presentation ($F(1,17) = 2.26$, $p = 0.151$, $\eta_p^2 = 0.117$). An interaction was also observed between memory type and hemisphere ($F(3,51) = 4.09$, $p = 0.011$, $\eta_p^2 = 0.194$). Paired t -tests revealed that all memory types showed significantly (with Bonferroni correction) greater right than left angular gyrus activity (hits - $t(17) = -7.84$, $p < 0.001$, $d = -1.85$; false alarms - $t(17) = -5.54$, $p < 0.001$, $d = -1.30$; correct rejections - $t(17) = -10.05$, $p < 0.001$, $d = -2.37$; misses = -6.26 , $p < 0.001$, $d = -1.47$). False alarms were associated with left angular gyrus activity that was less negative than correct rejections ($t(17) = 2.11$, $p = 0.05$, $d = 0.50$) though this difference did not survive correction for multiple comparisons. Left angular gyrus activity for false alarms was not significantly different from activity in the same area for hits or misses ($t(17) = 1.388$ and 1.318 respectively, $p > 0.05$).

We observed the same strong effect of hemisphere on the angular gyrus BOLD signal in the Old/Old test format ($F(1,17) = 122.23$, $p < 0.001$, $\eta_p^2 = 0.878$), independent of memory (chosen-target versus unchosen target) ($F(1,17) = 1.12$, $p = 0.304$, $\eta_p^2 = 0.062$) or original side of presentation ($F(1,17) = 1.10$, $p = 0.310$, $\eta_p^2 = 0.061$). We also observed no significant interactions between any of these factors (selection*side - $F(1,17) = 0.20$, $p = 0.658$, $\eta_p^2 = 0.012$; selection*hemisphere - $F(1,17) = 0.29$, $p = 0.599$, $\eta_p^2 = 0.017$; side*hemisphere - $F(1,17) = 0.27$, $p = 0.611$, $\eta_p^2 = 0.016$; selection*side*hemisphere - $F(1,17) = 0.02$, $p = 0.905$, $\eta_p^2 = 0.001$). A graphical summary of these results is presented in *Fig 4.4A*.

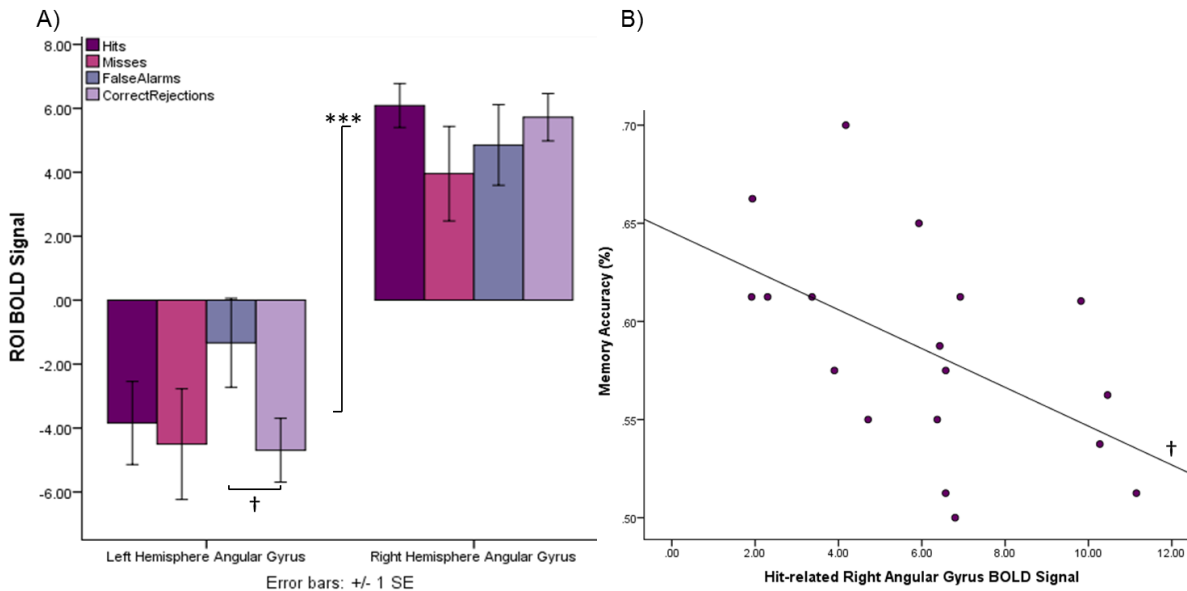


Figure 4.4: An illustration of the distinct processing of the angular gyrus of each hemisphere during the test phase of the Old/New forced choice recognition memory paradigm. **A)** We observed significantly different activity in the angular gyrus of the right and left hemisphere ($p < 0.001$). **B)** Memory accuracy in the recognition memory paradigm was only associated ($r = -0.531$) with hit-related activity in the right angular gyrus.

As mentioned previously, the angular gyrus is a node of the default mode network (Seghier, 2013). We performed the same 4x2x2 repeated measures ANOVA on five other key nodes of the default mode network (ventromedial (1) and dorsomedial prefrontal cortex (2), posterior cingulate cortex (3), lateral temporal cortex (4), and hippocampus (5)). A significant difference between left and right hemisphere was also observed in the posterior cingulate cortex ($F(1,17) = 4.99$, $p = 0.039$, $\eta_p^2 = 0.227$). This showed a small decrease in the BOLD signal in the left but not the right hemisphere during the task (*Supplementary Fig 4.3E and Supplementary Table 4.3*). However, the size of this effect was much smaller than the effect observed in angular gyrus (posterior cingulate - $\eta_p^2 = 0.227$ versus angular gyrus - $\eta_p^2 = 0.852$). Despite some activation, none of these areas displayed a similar pattern of activation to the angular gyrus in this comparison. Graphical representations and statistical summaries of these comparisons are provided in *Supplementary Fig 4.3*.

We also performed Pearson's linear correlation analyses to assess the relationship between BOLD signal in the angular gyrus of each hemisphere and behavioural memory performance. We observed a linear negative correlation ($r = -0.531$, $p = 0.024$) between activity in the right

angular gyrus during successful recognition (hits) and memory accuracy for all images (*Fig 4.4B*). This finding did not survive stringent Bonferroni correction ($p_{\text{Bonferroni threshold}} = 0.006$). We did not observe significant correlations between left or right angular gyrus activity and any of the other memory types (hits ($p_{\text{left}} = 0.644$), misses ($p_{\text{left}} = 0.699$, $p_{\text{right}} = 0.382$), false alarms ($p_{\text{left}} = 0.215$, $p_{\text{right}} = 0.635$), correct rejections ($p_{\text{left}} = 0.299$, $p_{\text{right}} = 0.335$)). Though this relationship is uncorrected and should be interpreted with some caution, the link between memory-related brain activity in the angular gyrus and memory accuracy suggests that activity in the right angular gyrus is more functionally relevant or more diagnostic of successful highly perceptual memory.

Discussion

This study aimed to assess the relationship between the informational content of a retrieved episode and the hemispheric specialisation of IPL function. We utilised a memory test that enabled direct contrast of perceptually-defined memory with perceptually-independent memory. Interestingly, both our review of previously published IPL activations associated with episodic memory and the current direct comparisons suggest that the retrieval of perceptually-defined episodic memories recruits the IPL in the right hemisphere. In contrast, previous findings strongly suggest that memory retrieval focussed on the semantic aspects of episodic memories is more likely to engage the left hemisphere IPL.

In particular, we observed greater activity in the right supramarginal gyrus for correctly rejected novel items than correctly recognised previously encountered items. The target image was visible during all hit trials but not, of course, during correct rejection trials. The activations that we have observed here do not survive correction for multiple comparisons and should be interpreted with caution. It is likely that the additional correct rejection-related activity we do observe is likely to reflect the recall of target features (not visible during lure presentations) to enable rejection of the novel image (i.e., recall-to-reject). In addition, we observed similar increases in supramarginal activity when comparing correct rejections with false alarms. This exploratory data further supports the idea that accurate correct-rejection-related activity is underpinned by perceptually specific, diagnostic recall-to-reject processing in the right IPL.

The lateralisation of the correct-rejection related activity (uncorrected) that we have observed is the same as seen in a recent study (Wais et al., 2017) using a similar comparison, which showed greater activity in the right IPL during the correct rejection of similar lures than during false alarms. In this previous study, the left angular gyrus also followed this trend but displayed substantially smaller extent of activation (41 against 154 voxels). This work also displayed regions in the entorhinal and parahippocampal cortex that showed greater activity during correct rejections than false alarms. Interestingly, the right entorhinal cortex displayed connectivity with both angular gyri. We did not observe medial temporal lobe effects here, however the (uncorrected) effects that we have observed in the angular and supramarginal gyri suggest that both medial temporal lobe effects and hemisphere lateralisation may have been observable with greater experimental power or a paradigm with a greater signal to noise ratio.

Our review of previous fMRI memory effects in the IPL has shown that episodic memory for semantic/conceptual information engages the left angular gyrus (and frequently the supramarginal gyrus). Presentations of previously encountered items that were not correctly recognised (misses) were associated with greater activity (uncorrected) in the left supramarginal gyrus when compared to hit-related activity in the current experiment. We speculatively propose that this difference suggests that in this contrast, individuals may recruit semantic/conceptual memory processing. In the absence of perceptually specific details with which to distinguish between the target and lure, focus is likely to have shifted to recollecting semantic/conceptual details of the object target to compensate or problem solve. That miss-related activity is observed in the left but not the right hemisphere *potentially* reflects the hemispheric lateralisation of function proposed by this study.

Previous work has revealed angular gyrus activations resulting from episodic memory contrasts and has focussed on the mechanisms that they likely underpin. This provided the *a priori* rationale for us to explore angular gyrus activity and compare the response of the angular gyrus of each hemisphere to the demands of our task. This investigation of the angular gyrus in the right and left hemisphere across conditions provided strong support for the functional specialisation of memory processing in each hemisphere. In this study, participants were encouraged to focus on the perceptual details of objects. Attempting to retrieve these perceptual aspects of episodic memory was associated with an increase in angular gyrus activity in the right hemisphere and a decrease in angular gyrus activity in the left hemisphere.

In contrast to previous work, we did not observe significant differences within the angular gyrus between memory conditions. A number of reasons could explain this discrepancy. Firstly, our use of similar lures as alternatives to previously encountered items is likely to have produced highly confident false alarms, and low confidence correct rejections and misses. In fact, memory for the similar, target-like features of the lures, in addition to the detection of novelty, may have obscured our ability to identify the sensitive recollection-based modulation of the angular gyrus. Secondly, our use of a shallow encoding strategy may have limited the instances of detailed recollection. Previous fMRI, neuropsychological, and TMS studies have linked angular gyrus activity to the process of memory feature integration within recollection (Bonnici et al., 2016; Nilakantan et al., 2017; Simons et al., 2010; Yazar et al., 2017).

One recent hypothesis of IPL memory function proposes that multifaceted information arising from memory is integrated in the IPL during memory retrieval (Bonnici et al., 2016; Yazar et al., 2017). To date, this hypothesis has focussed on memory supported by recollection and has yet to integrate the findings of previous research observing IPL activations associated with familiarity-based recognition (Frithsen & Miller, 2014; Kafkas & Montaldi, 2012; Sharot et al., 2004; Yonelinas et al., 2005). Memory accuracy in the current study was 57.3%. As a result, many trials with correct target recognition (events defined as hits) will have been characterised by low confidence recognitions and familiarity-based memory judgements. Despite the limited recollection that was required for accurate recognition, these trials still displayed the difference in activation between the left and right IPL. In the case of familiarity, information presented to the individual is compared with stored representations. Unlike with recollection, information is not *retrieved* from memory during familiarity judgements (Migo et al., 2009) and as a result, information integration should not be required for familiarity memory. Therefore, the hypothesis that links the IPL to a memory integration function requires updating to incorporate not only the recollective processes, but to account also for the IPL activations that have been associated with both recollection and familiarity. The observations of *Chapter 4* suggest that the assessment of the function of the IPL in low confidence memory can provide insight into the characteristics of these mechanisms.

The angular gyrus is a core component of the default mode network in both the left and the right hemisphere (Bellana et al., 2016; Fornito, Harrison, Zalesky, & Simons, 2012; Sestieri et al., 2011). The functional connectivity of the nodes of the default mode network was recently assessed with reference to episodic memory (Bellana et al., 2016). This previous study suggested that in the left hemisphere, the angular gyrus demonstrates strong connectivity with default mode network areas outside of the MTL. In contrast, strong connectivity was observed between the right angular gyrus and structures within the MTL. The results of the current study substantiate this hemispheric distinction in function and connectivity. First, in this episodic memory task we observed greater activations of the right angular gyrus than the left. Secondly and critically, the degree of activation in the right angular gyrus during the processing of correct item recognition displayed a significant negative correlation with behavioural memory accuracy. No linear relationships between angular gyrus activity in the right or left hemisphere were observed during any other type of memory processing (false alarms, correct rejections, misses).

In the current study, subjects with better memory accuracy displayed less activity in the right angular gyrus than subjects with less accurate memory. The direction of this relationship suggests that individuals with strong memory may have a reduced reliance on detailed re-experiencing of the target during hit decisions. These individuals may have more easily identified single features of the target image that enabled them to recognise the item. In contrast, those subjects with greater activity in angular gyrus may have been forced to assess the oldness of multiple features of target images and compare them in order to make a recognition decision. Alternatively, individuals that are highly accurate may more easily perform the task using MTL structures. Additional angular gyrus activity in less accurate individuals may reflect processes that coordinate with the MTL to enable better memory retrieval. A recent TMS study observed a similar relationship between angular gyrus and memory accuracy (Nilakantan et al., 2017). In this study, lower amplitudes of the parietal late-positive event-related potential were associated with better episodic memory of perceptual details. Decreases in the average power of theta-alpha frequency oscillatory activity over parietal electrodes also tracked better memory performance. A similar, more efficient memory process could potentially also explain these changes. Further research using targeted modulation of the angular gyrus is required to directly explore this potentially interesting hypothesis.

Implementing an Old/Old test format, using similar foils in the Old/New test format, and similar targets in the Old/Old format allowed for the manipulation of visuospatial information in a subtle and targeted manner. We did not observe any whole brain univariate differences between Old items that were judged as previously encountered (chosen) compared to Old items that were not chosen. This supports the proposal that correct rejection related activity in the IPL is related to recall-to-reject activity. Interestingly, the angular gyrus displayed the same pattern of activity for judgements made in the Old/Old and Old/New test format (*Supplementary Fig 4.4*). Importantly, this suggests that the angular gyrus processing of a previously encountered item displayed in the Old/New task was not dependent on novelty processing of the similar lure.

We did not observe a significant effect of side of original encounter in the current study. Memory accuracy in the Old/New test format was equal on each side of space. Performance in the Old/Old test format also displayed no preference for objects studied on one side over another. The goggles that were used to display the objects in our experiment provided a projector-like display. This created the perception of a large distance between target and

observer, and potentially enabled the processing of both stimuli by both hemispheres. This unforeseen feature of the study may have prohibited us from measuring the effect of truly unihemispheric presentations on memory retrieval. Furthermore, the variability in the dynamics of the hemispheric specialisation mechanism evidenced in this study has yet to be fully investigated. Many factors (including arousal and the distance between a target and the observer) have a substantial impact on the ventral attention network (including the IPL) (Lourenco & Longo, 2009; Newman et al., 2013). Similar idiosyncratic modulations of memory may occur as a function of varying the spatial location and/or the target-observer distance of a cue or attempting to retrieve a memory from a particular area of space (e.g., upper or lower).

In conclusion, this study provides a novel perspective on the role of the IPL in the retrieval of episodic memory. We propose for the first time that the IPL of each hemisphere perform similar but functionally dissociable roles in the retrieval of a complete episodic memory. The left IPL engages in the retrieval of the semantic and conceptual aspects of episodic memory, whereas the right IPL engages in the retrieval of the perceptual features of the memory. The findings of experiment 4.2 and our review of previously published IPL activations associated with episodic memory provide strong convergent evidence in support of our proposal of hemispheric specialisation.

Our interpretation also effectively links the brain mechanisms that support attention and memory. Whilst we recognise the potential for anatomically distinct systems dedicated to these two areas of cognitive function in the IPL (Hutchinson et al., 2015), the common hemispheric specialisation proposed here suggests a strong similarity between attention and memory retrieval processes. Understanding the spatial and temporal dynamics of the neural mechanisms that govern attention and memory in the left and right hemisphere will be crucial to the precise modelling of parietal cortex function. Future work should develop novel approaches that utilise the methodological strengths of the attention and memory literature in a more convergent approach. Moreover, it is crucial for the complete development of this work that studies involving the direct modulation of brain activity, e.g. through TMS, target and compare effects of stimulation in both hemispheres. Only through such strategic examinations will the functional relationship between the networks underpinning the effects in these studies be elucidated.

References

- Bellana, B., Liu, Z.-X., Anderson, J. A. E., Moscovitch, M., & Grady, C. L. (2016). Laterality effects in functional connectivity of the angular gyrus during rest and episodic retrieval. *Neuropsychologia*, 80, 24-34. <http://doi.org/10.1016/j.neuropsychologia.2015.11.004>
- Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: bilateral damage causes impaired free recall of autobiographical memory. *The Journal of Neuroscience*, 27(52), 14415-23. <http://doi.org/10.1523/JNEUROSCI.4163-07.2007>
- Bonnici, H. M., Richter, F. R., Yazar, Y., & Simons, J. S. (2016). Multimodal Feature Integration in the Angular Gyrus during Episodic and Semantic Retrieval. *Journal of Neuroscience*, 36(20), 5462-5471. <http://doi.org/10.1523/JNEUROSCI.4310-15.2016>
- Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: an attentional account. *Nature Reviews Neuroscience*, 9(8), 613-625. <http://doi.org/10.1038/nrn2459>
- Cabeza, R., Mazuz, Y. S., Stokes, J., Kragel, J. E., Woldorff, M. G., Ciaramelli, E., ... Moscovitch, M. (2011). Overlapping Parietal Activity in Memory and Perception: Evidence for the Attention to Memory Model. *Journal of Cognitive Neuroscience*, 22(11), 3209-3217. <http://doi.org/10.1162/jocn>
- Cai, Q., Van der Haegen, L., & Brysbaert, M. (2013). Complementary hemispheric specialization for language production and visuospatial attention. *PNAS*, 110(4), 322-30. <http://doi.org/10.1073/pnas.1212956110>
- Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain Activity Underlying Encoding and Retrieval of Source Memory. *Cerebral Cortex*, 12(10), 1048-1056. <http://doi.org/10.1093/cercor/12.10.1048>
- Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2012). Differential contribution of right and left parietal cortex to the control of spatial attention: A simultaneous EEG-rTMS study. *Cerebral Cortex*, 22(2), 446-454. <http://doi.org/10.1093/cercor/bhr127>
- Capotosto, P., Baldassarre, A., Sestieri, C., Spadone, S., Romani, G. L., & Corbetta, M. (2017). Task and Regions Specific Top-Down Modulation of Alpha Rhythms in Parietal Cortex. *Cerebral Cortex*, 27(10), 4815-4822. <http://doi.org/10.1093/cercor/bhw278>
- Chambers, C. D., & Heinen, K. (2010). TMS and the functional neuroanatomy of attention. *Cortex*, 46(1), 114-117. <http://doi.org/10.1016/j.cortex.2009.03.002>
- Chambers, C. D., Payne, J. M., & Mattingley, J. B. (2007). Parietal disruption impairs reflexive spatial attention within and between sensory modalities. *Neuropsychologia*, 45(8), 1715-1724. <http://doi.org/10.1016/j.neuropsychologia.2007.01.001>
- Chen, N.-F., Lo, C.-M., Liu, T.-L., & Cheng, S.-K. (2016). Source memory performance is modulated by transcranial direct current stimulation over the left posterior parietal cortex. *NeuroImage*, 139, 462-469. <http://doi.org/10.1016/j.neuroimage.2016.06.032>
- Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, 46(7), 1828-1851. <http://doi.org/10.1016/j.neuropsychologia.2008.03.022>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201-15. <http://doi.org/10.1038/nrn755>
- Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. *Annual Reviews Neuroscience*, 34, 569-99. <http://doi.org/10.1146/annurev-neuro-061010-113731>

- Darling, S., Logie, R. H., & Della Sala, S. (2012). Representational pseudoneglect in line bisection. *Psychonomic Bulletin & Review*, 19(5), 879-83. <http://doi.org/10.3758/s13423-012-0285-z>
- Davey, J., Cornelissen, P. L., Thompson, H. E., Sonkusare, S., Hallam, G., Smallwood, J., & Jefferies, E. (2015). Automatic and Controlled Semantic Retrieval: TMS Reveals Distinct Contributions of Posterior Middle Temporal Gyrus and Angular Gyrus. *Journal of Neuroscience*, 35(46), 15230-15239. <http://doi.org/10.1523/JNEUROSCI.4705-14.2015>
- Davidson, P. S. R., Anaki, D., Ciaramelli, E., Cohn, M., Alice, S. N., Murphy, K. J., ... Levine, B. (2010). Does lateral parietal cortex support episodic memory? Evidence from focal lesion patients. *Neuropsychologia*, 46(7), 1743-55. <http://doi.org/10.1016/j.neuropsychologia.2008.01.011>. Does
- Dennis, N. A., Bowman, C. R., & Vandekar, S. N. (2012). True and phantom recollection: An fMRI investigation of similar and distinct neural correlates and connectivity. *NeuroImage*, 59(3), 2982-2993. <http://doi.org/10.1016/j.neuroimage.2011.09.079>
- Dobbins, I. G., & Wagner, A. D. (2005). Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cerebral Cortex*, 15(11), 1768-1778. <http://doi.org/10.1093/cercor/bhi054>
- Frank, D., Gray, O.J., and Montaldi, D., (submitted). SOLID - Similar Object and Lure Image Database.
- Fornito, A., Harrison, B. J., Zalesky, A., & Simons, J. S. (2012). Competitive and cooperative dynamics of large-scale brain functional networks supporting recollection. *PNAS*, 109, 12788-93. <http://doi.org/10.1073/pnas.1204185109> /DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1204185109
- Frithsen, A., & Miller, M. B. (2014). The posterior parietal cortex: Comparing remember/know and source memory tests of recollection and familiarity. *Neuropsychologia*, 61(1). <http://doi.org/10.1016/j.neuropsychologia.2014.06.011>
- Gitelman, D. R., Nobre, A. C., Parrish, T. B., Labar, K. S., Kim, Y., Meyer, J. R., & Mesulam, M. (1999). A large-scale distributed network for covert spatial attention: Further anatomical delineation based on stringent behavioural and cognitive controls. *Brain*, 122, 1093-1106. <http://doi.org/10.1093/brain/122.6.1093>
- Gray, O.J., & Montaldi, D. (submitted). Attention Allocation Systems Selectively Specialised for Spatial or Semantic Processing: A Reversed Pseudoneglect Effect.
- Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, 30, 327-330. <http://doi.org/10.1212/WNL.30.3.327>
- Hutchinson, J. B., Uncapher, M. R., & Wagner, A. D. (2009). Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. *Learning & Memory*, (650), 343-356. <http://doi.org/10.1101/lm.919109.16>
- Hutchinson, J. B., Uncapher, M. R., & Wagner, A. D. (2015). Increased functional connectivity between dorsal posterior parietal and ventral occipitotemporal cortex during uncertain memory decisions. *Neurobiology of Learning and Memory*, 117(18), 71-83. <http://doi.org/10.1016/j.nlm.2014.04.015>
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, 38(1), 93-110. [http://doi.org/10.1016/S0028-3932\(99\)00045-7](http://doi.org/10.1016/S0028-3932(99)00045-7)
- Josse, G., & Tzourio-Mazoyer, N. (2004). Hemispheric specialization for language. *Brain Research Reviews*, 44(1), 1-12. <http://doi.org/10.1016/j.brainresrev.2003.10.001>

- Kafkas, A., & Montaldi, D. (2012). Familiarity and recollection produce distinct eye movement, pupil and medial temporal lobe responses when memory strength is matched. *Neuropsychologia*, 50(13), 3080-93. <http://doi.org/10.1016/j.neuropsychologia.2012.08.001>
- Knecht, S. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain*, 123(12), 2512-2518. <http://doi.org/10.1093/brain/123.12.2512>
- Lourenco, S. F., & Longo, M. R. (2009). The plasticity of near space: Evidence for contraction. *Cognition*, 112(3), 451-456. <http://doi.org/10.1016/j.cognition.2009.05.011>
- Maldjian, J. A., Laurienti, P. J., Kraft, R. A., & Burdette, J. H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *NeuroImage*, 19(3), 1233-1239. [http://doi.org/10.1016/S1053-8119\(03\)00169-1](http://doi.org/10.1016/S1053-8119(03)00169-1)
- Mayes, A. R., Montaldi, D., & Migo, E. (2007). Associative memory and the medial temporal lobes. *Trends in Cognitive Sciences*, 11, 126-135. <http://doi.org/10.1016/j.tics.2006.12.003>
- Mesulam, M. (1981). A cortical network for directed attention and unilateral neglect. *Ann Neurol*, 10, 309-25. <http://doi.org/10.1002/ana.410100402>
- Migo, E., Montaldi, D., Norman, K. A., Quamme, J., & Mayes, A. R. (2009). The contribution of familiarity to recognition memory is a function of test format when using similar foils. *Quarterly Journal of Experimental Psychology*, 62, 1198-1215. <http://doi.org/10.1080/17470210802391599>
- Montaldi, D., & Mayes, A. R. (2010). The role of recollection and familiarity in the functional differentiation of the medial temporal lobes. *Hippocampus*, 20, 1291-1314. <http://doi.org/10.1002/hipo.20853>
- Newman, D. P., O'Connell, R. G., & Bellgrove, M. A. (2013). Linking time-on-task, spatial bias and hemispheric activation asymmetry: a neural correlate of rightward attention drift. *Neuropsychologia*, 51(7), 1215-23. <http://doi.org/10.1016/j.neuropsychologia.2013.03.027>
- Neyens, V., Bruffaerts, R., Liuzzi, A. G., Kalfas, I., Peeters, R., Keuleers, E., ... Vandenberghe, R. (2017). Representation of Semantic Similarity in the Left Intraparietal Sulcus: Functional Magnetic Resonance Imaging Evidence. *Frontiers in Human Neuroscience*, 11(402), 1-18. <http://doi.org/10.3389/fnhum.2017.00402>
- Nicholls, M. E. R., Hobson, A., Petty, J., Churches, O., & Thomas, N. A. (2017). The effect of cerebral asymmetries and eye scanning on pseudoneglect for a visual search task. *Brain and Cognition*, 111, 134-143. <http://doi.org/10.1016/j.bandc.2016.11.006>
- Nilakantan, A. S., Bridge, D. J., Gagnon, E. P., VanHaerents, S. A., & Voss, J. L. (2017). Stimulation of the Posterior Cortical-Hippocampal Network Enhances Precision of Memory Recollection. *Current Biology*, 27(3), 465-470. <http://doi.org/10.1016/j.cub.2016.12.042>
- Price, A. R., Peelle, J. E., Bonner, M. F., Grossman, M., & Hamilton, R. H. (2016). Causal Evidence for a Mechanism of Semantic Integration in the Angular Gyrus as Revealed by High-Definition Transcranial Direct Current Stimulation. *Journal of Neuroscience*, 36(13), 3829-3838. <http://doi.org/10.1523/JNEUROSCI.3120-15.2016>
- Roy, L. B., Sparing, R., Fink, G. R., & Hesse, M. D. (2014). Modulation of attention functions by anodal tDCS on right PPC. *Neuropsychologia*, 74, 96-107. <http://doi.org/10.1016/j.neuropsychologia.2015.02.028>
- Schneider, W., Eschmann, A., & Zuccolotto, A. (2012). *E-Prime User's Guide*. Pittsburgh: Psychology Software Tool, Inc. Retrieved from https://www.researchgate.net/publication/260296789_E-prime_User%27s_Guide
- Seghier, M. L. (2013). The angular gyrus: Multiple functions and multiple subdivisions. *Neuroscientist*, 19(1), 43-61. <http://doi.org/10.1177/1073858412440596>

- Seghier, M. L., Fagan, E., & Price, C. J. (2010). Functional Subdivisions in the Left Angular Gyrus Where the Semantic System Meets and Diverges from the Default Network. *Journal of Neuroscience*, 30(50), 16809-16817. <http://doi.org/10.1523/JNEUROSCI.3377-10.2010>
- Sestieri, C., Corbetta, M., Romani, G. L., & Shulman, G. L. (2011). Episodic memory retrieval, parietal cortex, and the default mode network: functional and topographic analyses. *The Journal of Neuroscience*, 31(12), 4407-20. <http://doi.org/10.1523/JNEUROSCI.3335-10.2011>
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2010). Attention to Memory and the Environment: Functional Specialization and Dynamic Competition in Human Posterior Parietal Cortex. *Journal of Neuroscience*, 30(25), 8445-8456. <http://doi.org/10.1523/JNEUROSCI.4719-09.2010>
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2017). The contribution of the human posterior parietal cortex to episodic memory. *Nature Reviews Neuroscience*, 18(3), 183-192. <http://doi.org/10.1038/nrn.2017.6>
- Sharot, T., Delgado, M. R., & Phelps, E. A. (2004). How emotion enhances the feeling of remembering. *Nature Neuroscience*, 7(12), 1376-1380. <http://doi.org/10.1038/nn1353>
- Simons, J. S., & Mayes, A. R. (2008). What is the parietal lobe contribution to human memory? *Neuropsychologia*, 46(7), 1739-42. <http://doi.org/10.1016/j.neuropsychologia.2008.05.001>
- Simons, J. S., Peers, P. V., Hwang, D. Y., Ally, B. A., Fletcher, P. C., & Budson, A. E. (2008). Is the parietal lobe necessary for recollection in humans? *Neuropsychologia*, 46(4), 1185-1191. <http://doi.org/10.1016/j.neuropsychologia.2007.07.024>
- Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2010). Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex*, 20(2), 479-85. <http://doi.org/10.1093/cercor/bhp116>
- Slagter, H. A., Davidson, R. J., & Tomer, R. (2010). Eye-blink rate predicts individual differences in pseudoneglect. *Neuropsychologia*, 48, 1265-1268. <http://doi.org/10.1016/j.neuropsychologia.2009.12.027>
- St-Laurent, M., Moscovitch, M., & McAndrews, M. P. (2016). The retrieval of perceptual memory details depends on right hippocampal integrity and activation. *Cortex*, 84, 15-33. <http://doi.org/10.1016/j.cortex.2016.08.010>
- Szczepanski, S. M., & Kastner, S. (2013). Shifting attentional priorities: Control of spatial attention through hemispheric competition. *Journal of Neuroscience*, 33(12), 5411-21. <http://doi.org/10.1523/JNEUROSCI.4089-12.2013>
- Thakral, P. P., Madore, K. P., & Schacter, D. L. (2017). A role for the left angular gyrus in episodic simulation and memory. *Journal of Neuroscience*, 37(34), 1319-17. <http://doi.org/10.1523/JNEUROSCI.1319-17.2017>
- Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., ... Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, 15(1), 273-289. <http://doi.org/10.1006/nimg.2001.0978>
- Vilberg, K. L., & Rugg, M. D. (2008). Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia*, 46(7), 1787-1799. <http://doi.org/10.1016/j.neuropsychologia.2008.01.004>
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, 9(9), 445-53. <http://doi.org/10.1016/j.tics.2005.07.001>
- Wais, P. E., Jahanikia, S., Steiner, D., Stark, C. E. L., & Gazzaley, A. (2017). Retrieval of high-fidelity memory arises from distributed cortical networks. *NeuroImage*, 149(January), 178-

189. <http://doi.org/10.1016/j.neuroimage.2017.01.062>

- Yazar, Y., Bergström, Z. M., & Simons, J. S. (2012). What is the parietal lobe contribution to long-term memory? *Cortex*, 48(10), 1381-2. <http://doi.org/10.1016/j.cortex.2012.05.011>
- Yazar, Y., Bergström, Z. M., & Simons, J. S. (2014). Continuous theta burst stimulation of angular gyrus reduces subjective recollection. *PloS One*, 9(10), 1-7. <http://doi.org/10.1371/journal.pone.0110414>
- Yazar, Y., Bergström, Z. M., & Simons, J. S. (2017). Reduced multimodal integration of memory features following continuous theta burst stimulation of angular gyrus. *Brain Stimulation*, 10(3), 624-629. <http://doi.org/10.1016/j.brs.2017.02.011>
- Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the Brain Regions Involved in Recollection and Familiarity in Recognition Memory. *The Journal of Neuroscience*, 25(11), 3002-3008. <http://doi.org/10.1523/JNEUROSCI.5295-04.2005>
- Zago, L., Petit, L., Jobard, G., Hay, J., Mazoyer, B., Tzourio-Mazoyer, N., ... Mellet, E. (2017). Pseudoneglect in line bisection judgement is associated with a modulation of right hemispheric spatial attention dominance in right-handers. *Neuropsychologia*, 94(November 2016), 75-83. <http://doi.org/10.1016/j.neuropsychologia.2016.11.024>

Chapter 5: Episodic Memory Retrieval of Perceptual Experience is Spatially Biased

Abstract

The potentially causal role of the parietal cortex in episodic memory has been discussed at the frontier of cognitive neuroscience for two decades. Extensive research has characterised the heterogeneous functions of parietal activity and provided particular insight into the functional relevance of superior aspects of the parietal cortex to memory. However, the behavioural significance of the inferior parietal processing has been contentious to the extent that its role remains unclear and theoretically divisive. Neuropsychology and recent transcranial magnetic stimulation experiments have suggested that the angular gyrus integrates multifaceted perceptual information into an accessible subjective memory experience. Here, we present two experiments that explore the influence of the spatial location of encoded information on the recruitment of episodic retrieval mechanisms specialised for memory of perceptually defined experience. In the first experiment, we observed significantly more accurate recognition of items originally studied on the left side of visual space. Experiment 5.2 assessed the specific contribution of lateralised retrieval processing to this effect. The right hand of blindfolded subjects was systematically guided (we controlled the time spent exploring each object and the spatial pattern of perception) through a series of tactile arenas (each with a distinct tactile context, e.g. cotton wool) to encode through touch, a set of objects positioned in different areas of space. At test, subjects were cued with each tactile context and asked to recall the objects they had experienced in that context. Significantly more items were recalled from the bottom left of arena space than the right. In addition, memory accuracy in this task was correlated with lateralisation of reporting autobiographical memory space in another retrieval-focussed measure of hemispheric lateralisation. These three experiments revealed systematic differences in memory retrieval across the left and right sides of space, which cannot be explained by mental imagery, working memory bias, or perceptual prejudice at encoding.

Introduction

Our understanding of the brain systems that enable the storage and retrieval of the what, where, and when of life events, otherwise known as episodic memories, has vastly improved with the advent of neuroimaging techniques. For the last 15 years, the functional role played by the inferior parietal lobule (IPL) (angular gyrus and supramarginal gyrus) in the retrieval of episodic memory has been a contentious frontier in cognitive science (Davidson et al., 2010; Hutchinson et al., 2009; Simons & Mayes, 2008; Wagner et al., 2005; Yazar et al., 2014). Successful retrieval of episodic memories has been strongly associated with activation of the IPL in fMRI studies (Gray, & Montaldi, (in preparation (a)); Hutchinson et al., 2009; Yazar, Bergström, & Simons, 2012). Despite the consistency of this association, an interesting disconnect has existed between the seemingly minimal effects of damage to the IPL on memory abilities and the consistency of episodic memory-related IPL activity observed with neuroimaging techniques (Berryhill et al., 2007; Davidson et al., 2010; Simons et al., 2008).

In Gray and Montaldi (in preparation (a)), we classified previous fMRI investigations of episodic memory retrieval according to the content of the memory information. Memory assessments were classified according to both the content of the memory that had been encoded and the requirements of the retrieval challenge at test. A perceptually defined memory experience was characterised by two features: 1) detailed sensory information, most often in the visual domain, and 2) memory tests in which accurate performance was highly dependent on re-experiencing sensory information. For example, the detailed perceptual features of the encoded item (e.g. a semi-consumed lager beer) are crucial to distinguishing between two similar variants of the same item (e.g. distinguishing between your beer and the beer belonging to a second party). Two different criteria were used to classify a semantic and conceptually defined memory experience: 1) information stored in memory with limited perceptual detail, and 2) memory tests in which accurate performance could be effectively achieved through memory for a semantic or conceptual label for the information. For example, without needing to draw on the raw percept that led to that memory, one may recognise they had encountered the concept 'wine' earlier.

The classification in Gray and Montaldi (in preparation (a)) revealed that the IPL exhibits hemispheric specialisation in episodic memory function. We showed extremely consistent

activation of the right, but not left, IPL during perceptually defined memory experiences. In contrast, the left, but not right, IPL was active with great consistency during semantic and conceptually defined memory experiences. This conclusion is further supported by hemispheric differences in the connectivity of the IPL (Bellana et al., 2016). This study revealed that during unconstrained autobiographical retrieval, the right angular gyrus and the medial temporal lobe (MTL) show substantial functional connectivity. In contrast, the left angular gyrus showed functional connectivity with the default mode network but not the MTL during this task. These works provide evidence that a crucial role of the IPL is to recall and integrate the numerous features of perceptual experiences into a cohesive memory, and that this function may be specialised within the right hemisphere.

Establishing the causal role of the IPL in episodic memory retrieval has been limited by the scarcity of studies utilising patients and neuro-stimulating techniques. However, two investigations of patients with IPL lesions have observed an impairment in free recall of autobiographical memory (Berryhill et al., 2007; Davidson et al., 2010). Davidson et al., (2010) observed that this IPL-induced impairment was characterised by a reduction in objective episodic memory. The number of diagnostic episodic memory details recalled was reduced despite the preservation of the ability to describe semantic, non-specific information. In addition, patients produced fewer remember responses during a remember/know recognition task that indicated a lack of detailed recollection. However, Simons, Peers, Mazuz, Berryhill, & Olson, (2010) observed that IPL damage produced a reduction in recollection confidence, rather than performance, on a recognition memory task. This further causally implicates IPL processing in episodic retrieval mechanisms, although the distinction between deficits in objective memory and subjective memory confidence in these patients raises further questions as to the specific role of the IPL in this system.

Our understanding of the role of the IPL in episodic memory has been improved by studies combining fMRI and autobiographical memory challenges (Bellana et al., 2016; Brown et al., 2018; Rissman, Chow, Reggente, & Wagner, 2016). Accurate and detailed re-experiencing of autobiographical events is frequently reliant on the recall and integration of multiple perceptual features of a memory. As a result, successful autobiographical memory retrieval is frequently associated with right hemisphere IPL activations. In contrast, many recognition tasks require

little to no recollection of the perceptual features of an encoding experience. Frequently, the memory experiences in these tasks did not fit our classification as a perceptually defined memory experience and were, instead, classified as semantic and conceptual. For example, testing memory for simple word pairs is unlikely to induce the same detailed re-experiencing of the event as recollection of scenes (unless encoding instructions specifically encouraged this). Instead, accurate memory of semantic concepts, that is not necessarily functionally contingent on IPL processing, would be sufficient for accurate recognition memory (one may recognise they had encountered the concept 'bicycle' earlier, without needing to draw on the raw percept that led to that memory). This distinction may explain the divergent observations of the two neuropsychological studies detailed earlier. The patients in the Davidson et al., (2010) autobiographical memory study were more reliant on recall and integration of perceptual memory features, whereas the ability of patients to rely on semantic/conceptual memory produced a lack of sensitivity for detecting objective memory impairments in Simons et al., (2010).

Bisiach & Luzzatti (1978) and later, McGeorge *et al.*, (2007) showed that the majority of healthy individuals report more features of the left side of autobiographical memory space (the view of remembered features of a mental image from a fixed perspective) than the right. The term 'representational pseudoneglect' has been coined to describe this bias in reporting autobiographical memory space. Perceptual pseudoneglect describes the tendency for the majority of individuals to allocate more attention to the left side of perceptual space. The optimisation of highly perceptual and spatial attention allocation processing in the right frontoparietal attention network (including the IPL) has been implicated in the production of both the perceptual and representational pseudoneglect effects (Benwell, Harvey, et al., 2014; Brooks, Della Sala, & Darling, 2014; Corbetta & Shulman, 2011; Heilman & Van Den Abell, 1980; Mesulam, 1981). Interestingly, although representational pseudoneglect is, by definition, a bias in reporting from memory, the prospect that episodic retrieval mechanisms could also contribute to the spatial bias has never been well explored.

The attention-based explanation of representational pseudoneglect suggests that after a representation is retrieved, mental imagery or attention that is specialised in the right hemisphere, leads to more detailed visualisations or descriptions (respectively) of the left side

of the memory. This idea has been supported and developed by subsequent investigations of spatial lateralisation biases in working memory and mental imagery (Darling et al., 2012; Della Sala et al., 2010; Friedman et al., 2012; McGeorge et al., 2007). We hypothesised that representational pseudoneglect may also result from hemispheric differences in the specialisation of episodic retrieval mechanisms. As described earlier, we have provided evidence that the IPL in the right hemisphere is specialised for the retrieval of the perceptual features of memory. This may directly enable strong medial temporal lobe interaction (Bellana et al., 2016) and result in more effective memory retrieval of the perceptual features of the left side of memory space. Alternatively, a spatially-specific memory enhancement could also occur through the interaction of the IPL with superior parietal structures with a functional role in memory-retrieval (Sestieri et al., 2017). The perceptual pseudoneglect effect is reportedly driven by a process that is similar to this second/alternative proposed mechanism (Corbetta & Shulman, 2011). Activity in the ventral attention network (which includes the IPL) upregulates activity in the spatially-specific superior parietal lobule (which forms a part of the dorsal attention network). The hemispheric specialisation of attention processing in the right ventral attention network leads to greater activation of the right superior parietal lobule than the left, and subsequently, to greater spatial attention allocation to the contralateral, left side of perceptual space (the pseudoneglect effect).

The current study aims to investigate the possibility that spatially biased episodic memory retrieval of perceptual details, that is independent of mental imagery or attention to remembered space, is contributing to the representational pseudoneglect effect. Such an observation would both implicate retrieval mechanisms in the representational pseudoneglect effect and inform our understanding of the systems enabling episodic memory retrieval. We first provide details of a behavioural experiment with a similar design to the fMRI study presented in Gray & Montaldi (in preparation (a); experiment 4.2). We assessed whether a spatial bias in memory could be demonstrated in the absence of mental imagery. Our recognition-based paradigm removed the requirement for subjects to mentally imagine a scene or space. This experiment also required subjects to focus closely on the perceptual details of objects by providing multiple encoding experiences, and employing a forced choice, recognition memory paradigm with similar lures. Like the fMRI study, this experiment also employed two test formats. Trials in the traditional Old/New test format displayed a previously presented object

(target) and a new similar object (lure). Contrastingly, our recently developed Old/Old test format required participants to choose between two targets. Subjects were always asked to identify which of two similar objects they had encountered previously. The Old/Old format removed the processing of novelty from decision making and allowed us to better assess the relative strength of recognition on each side of space.

Methods - Behavioural Experiment - 5.1

Participants

Data were collected from 28 (4 males, 18-22 years, mean = 19.55) volunteers. This sample size is in accordance with the size of samples in previous similar memory experiments (Cansino & Trejo-Morales, 2008). All participants were right-handed with normal or corrected-to-normal vision and no history of neurological disorder. All participants read the participant information sheet, and provided written, informed consent at the start of the experimental session. Individuals were compensated with £7 for 60 minutes of participation in the behavioural study. All procedures were approved by the University of Manchester Research Ethics Committee. Three participants did not follow instructions and missed the interval between study and test. These participants were removed from the analysis.

Stimuli

All images were digital photographs of everyday objects (see *Fig 5.1*) and were provided by Migo *et al.*, (2013). Stimuli were selected from a database of images consisting of 48 object sets (for example, scissors, keys, apple), each containing between 16 and 25 variants of the object (e.g., 16 different apples). Two (for use in the Old/Old test format) or three (for use in the Old/New test format) images from each object set were used in the behavioural study. Representative stimuli are provided in *Fig 5.1*.

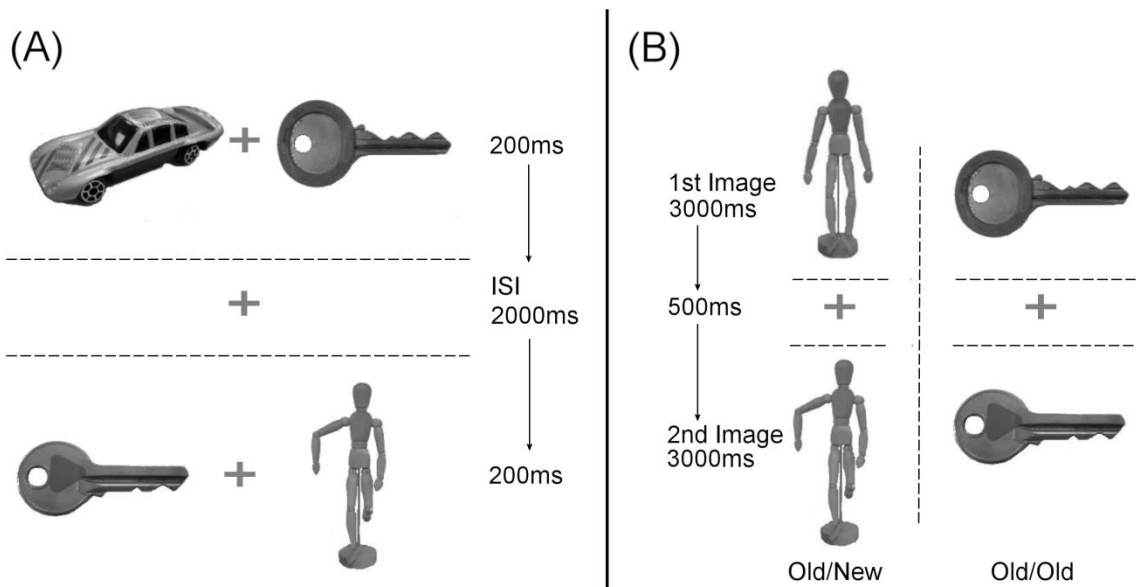


Figure 5.1: A schematic representation of the common study phase and two formats of the test phase of the forced choice recognition paradigm. Note in the Old/Old test phase the presence of two similar items both having been seen at study, in contrast to the presence of a similar foil, not seen at study, in the Old/New test condition.

Materials

All behavioural experimental sessions took place in a dedicated testing room at the University of Manchester. A 17 inch monitor on a desktop computer was used to complete all visual tasks in the behavioural task. Participants viewed the screen from 1 metre away. A standard QWERTY keyboard was used for all tasks and all responses were made on the number pad. Stimuli were presented and responses recorded through E-Prime (Psychology Software Tools, Inc.).

Procedure

Participants first completed an observation (study) phase in which two images were presented on either side of a central fixation cross. The width of each image was 25% of the total screen width. The height of the image was variable but never exceeded 25% of total screen width. Participants were instructed to maintain fixation on the cross and use their peripheral vision to take in as much information as they could about both images at the same time. The left hand edges of each image were presented at 35% and 65% of total screen width. The two images were presented simultaneously for 200ms and the inter-stimulus interval was 1800ms. 48 pairs of images (96 images) were shown in the study phase. To ensure accurate memory, the study phase

was repeated four times for each participant with a short break (approx. 30 seconds) between each repetition. Participants were unaware for the first two repetitions that the block would be repeated four times in total. This information was divulged after the second repetition. The instruction to remain centrally fixated during trials and to use peripheral vision to perceive both sides was reiterated between every repetition.

Both the pairing of images and their position in space remained constant throughout the study repetitions. However, the order of trial presentations was random and varied between repetitions. The location of each image during study was fully counterbalanced across participants. Two objects from the same object set (e.g. two apples) were never shown in the same study pair. During the study phase, participants were not required to respond. During practice, eight study pairs were shown in an identical format to the study phase. This practice study block ensured that participants were accustomed to the speed of the task, fully comprehended the study instructions, and were able to maintain the central fixation (verbal confirmation).

A 10 minute unfilled period of rest followed the encoding task. Participants were instructed to relax and not continue the experiment. Following rest, the test phase of the task was conducted. At test, two images were presented centrally one after the other. Images were the same size as presented in the study phase. The first image was presented for 3000ms and then immediately replaced by a fixation cross for 500ms. The second image was then presented for up to 3000ms. Participants were required to indicate which of the two images had been seen before (the “1” key if the first image was seen before, the “2” key if the second image was seen before). Participants were required to respond before the second image left the screen. Images from each study location (left and right) were equally and randomly distributed between the first and second presentations at test.

Two different test formats were used: an Old/New format (Target versus Similar Foil - 24 tests) and an Old/Old format (Target versus Target - 24 tests). The Old/New condition consisted of a previously presented target and a similar foil. The Old/Old condition comprised two similar images of the same object type that had both been shown separately, and in different left/right locations, in the study condition, (see *Fig 5.1*). The order of presentation of the image pairs and

the order of presentation of each test format was random. A practise that immediately preceded the test phase was conducted with six test pairs sourced from the practise study list.

Results - Visual Memory Lateralisation Experiment

Pilot testing indicated that participants were reliably able to name both objects in a pair within the study phase presentation time. A similar procedure used in an eye-tracking study (Gray and Montaldi, submitted) confirmed that subjects could maintain central fixation whilst images were presented on the left and right side of space. This guaranteed that both objects could be perceived and potentially encoded.

Statistical analyses were conducted on data from 25 participants. Collapsed across location of target at study, the mean accuracy of the sample in the Old/New condition was 63.16% (SD=11.45%, 95% CI [58.44% - 67.89%]). Critically, this accuracy was significantly greater ($t(24) = 5.75$, $p = <0.001$) than chance (50%) when explored with a one sample t-test. For obvious reasons, collapsed accuracy for the Old/Old condition was 100%.

Two one-sample T-tests, one each for the Old/New and Old/Old test formats, compared the difference between the recognition rates of targets encountered at study on the left and right side (left hit rate -right hit rate) of visual space with chance/unbiased identification (no difference) = 0. This analysis showed that in the Old/New test format the hit rate for identification of targets originally encountered on the left side of visual space was significantly greater ($t(24) = 2.15$, $p = 0.042$, $d = 0.43$) than for those originally presented on the right side (Mean Difference = 7.67%, SD = 17.83%, CI = [0.30% - 15.02%]). The Old/Old test format revealed a laterality bias that was also significantly biased in favour of items encoded on the left side of space ($t(24) = 2.37$, $p = 0.027$, $d = 0.47$). *Fig 5.2* displays the difference in item recognition from each side of space in the Old/New and Old/Old format.

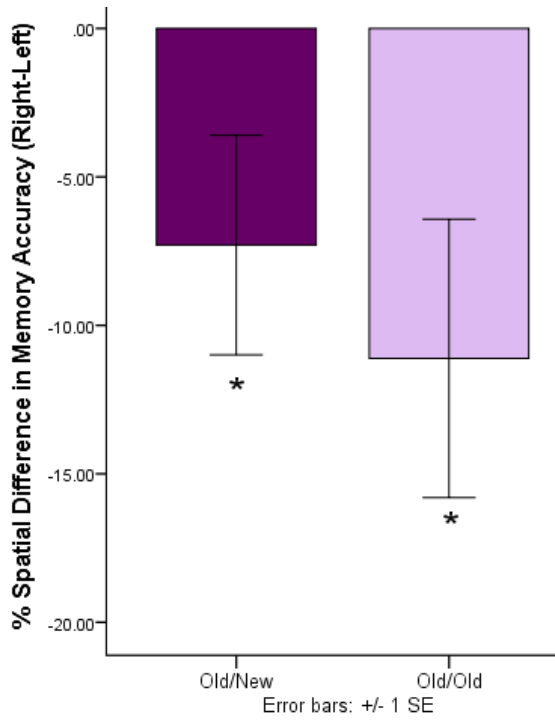


Figure 5.2: A comparison between the mean percentage hit rates for targets presented on the left and right at study in each test format. In both the Old/New and Old/Old test format, identification of targets for items originally presented on the left were significantly higher (asterisk indicates significance, $p = 0.042$ and $p = 0.027$ respectively) than for those presented on the right. Error bars indicate 95% confidence intervals.

Discussion - Visual Memory Lateralisation Experiment

The representational pseudoneglect effect has formerly been attributed to the specialisation of mental imagery processing in the right hemisphere (McGeorge et al., 2007). In the current experiment, individuals are not required or encouraged to form any mental images. Instead, each object is presented to the subjects at test. This provides all of the image information required for a recognition decision and focuses on the more implicit effect of spatial position on item memory.

In revealing a memory advantage for items presented on the left side of space, this experiment has provided the first evidence that the representational pseudoneglect effect can be observed in the absence of mental imagery. The effect observed here was not seen in the behaviour of the fMRI task (Gray & Montaldi (submitted, Chapter 4). In the current experiment (5.1), memory accuracy was greater than the fMRI task (63.16% here compared to 57.3% in the fMRI task). This increased accuracy is likely to be a function of the multiple encoding experiences of each item. It is also likely that this increased memory accuracy will have increased the number of recollective memory experiences characterising the test trials. Recollection has been more closely linked to IPL activity than familiarity memory (Yonelinas et al., 2005), and the difference in the effects observed across the two experiments potentially reflects the closer association of recollection with parietal cortex-related spatially-specific memory. We do not have a measure of the relative contribution of recollection and familiarity to memory on these experiments and further work is required to explore this potential mechanistic difference in the driver of spatially-specific memory.

Whereas spatially biased attention to a fully remembered and visualised mental image cannot explain the present findings, hemispheric specialisation of episodic retrieval mechanisms may provide insight. The angular gyrus has been causally linked with the recall and integration of perceptual memory features (Yazar et al., 2017). Though the left, but not right, angular gyrus has been investigated in experiments utilising non-invasive neural modulations (e.g., repetitive transcranial magnetic stimulation (TMS), theta burst TMS), two strands of evidence actually suggest the right IPL might be specialised for this function. First, functional connectivity analysis has revealed strong associations between the right angular gyrus and the MTL during episodic retrieval (Bellana et al., 2016). Second, Gray & Montaldi (in preparation (a)) observed that the right, but not left, IPL is consistently active during episodic memory retrieval of perceptually

defined experiences. We argue that it is feasible that the role of the IPL, and its specialisation in the right hemisphere, may result in more effective memory retrieval of the perceptual features of the contralateral, left side of memory space than the ipsilateral, right side. This could occur directly, through stronger right IPL interaction with the medial temporal lobe (Bellana et al., 2016), and/or through right IPL driven upregulation of memory-relevant superior parietal structures that subsequently increases memory search (Sestieri et al., 2017).

Tactile and Autobiographical Memory Experiments

Perceptual pseudoneglect asymmetries may change the perception of targets in different areas of space (Dickinson & Intraub, 2009; Reuter-Lorenz et al., 1990), and influence the order in which participants perceive stimuli (the first saccade during a scene presentation generally explores the left visual field (Thomas et al., 2014)). Avoiding perceptual pseudoneglect in the encoding phase of a memory paradigm therefore presents a substantial challenge to assessing episodic memory retrieval mechanisms. Control and manipulation of visual fixations, saccades, and covert shifts in attention through space is inherently difficult to achieve. In complete contrast, far greater control over the experience of an individual can be achieved in the tactile domain. Physical manipulation of the position of the subject's hand or body can control both the pattern and order of spatial exploration, along with the time spent exploring each item. Pseudoneglect has been readily detected in the tactile domain (Brooks et al., 2011). To the authors knowledge, these findings have been almost exclusively used a tactile line/rod bisection task. Unlike previous studies observing tactile pseudoneglect, systematic control over pattern, order, and time encoding items in the tactile domain should eliminate the influence of all perceptual pseudoneglect. We utilise such control in a novel tactile cued recall task in the following experiment. We created spatial arenas containing objects that were encoded by blindfolded subjects using touch whilst being manually guided around the arena by the experimenter.

Similar to experiment 5.1, subjects were oriented to the details of the perceptual experience at encoding and retrieval. This increased the probability that right rather than left hemisphere IPL retrieval mechanisms would be recruited, and the likelihood of a spatial bias in memory recall to the left. Critically, subjects were told that their memory for individual objects, but not their position in space, would be tested. This approach guided individuals away from a strategy of

memorising all of the objects in an entire arena as one representation, potentially encouraging mental imagery that could be subject to perceptual pseudoneglect. Rather we measured the more implicit effect of spatial position on memory retrieval of individual object-arena associations.

Additionally to the systematic encoding and tactile cued recall task, we employed a highly similar version of the test of autobiographical memory retrieval of the Piazza del Duomo that was developed by Bisiach & Luzzatti (1978). Like this previous experiment, we asked participants to mentally adopt a perspective at a specific location (the Stopford Building or University Place at the University of Manchester) and describe as many features of the visible scene as possible. After a filled interval, participants were asked to adopt the opposite perspective and describe the scene again. Interestingly, this procedure contains episodic memory retrieval, mental imagery, and probably attention to a remembered scene. Moreover, the procedure has been associated with the representational pseudoneglect effect (Bisiach & Luzzatti, 1978; McGeorge et al., 2007). As a result, it provides the ideal opportunity for comparison with the tactile cued recall task, which contains episodic memory retrieval, but not mental imagery or attention to a remembered scene. This comparison will serve as an effective assessment of the contribution of hemispheric lateralisation of memory retrieval mechanisms to the representational pseudoneglect effect.

Methods - Tactile and Autobiographical Memory Experiments - 5.2

Participants

Data were collected from 36 (23 females, 18-25 years, mean = 19.97) volunteers. This sample is larger than that in experiment 5.1. In a similar experiment to the autobiographical task, McGeorge et al., (2007) recruited 100 individuals. This previous experiment revealed subtle lateralisation effects. We increased our sample size from experiment 5.1 in an attempt to capture these subtle effects. All participants were right-handed with normal or corrected-to-normal vision and no history of neurological disorder. All participants read the participant information sheet, and provided written, informed consent at the start of the experimental session. Individuals were compensated with course credit for 120 minutes of participation in the study. All procedures were approved by the University of Manchester Research Ethics Committee.

Stimuli and Materials

A total of 128 different, distinct objects were employed in the tactile cued recall task. These objects were spatially distributed across eight tactile arenas. Each arena was composed of four cardboard boxes arranged in a 2x2 structure (2 horizontally adjacent boxes with 2 boxes secured on top). A single material, distinctive to touch, covered the surface within each arena: cotton wool, corrugated rubber, tin foil, polyethylene plastic, sand paper, bubble wrap, dishcloth, or woollen blanket. Each object was secured (tied with string) to the boxes' back wall in one of the four corners. This created a 4x4 distribution of objects across each arena. The arenas were positioned on tables spanning the width of a dedicated testing room at the University of Manchester. See *Fig 5.3* for an illustration of the structure and arrangement of each arena.

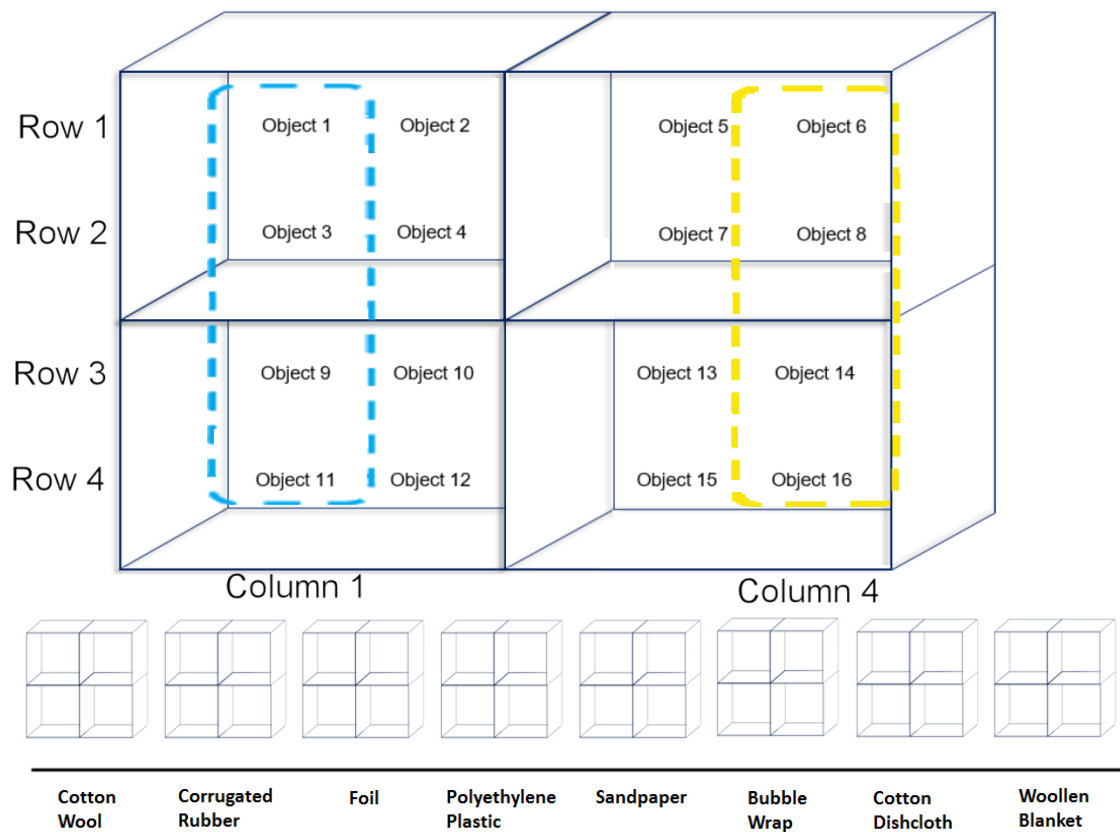


Figure 5.3: An illustration of the layout of objects within a single arena. Each arena was characterised by a distinct material. Only data from the first (blue) and fourth (yellow) column of the arena was eligible for analysis.

Procedure - Tactile Cued Recall Task

Subjects were blindfolded and seated prior to entering the testing room. This ensured that subjects were not exposed to the test materials prior to the experiment. Participants sat on an office chair with wheels. This chair was used to position participants at the correct height and centrally in front of each tactile arena. Counterbalancing controlled for item dependent memory effects. This included the order in which arenas were encountered, and the position of objects within the arenas, such that across participants, each object was encountered in each position of the box. The tactile memory testing was split into two blocks. Each block contained a memory assessment (encoding and retrieval) of four of the eight tactile arenas. Participants rested for 5 minutes between each block.

Each subject's right hand was systematically guided throughout each arena to feel and identify the objects that were positioned within each arena. The order in which subjects encountered

the objects at encoding was changed for each box and participant. This change ensured that encoding began on the left and the right side of the box equally and that the pattern of exploration of the box was unpredictable. Upon each encounter, subjects were asked to remember the perceptual experience combining each object's identity in association with the matching arena material for a later cued recall memory test. The materials were not referred to by name by the experiments, instead being referred to as 'this/the material'. This approach mitigated semantic associations between the objects and materials. The left hand of the individual remained on the material to assist with the process of associating objects with the perceptual features of each arena during encoding. On encountering each object, participants were required to verbally state the object's identity. These verbal descriptions were used to assess subsequent memory accuracy. Critically, the systematic guiding of the right hand controlled the order in which objects were encountered and the time spent exploring each object (5 seconds). After encountering all objects in an arena, the encoding process was repeated for a second time in the same order. Following the encoding phase, participants completed the test phase of the tactile cued recall task. Subjects were returned to the first arena that was studied. Whilst still blindfolded and positioned once again in front of each arena, participants felt the material, and were asked to recall as many objects as they could from the arena with that material.

Procedure - Autobiographical Memory Task

The autobiographical memory task was conducted prior to, and following the tactile task. Prior to the tactile task, participants were asked to adopt a perspective in their memory from one of two very familiar locations at the University of Manchester: University Place or the Stopford Building. Participants imagined themselves walking down Oxford Road from one of these locations to the other (e.g. University Place to the Stopford Building) and were instructed to describe their surroundings in as much detail as possible. See *Fig 5.4* for an illustration of the layout of Oxford Road between University Place and the Stopford Building. After completing the tactile task, participants completed the autobiographical memory task again. Participants described the surroundings of the reverse journey to the one they described prior to the tactile task (in this example, the Stopford Building to University Place). A dictaphone recorded the participant's recall of the scene and these were later compared against a reference video, created one day prior to experimentation, to enable accurate confirmation of subjects' memory

details. In addition to recording recall of confirmable memory details, we also noted the number of words used to describe the scene. These included non-confirmable, and incorrect information, as well as non-memory related words. The spatial location (left or right) that these non-diagnostic words were attributed to was also recorded for subsequent analysis.

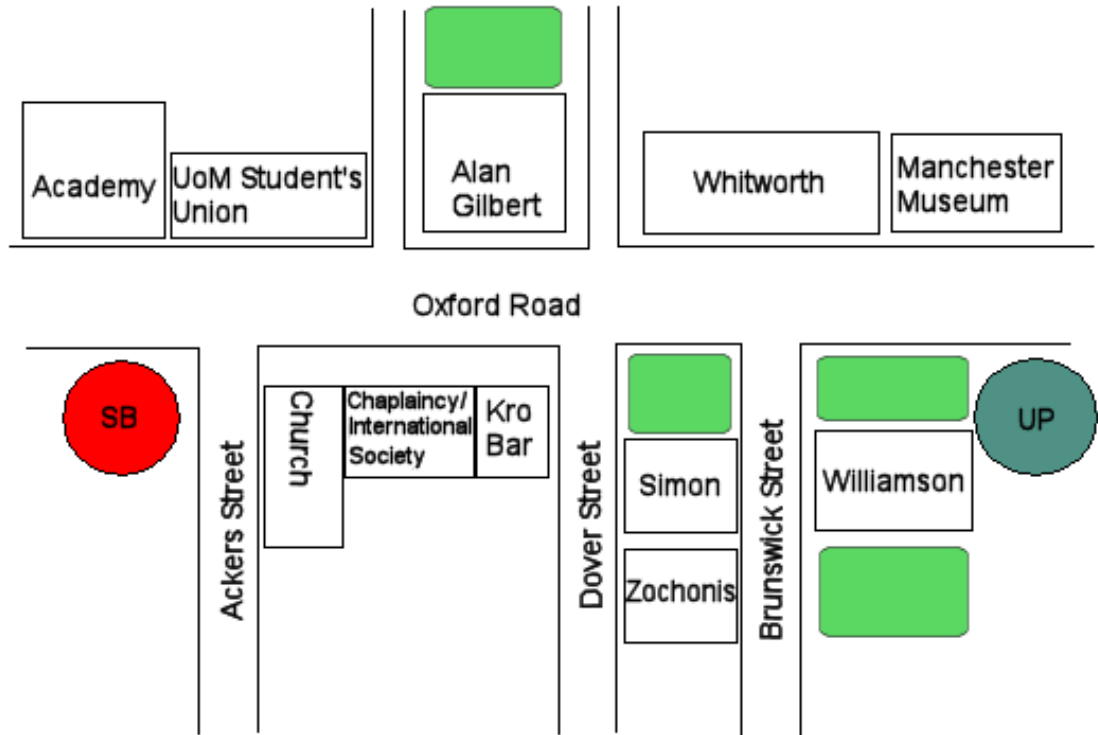


Figure 5.4: An illustration of the basic layout of Oxford Road, Manchester and the prominent University buildings. (SB = Stopford Building, UP = University Place).

Results

Tactile Cued Recall Memory

Statistical analyses were conducted on data from 35 participants. One participant was excluded prior to analysis of the contrast of interest because of a failure to follow task instructions. Objects in columns two and three were presented directly in front of participants. As a result, these columns did not contribute to our comparison of the left and right side of memory space, and are not referred to further here. Data from the first and fourth columns of the arena were eligible for analysis (see *Fig 5.3* for an illustration of the eligible object positions and *Table 5.1* for summary statistics).

Cued Recall	Left		Right	
	Mean % (SD)	CI	Mean % (SD)	CI
Row 1	28.57 (18.58)	[22.19, 34.95]	32.86 (21.24)	[25.56, 40.15]
Row 2	37.50 (17.94)	[31.34, 43.66]	34.64 (17.44)	[28.65, 40.63]
Row 3	30.36 (17.23)	[24.44, 36.27]	34.29 (15.85)	[28.84, 39.43]
Row 4	47.14 (21.67)	[39.70, 54.60]	36.07 (21.60)	[28.65, 43.49]

Table 5.1: Descriptive statistics for the tactile cued recall memory task.

Collapsed across target locations, 35.18% (SD = 5.48) of objects were recalled. A within-subjects 2x4 (left/right x row 1/2/3/4) repeated measures ANOVA compared number of item hits across each object location. Descriptive statistics for these conditions are provided in *Table 5.1*. We observed a significant main effect of vertical position ($F(2.35, 77.53) = 4.40$, $p = 0.011$, $\eta^2 = 0.117$ (sphericity not assumed)) but no main effect of horizontal position ($F(1, 33) = 0.819$, $p = 0.37$, $\eta^2 = 0.072$). An interaction between vertical and horizontal position approached significance ($F(3, 99) = 2.56$, $p = 0.059$, $\eta^2 = 0.072$). We investigated the potential interaction using paired samples *t*-tests that compared recall between the left and right positions of each row of the arena. Interestingly, we observed significantly (though uncorrected for multiple comparisons) better recall for items originally presented on the left side than the right side in the fourth row of arena ($t(34) = 2.53$, $p = 0.016$, $d = 0.512$). Comparison of recall of objects originally presented on the left and right side of space in the other rows of the arena did reveal any significant differences (row 1 - $t(34) = 1.03$; row 2 - $t(34) = 0.77$; row 3 - $t(34) = 0.85$; all p

values > 0.05). Illustrations of these comparisons are provided in Fig 5.5. Further investigation with a Pearson’s correlation analysis did not reveal a relationship connecting the difference between memory on the left and right side of space, and overall performance on the tactile cued recall memory task ($r = 0.309$, $p = 0.071$).

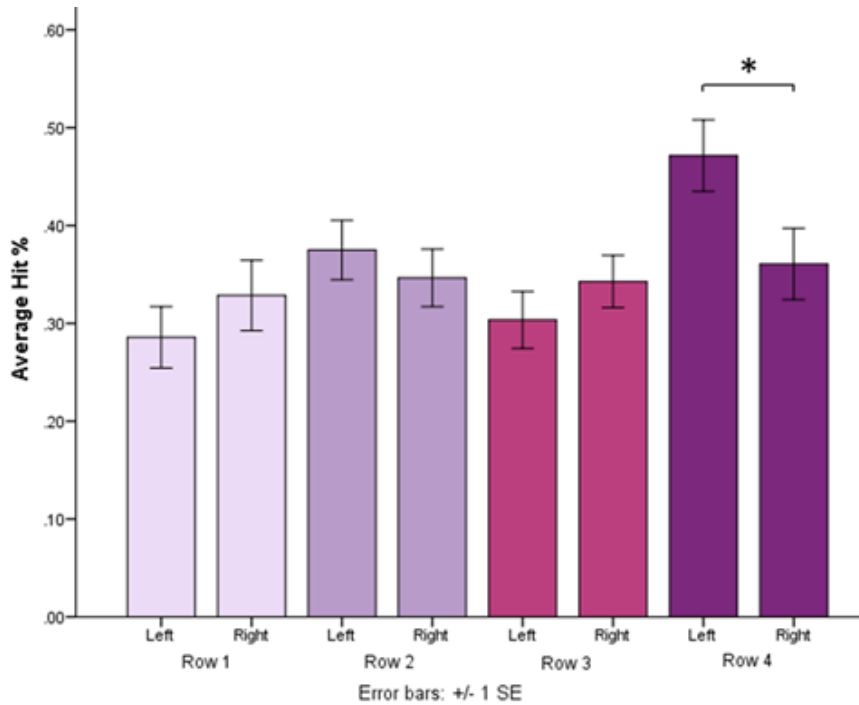


Figure 5.5: A comparison between the mean hit percentages of cued recall from each of the object positions in the tactile memory task. Error bars indicate one standard error of the mean. Asterisk indicates significance - $p = 0.016$.

Autobiographical Memory

Collapsed across direction of mental memory travel and locations within the mental representation, subjects recalled an average of 14.49 confirmable landmarks using 107.69 words. Descriptive statistics are presented in Table 5.2.

Autobiographical Memory	Left		Right	
	Mean (SD)	CI	Mean (SD)	CI
Confirmable Landmarks	7.29 (2.83)	[6.31, 8.26]	6.97 (3.17)	[5.88, 8.06]
Words	51.91 (24.25)	[43.58, 60.25]	55.77 (27.79)	[46.22, 65.32]

Table 5.2: Descriptive statistics pertaining to the autobiographical memory task.

Two dependent variables were assessed by one-sample *t*-tests, illustrated in Fig 5.6. The first of these variables was a measure of the difference between the number of confirmable landmarks that were recalled from each side of representational space (right-left). In addition, we measured the difference between the number of words used to describe each side of representational space (right-left). Within our sample, more words were used to describe the right side of representational space than the left (mean difference = 4.77 words), and this difference was close to significance ($t(34) = 2.01, p = 0.053, d = 0.339$). We found no significant difference between the number of confirmable landmarks recalled on each side of representational space (mean difference = -0.31 landmarks, $t(34) = 0.9, p = 0.375, d = 0.152$). The laterality biases that were measured by each of our dependent variables were compared using a paired samples *t*-test. This revealed a significant difference (mean difference = 5.09, $t(35) = 2.28, p = 0.029$) between the two measures of laterality (Fig 5.6).

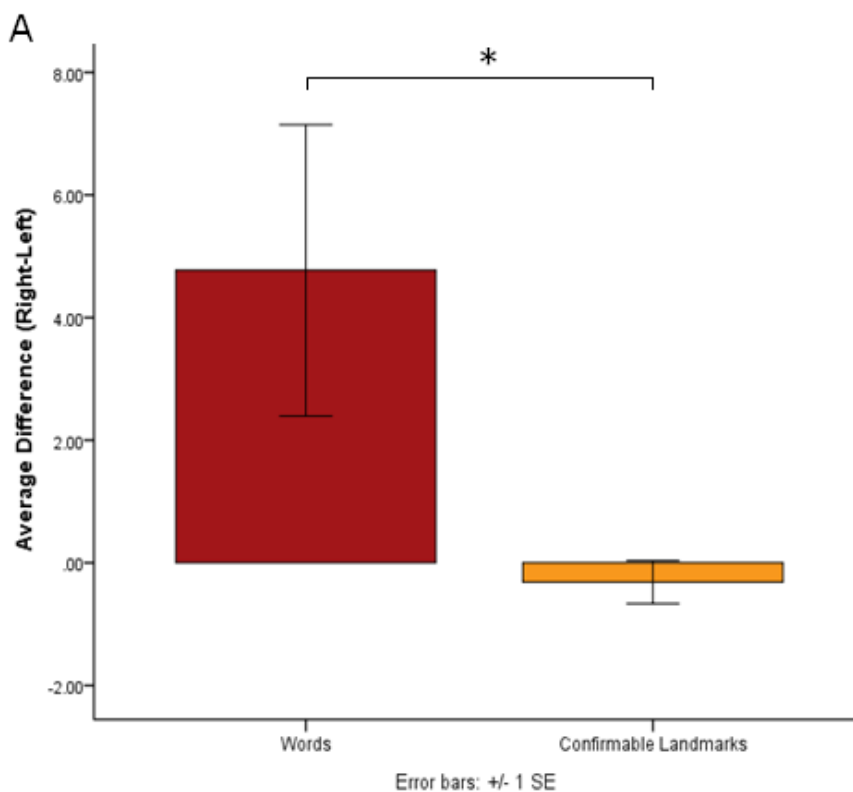


Figure 5.6: We observed a strong but non-significant trend for more words to be used to describe the right side of autobiographical memory space than the left ($p = 0.053$). There was no difference in the number of confirmable landmarks recalled from the left and right side of autobiographical memory space ($p = 0.375$).

We used a Pearson's correlation analysis to investigate whether the total number of confirmable landmarks recalled was associated with the direction and extent of the memory and word lateralisations. In our sample, we found that individuals who recalled more confirmable landmarks from the left side of autobiographical memory space, also tended to recall the most confirmable landmarks overall, though this effect did not quite reach the threshold for statistical significance ($r = -0.325$, $p = 0.057$).

Cross Task Investigations

We performed a Pearson's correlation analysis to investigate the potential relationship between the laterality bias in the autobiographical, and tactile cued recall, memory tasks. Interestingly, we observed that subjects who recalled more confirmable landmarks from the left side of autobiographical memory space demonstrated significantly better memory for items originating from the right side of the tactile cued recall task ($r = -0.456$, $p = 0.006$) (*Fig 5.7A*). This relationship was not observed for memory on the left side in the tactile cued recall memory task ($r = -0.092$, $p = 0.6$) (*Fig 5.7B*). There was also no significant relationship between the difference in the number of words used to describe each side of autobiographical memory space (right-left), and the difference in memory recall for items originating from the left and right side of space in the tactile cued recall task ($r = -0.234$, $p = 0.177$).

We also assessed whether there was any relationship between lateralisation measured by the autobiographical memory and tactile cued recall tasks. Better memory (more items recalled) in the tactile cued recall task was characterised by an increasingly leftward laterality bias in recall of confirmable landmarks during the autobiographical memory task ($r = -0.349$, $p = 0.04$) (*Fig 5.7C*). In contrast, no significant relationship was observed between the difference in the number of words used to describe each side of autobiographical memory space and tactile cued recall memory accuracy ($r = -0.097$, $p = 0.581$) (*Fig 5.7D*).

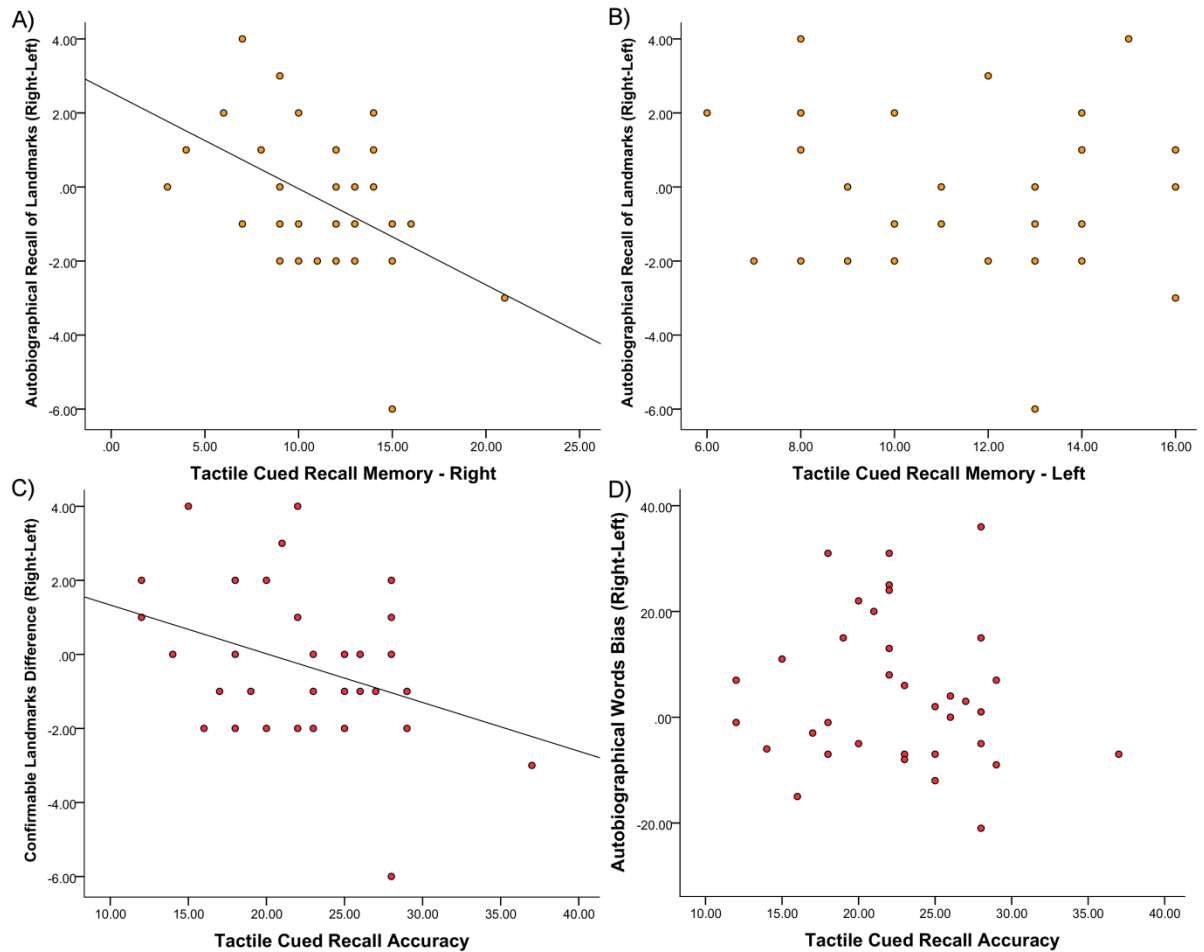


Figure 5.7: **A)** An illustration of the linear relationship between the difference in recall from right and left autobiographical memory space and memory of the right side in the tactile cued recall task ($p = 0.006$). **B)** There was no linear relationship between the difference in recall from right and left autobiographical memory space, and memory of the left side in the tactile cued recall task. ($p = 0.6$). **C)** An illustration of the significant relationship between more accurate tactile cued recall and greater leftward biases in autobiographical memory space ($p = 0.04$). **D)** The number of words used to describe each side of autobiographical memory space showed no significant relationship with tactile cued recall accuracy ($p = 0.581$).

General Discussion

The experiments in this study assessed the cognitive mechanisms that support the retrieval of the perceptual detail of episodic memories. As mentioned, we proposed in Gray and Montaldi (in preparation (a)) that the recruitment of the IPL of each hemisphere depends on the nature of the information being retrieved from memory. More specifically, the right IPL is engaged particularly by the retrieval of perceptually defined memory experiences, while the left IPL is engaged principally by the retrieval of semantic and conceptual memories. In this study, we hypothesised that the right hemisphere specialisation of perceptual memory retrieval processing could lead to a spatially-specific enhancement of perceptually driven memory. We suggested that right IPL processing could increase communication with the medial temporal lobe structures either directly (Bellana et al., 2016) or through excitatory modulation of more superior parietal structures involved in memory search or decision making (Cabeza et al., 2011; Sestieri et al., 2017). This mechanism may produce better memory for items encoded on the contralateral, left side of space. The memory biases that have been described in our experiments strongly suggest that at least one of these mechanisms produces better retrieval of the perceptual details of episodic memories for events encountered on the left side of space.

Previous investigations of the influence of hemispheric specialisation on episodic memory have implicated mental imagery and attention to a remembered image as key components of the representational pseudoneglect effect. In experiment 5.1, we conducted a recognition memory paradigm that demonstrated a leftward bias in episodic memory space that was independent of the effects of mental imagery and attention to a remembered image. We then employed systematic tactile encoding and item focussed (rather than scene focussed) memory retrieval in the tactile cued recall task of experiment 5.2. This carefully ensured that neither spatially-biased encoding, nor biased mental imagery at retrieval influenced the degree of lateralisation bias during this task. Despite these controls, we observed that memory accuracy in the tactile cued recall task was best on the left side (in the fourth (lowest) row). This effect should be interpreted with caution as the omnibus ANOVA test demonstrated only a trend that did not reach significance. During encoding, we attempted to promote perceptual memory using an engaging, rich and stimulating perceptual experience. As a result, the leftward bias in cued recall that we observe likely reflects the hemispheric difference in IPL engagement during

perceptual episodic memory retrieval. More work of this nature is required to replicate, and more clearly reveal this effect and its neural underpinnings.

Our novel hypothesis regarding the hemispheric specialisation of the IPL in episodic memory retrieval is further strongly supported by our validation procedure using the autobiographical memory task. We observed a tendency for individuals who recall more features from the left, than the right side of autobiographical memory space, to recall the most confirmable landmarks. Interestingly, these same subjects also performed significantly better on the tactile cued recall memory task. These two correlations suggest that across these two tasks, a strategy with a greater focus on the perceptual details was advantageous to memory performance. The autobiographical memory task used here is similar to the well-known Piazza del Duomo autobiographical memory task (Bisiach et al., 1981; McGeorge et al., 2007). Representational pseudoneglect (a leftward bias in memory not formerly attributed to retrieval mechanisms) has previously been observed using this paradigm. The relationship we have observed here between the extent of lateralisation in autobiographical memory space and tactile cued recall accuracy (*Fig 5.7C*) provides novel and compelling evidence that the hemispheric specialisation of episodic retrieval mechanisms contributes to the production of the representational pseudoneglect effect.

Additional evidence presented in the current study further supports our suggestion regarding the hemispheric specialisation of IPL function in memory. Recalling more confirmable landmarks from the left side of autobiographical memory space was associated with better memory for the right, but not the left side in the tactile cued recall task (*Fig 5.7A*). More specifically, those who better employ memory for perceptual details (*i.e.* those who show a leftward bias in autobiographical memory space) show very good memory for items from both sides of the tactile arenas. This effect mirrors the hemispheric specialisation characteristics of the ventral attention network (which also contains the IPL) (Corbetta & Shulman, 2002, 2011). Long standing evidence suggests that the right IPL is engaged during bilateral attention allocation in visual space. In contrast, the same network in the left hemisphere is recruited only during attention allocation to the contralateral visual field (Duecker et al., 2013; Heilman & Van Den Abell, 1980; Sheremata, Bettencourt, & Somers, 2010). The IPL is engaged in both attention and memory (though specific cortical regions may not overlap - Hutchinson et al. (2014)). We suggest that the strong performance in bilateral memory space of participants who best employ memory for

perceptual details shows that the spatial lateralisation of episodic retrieval observed in these experiments is a reflection of the characteristic processing of the IPL.

We observed a strong trend for descriptions of the right side of autobiographical memory space to contain more non-diagnostic words. In addition, the laterality bias measured by non-diagnostic words was significantly more rightward than that indexed by the number of confirmable landmarks that were recalled. We expect that the use of more non-diagnostic words to describe the right side of autobiographical memory space is a function of specialised language processing in the left hemisphere (Cai et al., 2013; Josse & Tzourio-Mazoyer, 2004; Purves et al., 2012). Similar induction of left hemisphere specialised language processing has been closely linked with greater spatial attention allocation to the right visual field (Gray and Montaldi (submitted)). Unlike previous studies of autobiographical memory space (Bisiach & Luzzatti, 1978; McGeorge et al., 2007), our instructions asked participants to describe their autobiographical memory space in as much detail as possible. This may have unexpectedly increased the engagement of the left hemisphere specialised language system in our study.

In contrast to the rightward bias in non-diagnostic words, we did not observe a laterality bias in the retrieval of confirmable landmarks. The interhemispheric competition account of frontoparietal attention network processing states that greater engagement of the left hemisphere frontoparietal attention network may suppress activity in the same network in the right hemisphere. The IPL is part of this network and the greater engagement of the left IPL in our paradigm may have reduced right IPL activity and masked the previously observed leftward recall bias in autobiographical memory space. However, the extent of the lateralisation of confirmable landmark recall correlated well with memory in the tactile cued recall task. In further contrast, we did not observe any correlations between the use of non-diagnostic words and lateralisation biases in the tactile cued recall memory task. This further supports our proposition that the IPL in the right, but not the left hemisphere, supports episodic memory retrieval of perceptual experience. Furthermore, these findings also support the lateralisation in functional connectivity observed in angular gyrus. The right angular gyrus showed greater connectivity with the MTL. In contrast, the left angular gyrus showed default mode network connectivity (Bellana et al., 2016). More specifically, the present study demonstrates that this hemispheric specialisation and difference in functional connectivity can be expressed as a spatial bias in objective memory retrieval.

Summary

We have previously proposed that the memory-related recruitment of the IPL of each hemisphere is dependent on the content of the memory being retrieved (Gray and Montaldi (in preparation (a))). More specifically, episodic memory retrieval of perceptual details engages the right IPL, whereas the retrieval of semantic/conceptual detail engages the left IPL. We suggested that, under certain conditions, this functional difference between the right and left hemisphere IPL may result in differences in the accuracy of episodic memory across egocentric space. More specifically, perceptual episodic memory retrieval would recruit the right hemisphere IPL and enable better memory in contralateral, left space. In this study, we observed two leftward biases in memory retrieval accuracy and specific correlations that fit with this interpretation.

We first recruited a forced choice recognition memory paradigm that demonstrated a leftward memory accuracy bias in the absence of spatially biased mental imagery. We then employed a cued recall memory task with systematic tactile encoding that carefully ensured that perceptual pseudoneglect and mental imagery did not bias the lateralisation of spatial memory. In line with our hypothesis and despite systematically controlling for perceptual pseudoneglect and minimising mental imagery, we reported a tendency for the left side of egocentric space to be more accurately remembered than the right. We also utilised an autobiographical memory task that was a close analogue of the seminal studies of spatial memory using the Piazza del Duomo (Bisiach & Luzzatti, 1978; McGeorge et al., 2007). Correlation of the lateralisation of memory across both tasks revealed that individuals with good accuracy showed evidence of a more perceptual memory strategy (indicated by the leftward memory bias in autobiographical memory task). This association between better bilateral memory on the tactile cued recall task and the lateralisation in reporting autobiographical memory space provides strong evidence for a memory analogue of the attention allocation processing that characterises the IPL. In addition, this cross-task correlation suggests that episodic retrieval mechanisms played a significant role in producing the previously reported representational pseudoneglect effect (Bisiach & Luzzatti, 1978; McGeorge et al., 2007).

This set of experiments has demonstrated the value of considering the characteristics of cortical processing in one domain, (e.g. attention), in mapping functional processing in another domain

(i.e., memory). We utilise our prior understanding of hemispheric specialisation and network features to directly investigate memory retrieval processing and the neural system that underpins it. Future work should continue to characterise the idiosyncratic features of the IPL in episodic memory processing. Fatigue, viewing distance, and age all affect the distribution of attention allocation as a function of varying the balance of IPL activation across the hemispheres (Benwell, Thut, et al., 2014, 2013; Learmonth et al., 2017; Longo & Lourenco, 2006). It is probable that the engagement of the IPL in episodic memory varies in a similar way. The prospect that changes in the balance of IPL activation across the hemispheres might also account for subjective and objective memory impairments in age and disease is promising and deserves additional investigation.

References

- Bellana, B., Liu, Z.-X., Anderson, J. A. E., Moscovitch, M., & Grady, C. L. (2016). Laterality effects in functional connectivity of the angular gyrus during rest and episodic retrieval. *Neuropsychologia*, 80, 24-34. <http://doi.org/10.1016/j.neuropsychologia.2015.11.004>
- Benwell, C. S. Y., Harvey, M., & Thut, G. (2014). On the neural origin of pseudoneglect: EEG-correlates of shifts in line bisection performance with manipulation of line length. *NeuroImage*, 86, 370-80. <http://doi.org/10.1016/j.neuroimage.2013.10.014>
- Benwell, C. S. Y., Thut, G., Grant, A., & Harvey, M. (2014). A rightward shift in the visuospatial attention vector with healthy aging. *Frontiers in Aging Neuroscience*, 6, 113-124. <http://doi.org/10.3389/fnagi.2014.00113>
- Benwell, C. S. Y., Thut, G., Learmonth, G., & Harvey, M. (2013). Spatial attention: differential shifts in pseudoneglect direction with time-on-task and initial bias support the idea of observer subtypes. *Neuropsychologia*, 51(13), 2747-56. <http://doi.org/10.1016/j.neuropsychologia.2013.09.030>
- Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: bilateral damage causes impaired free recall of autobiographical memory. *The Journal of Neuroscience*, 27(52), 14415-23. <http://doi.org/10.1523/JNEUROSCI.4163-07.2007>
- Bisiach, E., Capitani, E., Luzzatti, C., & Perani, D. (1981). Brain and conscious representation of outside reality. *Neuropsychologia*, 19, 543-51.
- Bisiach, E., & Luzzatti, C. (1978). Unilateral neglect of representational space. *Cortex*, 14, 129-133. [http://doi.org/10.1016/S0010-9452\(78\)80016-1](http://doi.org/10.1016/S0010-9452(78)80016-1)
- Brooks, J. L., Della Sala, S., & Darling, S. (2014). Representational pseudoneglect: A review. *Neuropsychology Review*, 24, 148-165. <http://doi.org/10.1007/s11065-013-9245-2>
- Brown, T. I., Rissman, J., Chow, T. E., Uncapher, M. R., & Wagner, A. D. (2018). Differential Medial Temporal Lobe and Parietal Cortical Contributions to Real-world Autobiographical Episodic and Autobiographical Semantic Memory. *Scientific Reports*, (April), 1-14. <http://doi.org/10.1038/s41598-018-24549-y>
- Cabeza, R., Mazuz, Y. S., Stokes, J., Kragel, J. E., Woldorff, M. G., Ciaramelli, E., ... Moscovitch, M. (2011). Overlapping Parietal Activity in Memory and Perception: Evidence for the Attention to Memory Model. *Journal of Cognitive Neuroscience*, 22(11), 3209-3217. <http://doi.org/10.1162/jocn>
- Cai, Q., Van der Haegen, L., & Brysbaert, M. (2013). Complementary hemispheric specialization for language production and visuospatial attention. *PNAS*, 110(4), 322-30. <http://doi.org/10.1073/pnas.1212956110>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201-15. <http://doi.org/10.1038/nrn755>
- Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. *Annual Reviews Neuroscience*, 34, 569-99. <http://doi.org/10.1146/annurev-neuro-061010-113731>
- Darling, S., Logie, R. H., & Della Sala, S. (2012). Representational pseudoneglect in line bisection. *Psychonomic Bulletin & Review*, 19(5), 879-83. <http://doi.org/10.3758/s13423-012-0285-z>

- Davidson, P. S. R., Anaki, D., Ciaramelli, E., Cohn, M., Alice, S. N., Murphy, K. J., ... Levine, B. (2010). Does lateral parietal cortex support episodic memory? Evidence from focal lesion patients. *Neuropsychologia*, 46(7), 1743-55. <http://doi.org/10.1016/j.neuropsychologia.2008.01.011>.Does
- Della Sala, S., Darling, S., & Logie, R. H. (2010). Items on the left are better remembered. *Quarterly Journal of Experimental Psychology*, 63(5), 848-55. <http://doi.org/10.1080/17470211003690672>
- Dickinson, C. A., & Intraub, H. (2009). Spatial Asymmetries in Viewing and Remembering Scenes: Consequences of an Attentional Bias? *Attention Perception and Psychophysics*, 71(6), 1251-1262. <http://doi.org/10.3758/APP.71.6.1251>
- Duecker, F., Formisano, E., & Sack, A. T. (2013). Hemispheric differences in the voluntary control of spatial attention: Direct evidence for a right-hemispheric dominance within frontal cortex. *Journal of Cognitive Neuroscience*, 25, 1332-1342. <http://doi.org/10.1162/jocn>
- Friedman, A., Mohr, C., & Brugger, P. (2012). Representational pseudoneglect and reference points both influence geographic location estimates. *Psychonomic Bulletin & Review*, 19(2), 277-284. <http://doi.org/10.3758/s13423-011-0202-x>
- Gray, O.J., & Montaldi, D. (submitted). Attention Allocation Systems Selectively Specialised for Spatial or Semantic Processing: A Reversed Pseudoneglect Effect.
- Gray, O.J., & Montaldi, D., (in preparation). Convergent Evidence for Hemispheric Specialisation of Episodic Memory Retrieval Mechanisms in the Inferior Parietal Lobule.
- Heilman, K. M., & Van Den Abell, T. (1980). Right hemisphere dominance for attention: The mechanism underlying hemispheric asymmetries of inattention (neglect). *Neurology*, 30, 327-330. <http://doi.org/10.1212/WNL.30.3.327>
- Hutchinson, J. B., Uncapher, M. R., & Wagner, A. D. (2009). Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. *Learning & Memory*, (650), 343-356. <http://doi.org/10.1101/lm.919109.16>
- Hutchinson, J. B., Uncapher, M. R., Weiner, K. S., Bressler, D. W., Silver, M. A., Preston, A. R., & Wagner, A. D. (2014). Functional heterogeneity in posterior parietal cortex across attention and episodic memory retrieval. *Cerebral Cortex*, 24(1), 49-66. <http://doi.org/10.1093/cercor/bhs278>
- Josse, G., & Tzourio-Mazoyer, N. (2004). Hemispheric specialization for language. *Brain Research Reviews*, 44(1), 1-12. <http://doi.org/10.1016/j.brainresrev.2003.10.001>
- Learmonth, G., Benwell, C. S. Y., Thut, G., & Harvey, M. (2017). Age-related reduction of hemispheric lateralisation for spatial attention: An EEG study. *NeuroImage*, 153, 139-151. <http://doi.org/10.1016/j.neuroimage.2017.03.050>
- Longo, M. R., & Lourenco, S. F. (2006). On the nature of near space: Effects of tool use and the transition to far space. *Neuropsychologia*, 44(6), 977-981. <http://doi.org/10.1016/j.neuropsychologia.2005.09.003>
- McGeorge, P., Beschin, N., Colnaghi, A., Rusconi, M. L., & Della Sala, S. (2007). A lateralized bias in mental imagery: evidence for representational pseudoneglect. *Neuroscience Letters*, 421(3), 259-63. <http://doi.org/10.1016/j.neulet.2007.05.050>
- Mesulam, M. (1981). A cortical network for directed attention and unilateral neglect. *Ann Neurol*, 10, 309-25. <http://doi.org/10.1002/ana.410100402>

- Purves, D., Augustine, G., Fitzpatrick, D., Hall, W., LaMantia, A., & White, L. (2012). *Neuroscience*. Sunderland (MA): Sinauer Associates Inc.
- Reuter-Lorenz, P. A., Kinsbourne, M., & Moscovitch, M. (1990). Hemispheric control of spatial attention. *Brain and Cognition*, 12, 240-6. [http://doi.org/10.1016/0278-2626\(90\)90018-J](http://doi.org/10.1016/0278-2626(90)90018-J)
- Rissman, J., Chow, T. E., Reggente, N., & Wagner, A. D. (2016). Decoding fMRI Signatures of Real-world Autobiographical Memory Retrieval. *Journal of Cognitive Neuroscience*, 28(4), 604-620. http://doi.org/10.1162/jocn_a_00920
- Schneider, W., Eschmann, A., & Zuccolotto, A. (2012). *E-Prime User's Guide*. Pittsburgh: Psychology Software Tool, Inc. Retrieved from https://www.researchgate.net/publication/260296789_E-prime_User%27s_Guide
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2017). The contribution of the human posterior parietal cortex to episodic memory. *Nature Reviews Neuroscience*, 18(3), 183-192. <http://doi.org/10.1038/nrn.2017.6>
- Sheremata, S., Bettencourt, K. C., & Somers, D. C. (2010). Hemispheric Asymmetry in Visuotopic Posterior Parietal Cortex Emerges with Visual Short-Term Memory Load. *Journal of Neuroscience*, 30(38), 12581-12588. <http://doi.org/10.1523/JNEUROSCI.2689-10.2010>
- Simons, J. S., & Mayes, A. R. (2008). What is the parietal lobe contribution to human memory? *Neuropsychologia*, 46(7), 1739-42. <http://doi.org/10.1016/j.neuropsychologia.2008.05.001>
- Simons, J. S., Peers, P. V., Hwang, D. Y., Ally, B. A., Fletcher, P. C., & Budson, A. E. (2008). Is the parietal lobe necessary for recollection in humans? *Neuropsychologia*, 46(4), 1185-1191. <http://doi.org/10.1016/j.neuropsychologia.2007.07.024>
- Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2010). Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex*, 20(2), 479-85. <http://doi.org/10.1093/cercor/bhp116>
- Thomas, N. A., Loetscher, T., & Nicholls, M. E. R. (2014). Asymmetries in attention as revealed by fixations and saccades. *Experimental Brain Research*, 232, 3253-67. <http://doi.org/10.1007/s00221-014-4015-9>
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, 9(9), 445-53. <http://doi.org/10.1016/j.tics.2005.07.001>
- Yazar, Y., Bergström, Z. M., & Simons, J. S. (2012). What is the parietal lobe contribution to long-term memory? *Cortex*, 48(10), 1381-2. <http://doi.org/10.1016/j.cortex.2012.05.011>
- Yazar, Y., Bergström, Z. M., & Simons, J. S. (2014). Continuous theta burst stimulation of angular gyrus reduces subjective recollection. *PloS One*, 9(10), 1-7. <http://doi.org/10.1371/journal.pone.0110414>
- Yazar, Y., Bergström, Z. M., & Simons, J. S. (2017). Reduced multimodal integration of memory features following continuous theta burst stimulation of angular gyrus. *Brain Stimulation*, 10(3), 624-629. <http://doi.org/10.1016/j.brs.2017.02.011>

Chapter 6: Summary and Conclusions

The neural mechanisms governing spatial attention allocation and episodic memory have been investigated using predominantly distinct techniques. Until now, the tools developed by one of these fields of research have yet to be effectively and creatively adapted to investigate the other field. This thesis is concerned with hemispheric specialisation and its effect on spatial attention allocation and the retrieval of episodic memories. Over many years, the fields of both attention and memory have focused on the functional role of the IPL. However, the scope of this focus has been restricted to the role played by the IPL in supporting their respective cognitive processes. For the first time, the research in this thesis aimed to consider, empirically investigate, and observe the shared and unique contributions of the left and right hemisphere's IPL to memory retrieval and spatial attention allocation. To this end, the methods and investigative approaches of previous memory and attention allocation research have been adapted to establish targeted behavioural and neuroimaging measurements of hemispheric lateralisation in both spatial attention and long-term memory. This approach has yielded findings that underpin a fundamental change to our understanding of the functional characteristics of the IPL in memory and attention.

Spatial attention research has developed excellent tools for measuring inherent hemispheric specialisations in attention allocation processing (e.g. line bisection task, landmark task, greyscale task). The tendency for healthy individuals to preferentially allocate more attention to the left side of perceptual space than the right has been termed the pseudoneglect effect. This effect has been closely linked with hemispheric specialisation of spatial attention processing supported by the VAN (including the IPL) of the right hemisphere (Corbetta & Shulman, 2011). The pseudoneglect effect is a robust, behaviourally observable phenomenon that enables strong inferences about underlying neural mechanisms that support spatial attention. Many factors influence the strength and direction of the pseudoneglect effect (e.g., the distance between the stimulus and the observer (Longo et al., 2015) and the observer's state of arousal (Newman et al., 2013)). For this reason, spatial attention research has tended to reduce the complexity of its stimuli and judgements to mitigate these factors and allow for better insight into underlying neural processes. I proposed at the beginning of this thesis that this reduction in complexity predisposes individuals to exhibit the pseudoneglect effect and that key idiosyncratic features of the system governing spatial attention may have been overlooked as a result.

In *Chapter 2*, the research provides, for the first time, strong evidence that the left hemisphere attention network is optimised for allocating attention to semantically engaging stimuli. Subjects displayed attention allocation biases that were to the right of objective centre, to the right of their line bisection judgements, and even to the right of biases that were associated with their judgements of small horizontal lines (small lines produce the most rightward line-bisection attention bias). With the use of object-like abstract shapes, the degree to which subjects could interpret the stimulus was manipulated and thus the engagement of the semantic aspect of object recognition processing was varied. This behavioural modulation of the system illustrated that shapes that were more difficult to interpret displayed the greatest rightward attention bias. The additional semantic processing that was required to identify difficult to interpret shapes was implicated in underpinning this relationship.

A novel implicit primed attention (IPA) task was developed specifically to further investigate the link between semantic processing and spatial attention allocation. This task identified an additional dynamic of the semantically weighted attention allocation system that was also presented in *Chapter 2*. More specifically, this task established that the semantic processing-induced reversal of the traditional pseudoneglect effect that was observed in the object bisection task was also evident with covert attention allocation. Whereas subjects could move their eyes and voluntarily allocate their attention to specific features in the object bisection task that is discussed above, the IPA task ensured that subjects reactively oriented to stimuli whilst relying on covert attention allocation. Eye-tracking ensured that subjects fixated centrally. Despite this control, the IPA task showed that subjects were faster at orienting to the right side of visual space following the priming of attention by a semantic decision.

The IPL has been causally linked with both reactive covert attention allocation (Chambers & Heinen, 2010) and semantic processing (Davey et al., 2015; Price et al., 2016). The semantic priming and covert attention allocation to the X-target in the IPA task clearly implicates IPL processing as the probable instigator of the right visual field attention bias measured here. This novel insight substantially changes our perspective of the pseudoneglect from an idiosyncratic effect that is either present or absent, to a measure that is indicative of the hemispheric specialisation of IPL processing. This new perspective allows for exciting new insight into the dynamics of the IPL in spatial attention allocation and its other functions such as semantic processing and memory retrieval.

Line centre judgements of shorter lines are associated with more rightward attention allocation biases (Benwell, Harvey, et al., 2014). Rightward lateralisation biases are also associated with the distribution of attention to stimuli in distant space (Lane et al., 2015). It is well established that the size and distance of an object are easily confused and that this confusion underpins the perceptual illusion of forced perspective. *Chapter 3* provides the first evidence of common neural mechanisms that underlie the well-characterised line length and observer-target proximity effects. First, we observed that larger object images were associated with significantly greater leftward attention allocation biases. Forced perspective, the perceptual ambiguity between size and distance that occurs in the absence of informative distance cues (e.g., the Beuchet Chair illusion), provides an excellent explanation of both this effect and the line length effect. Large lines and objects could be misperceived as closer to the observer than small lines and objects. The target-observer proximity effect describes the left visual field bias associated with attention allocation in peripersonal space, and the shift in this bias to the right visual field with increasing distance between the target and observer. If the shape of stimuli, rather than forced perspective misperception of distance, were to modulate the laterality of attention, one would expect objects more similar in shape to small lines to exhibit the strongest rightward attention biases. The relationship between object size and attention bias described in *Chapter 3* is in the opposite direction to this shape dependent relationship.

Secondly in *Chapter 3*, fMRI evidence is presented that suggests that the processing recruited by the perception of objects is also recruited by the perception of line stimuli. Moreover, we observed a brain-behaviour relationship between regions traditionally associated with object recognition and the degree of lateralisation bias on the landmark task. This illustrated that the forced perspective confusion associated with objects could equally occur with line stimuli. This showed that an explanation of the line length effect with forced perspective misperception of size and distance was not only plausible, but a more effective account of the line length effect than shape-specific processing. Critically, this study also provides further impetus to investigate the pseudoneglect effect, and spatial attention allocation more generally, in ways that better reflect the complexity of our environments.

These studies have drawn on and manipulated behavioural idiosyncrasies, e.g. the pseudoneglect effect, the target-observer proximity effect, the line length effect, to provide a crucial progression of our understanding of the functioning of the neural mechanisms supporting

attention allocation. Importantly, this development has also enabled better understanding and prediction of the functional characteristics of the areas of the brain governing this spatial attention. As explained, the IPL of each hemisphere has been closely associated with the direction of attention to contralateral space. In addition, the IPL has been strongly linked to the retrieval of long-term memories. This thesis builds upon the AToM model, the previous suggestion that the IPL has a shared function in the allocation of attention externally in perception, and internally during memory retrieval. Though the role of the supramarginal gyrus and angular gyrus in the retrieval of long-term memory is not fully explained by the AToM model, this research has demonstrated common hemispheric specialisations that support both attention allocation and long-term memory retrieval. *Chapters 4 and 5* present the methodological developments and results of focused tests that reveal this hemispheric specialisation.

Chapter 4 presents two tests of hemispheric specialisation characterising episodic memory retrieval mechanisms, one of which utilises the similar object and lure images. First, a review of the lateralisation of IPL activations in previous neuroimaging studies was performed to investigate the potential link between the informational content of a retrieved memory and differences in the lateralisation of IPL activation. More specifically, the review asked whether the patterns of activity suggest that the retrieval of more richly perceptual memories is associated with greater right hemisphere IPL activity, while the retrieval of more semantic and/or conceptual memories is associated with left hemisphere IPL activity. In line with this hypothesis, this striking pattern of activation was clearly observed in the review.

A highly specific and targeted fMRI investigation of the functional correlates of perceptually-driven episodic memory is presented alongside the results of the neuroimaging review. Attempts to retrieve the perceptual aspects of object memories resulted in greater activation of the right than the left hemisphere IPL. In this experiment, the design ensured that the semantic/conceptual information was unimportant, and not diagnostic and therefore insignificant to the memory retrieval process. Interestingly, this processing was associated with substantially reduced activity of the left angular gyrus. Furthermore, compensation for weak perceptual memory by the engagement of semantic processing produced greater recruitment of the left supramarginal gyrus (this effect was uncorrected for multiple comparisons). This convergent primary and secondary evidence from fMRI studies of episodic memory retrieval

provides strong evidence for a clear hemispheric specialisation of episodic retrieval mechanisms.

Two clear and important conclusions can be drawn from the numerous observations of left hemisphere and bilateral activations identified in the neuroimaging review of *Chapter 4*. Firstly, common bilateral activations indicate that in many cases retrieval of both perceptual and semantic aspects of an episode can underpin an accurate memory experience. The probable redundancy in this mechanism may enable compensation for brain damage-induced processing failures (likely from a stroke or brain tumour) and thus provide a convincing explanation for the relative lack of clear memory impairments in parietal lesion patients. Though these impairments have not been easy to identify in patients with IPL damage, deficits in memory retrieval have been revealed in some of these patients primarily through careful manipulation and measurement of perceptually-driven memory (Berryhill et al., 2007; Simons et al., 2010). Interestingly, some of the limited available neuropsychological evidence suggests that patients with bilateral damage exhibit memory impairment when unilaterally damaged patients do not (Simons et al., 2010).

Secondly, the neuroimaging review of *Chapter 4* showed a greater prevalence of left than right hemisphere IPL activations during episodic retrieval. This is consistent with the idea that the retrieval of distinct semantic/conceptual features are often highly diagnostic of episodic memories, perhaps more reliably so than the more perceptual features. At least, this is likely the case with most experimental memory tests (see *Supplementary Table 4.1*). This characteristic highlights a mechanism that may represent memory efficiency. For example, distinction between old and new scenes using purely perceptual memory would require encoding and retrieval of numerous visual features. In contrast, memory for old scenes using semantic/conceptual information could be achieved quite efficiently by the retrieval of a small number of informative semantic labels. This is likely to characterise a majority of standard memory paradigms and therefore explain the left, or bilateral, hemisphere activation often seen in the studies that utilise them.

The specialisation of the IPL of each hemisphere revealed in this research provides an interesting and informative comparison between the neural mechanisms that govern attention allocation and those that underpin memory retrieval. Previous assessment of the comparison between attention and memory processing has provided evidence that similar roles are played by the dorsal and ventral attention networks in the retrieval of episodic memories (Cabeza et al., 2011,

2008; Sestieri et al., 2010). More specifically, the SPL has been linked to the guidance of voluntary, top-down memory search in these studies. This is comparable to the role of the same area of cortex in the allocation of attention to external stimuli in perception (Corbetta & Shulman, 2002, 2011). As mentioned, the role of the IPL, however, has been far more contentious. The ventral attention network (including the IPL) has been strongly associated with the reorientation of attention to unexpected or salient task-relevant perceptual information (Corbetta & Shulman, 2002, 2011). Similarly, the AToM model of LPC function suggests that the IPL reorients cognition to unexpected or salient aspects of episodic memory (Cabeza et al., 2008). However, IPL activations that do not reflect this attention-like processing mechanism have been commonly observed and the AToM model has been heavily criticised (Hutchinson et al., 2014, 2009; Shimamura, 2011).

As discussed in *Chapter 4*, perceptually-driven and semantic/conceptually-driven memory experiences are likely to differ considerably in the memory signals that are represented in the IPL. For example, a detailed memory for the original percept and many comparisons between target and the remembered percept would be required to distinguish between a previously seen 'Old' stimulus and a very similar 'New' stimulus using perceptually-defined memory (e.g. to identify which of three adjacent wine glasses belonged to you, you may need to remember and compare the many perceptual features (colour, quantity, exact location, smudges on the rim) of your wine glass with the other glasses). In contrast, semantic/conceptually-driven memory may be more frequently characterised by fewer memory details and comparisons. Without remembering details of the raw percept, one can remember that they encountered the concept 'wine' earlier.

The processing of each hemisphere's IPL may reflect the different characteristics of the memory experiences that they process. The numerous details and comparisons that frequently accompany perceptually-driven memory experiences may be best represented on a scale of memory strength with a threshold for an 'old' judgement (I.E. the process predicted by the mnemonic accumulator hypothesis (Wagner et al., 2005)) in the right IPL. In contrast, semantic/conceptually-driven memory experiences, represented in the left IPL, may be simpler and/or contain fewer memory comparisons to determine oldness. As a result, identification of only a few features of these less detailed memories may be highly diagnostic of the items memory state. Detection of stimulus traces that may arise from memory (I.E. the attention to

internal representation (Wagner et al., 2005)) may be more helpful (than a wide scale of memory strength signal) as an indicator of memory in less detailed semantic/conceptual memory decisions.

The novel perspective of LPC hemispheric specialisation for the processing of perceptually-driven and semantic/conceptually-driven memory retrieval that is presented in *Chapter 5* of this thesis provides the opportunity to assess the potential differences in processing characteristics across the IPLs of each hemisphere. Furthermore, our perspective suggests that the evidence supporting the criticism of the AToM model of parietal memory function may have lacked the specificity to reveal an overlap between the attention and memory systems. As a result, the distinction in the function of the LPC of each hemisphere illustrated in the current research should inform a reassessment of previous theories of the functional role of the LPC in episodic memory. This should include, but not be limited to future evaluations of the theories described by Wagner et al. (2005).

Variability in the level of ventral attention network activity has been causally linked to changes in the distribution of attention across space (Chambers et al., 2007). Processing in the ventral attention network, that responds equally to all areas of perceptual space, has the ability to drive activity in the spatially-specific dorsal attention network (Corbetta & Shulman, 2002, 2011; Gigliotta, Malkinson, Miglino, & Bartolomeo, 2017). This system dynamic provides the basis for our novel conceptual and mechanistic understanding of both the pseudoneglect effect and the rightward attention allocation bias that is associated with semantic object processing (see *Chapter 2*). The possibility that processing in the IPL, invoked by episodic memory related activity, might drive dorsal attention network activity in the same way as does the IPL attention modulation, has not been considered until now. For the first time, *Chapter 5* presents behavioural evidence that supports this previously unrecognised neural mechanism.

In this final experimental chapter (*Chapter 5*), a tactile cued recall task that varied the spatial location of objects whilst systematically controlling other features of encoding is presented. Interestingly, memory accuracy was better for objects in the bottom left side of space than the right. This exploratory analysis was further supported by a correlation between lateralisation of tactile cued recall and autobiographical spatially-specific memory. More specifically, the strength of the horizontal lateralisation bias (difference between memory accuracy from left and right space) was associated with performance on a putative retrieval-based assessment of

autobiographical memory (McGeorge et al., 2007). Critically, these effects clearly suggest differences in the mechanisms governing the retrieval of episodic memory. This is the first time that such an association has been observed, providing novel evidence for a memory driven interaction between the IPL and SPL. *Chapter 5* proposes that an attempt to remember the tactile perceptions from the encoding phase induces greater activity in the right than the left IPL. This activity drives recruitment of the right SPL more than the left SPL. The activity of each SPL is tightly modulated by interhemispheric inhibition (Duecker & Sack, 2015) and as a result, greater engagement of the right IPL could easily produce a highly active right SPL and a less active left SPL. Given the spatial specificity of the SPL and its role in top down memory processing, this difference in activity between the hemispheres may allow for better top-down memory search for memories encoded in the contralateral left side of space.

The representational pseudoneglect effect is currently believed to be underpinned by the unequal distribution of attention to a mental image (Della Sala et al., 2010; McGeorge et al., 2007). This suggests that the information from all areas of space is retrieved equally and that subsequent attention to representation processing induces the lateralisation in memory strength. The tasks measuring representational pseudoneglect effect are highly perceptual in their nature. In fact, these tasks often require the allocation of attention to these remembered perceptual features. This would be highly likely to produce greater IPL activity in the right, than the left hemisphere. The knock-on effects of this IPL imbalance on the SPL, and subsequently on internal spatial attention allocation could easily account for the leftward bias in describing memory space. However, the same mechanism does not provide a sufficient account of the lateralisation bias observed in *Chapter 5*. The tactile cued recall task prompts recall of perceptual experiences but not recall of a true mental image. The autobiographical memory task provided a useful comparison task that induces the retrieval of a mental image of a scene, whilst also providing a sensitive assessment of the lateralisation of memory retrieval. The correlations observed in this experiment between the tactile cued recall, and autobiographical memory tasks highlight the potentially fundamental role that hemispheric specialisation of retrieval is performing in inducing the representational pseudoneglect effect in long term memory.

This research emphasizes the importance of considering the functional role of the right, as well as the left IPL in episodic retrieval mechanisms. In combination, the chapters of this thesis illustrate the similarities in hemispheric specialisation of the LPC across different cognitive

functions. The focus of long term memory research on highly semantic memory tests and attention research on highly perceptual represent methodological and investigative biases. These biases have led to the widely accepted account that in the LPC, attention is right hemisphere lateralised and episodic memory retrieval is lateralised to the left hemisphere. Under specific, but arguably more ecologically relevant (i.e. less reductionist) conditions, the experiments presented in this thesis have demonstrated a mirror image of these perspectives. Moreover, these findings suggest that the previously proposed hemispheric lateralisation of LPC function in attention and memory may be primarily a function of the manner in which they have been measured. In attempting to reduce attention allocation to its simplest neural foundations, the influence of semantic and conceptual processing on the lateralisation of attention has been overlooked. Similarly, the understandable adoption of semantic words and concepts in investigations of episodic memory has produced an under appreciation of perceptually-specific memory effects and the contribution of perceptually-defined retrieval to memory.

Future Directions

The semantic/conceptual processing induced bias of attention allocation that was observed directly for the first time and reported in *Chapter 2* requires further detailed examination. Additional within-subject assessments of the response characteristics of the system, and the shift in attention bias under increasingly ecologically realistic scenarios are required. Furthermore, some sports require high degrees of perceptual accuracy (e.g. snooker, darts, motor racing, golf, and cricket) and the potential that the semantic attention allocation system can promote or impair performance of the skills involved in these sports has not been considered. For example, self-talk is a technique promoted to sports people to improve performance. The mechanism underlying this improvement may result from the improved balance of an otherwise leftward bias induced by strongly perceptually-driven attention processing that impairs performance. Future work should seek to develop and test the way cognitive idiosyncrasies might drive performance in different scenarios.

The research reported in *Chapter 3* revealed a strong link between the well-established line length, and target-observer proximity effects. These effects have both been associated with the extent to which the LPC in the right hemisphere is engaged by a perceptual stimulus (Benwell,

Harvey, et al., 2014; Longo et al., 2015). Many other factors also influence the extent of the pseudoneglect effect (e.g. age, time on task, stimulus contrast). Future investigations should attempt to improve our understanding of the commonalities and distinctions between the neural mechanisms that underpin these modulating factors. Not only is this important to our understanding of attention allocation, but, as has been demonstrated by investigations and subsequent findings the long-term memory research in this thesis, this progressive assessment of attention can inform the approach and mechanistic models of other areas of research.

Though it is widely accepted that the pseudoneglect effect can be produced by the modulation of SPL activity by the IPL, the characteristics of this interaction have yet to be clearly and fully characterised. However, the extent and direction of the attention allocation bias, and the output of the SPL have been used as an accurate, indirect measure of attention-related IPL activity for a long time (Corbetta & Shulman, 2002). The experiments presented here demonstrate that the IPL/SPL interaction can also be utilised as a measure of the degree to which hemispheric lateralisation exists for other functions of the IPL. Utilising behavioural lateralisation biases as a measure of IPL activity provides a tool for better understanding the functional idiosyncratic dynamics of the IPL in episodic memory retrieval, attention allocation, and semantic processing.

The previously proposed theory that the IPL of each hemisphere is responsible for a particular function (left = memory, right = attention) may have both restricted our understanding of the functions of these regions and limited the development of applications of this understanding to true to life scenarios. Unlike research into attention allocation, neurostimulation experiments that have assessed episodic memory have focused exclusively on the functional role of the left IPL. The insights provided by the experiments presented in this thesis strongly suggest that the role of the right IPL should also be investigated with these techniques. TMS and tDCS modulation of right IPL activity has been closely linked to altered spatial attention (Agosta, Herpich, Miceli, Ferraro, & Battelli, 2014; Chambers & Heinen, 2010; Göbel et al., 2006). Any attempt to modulate the memory-related processing of the right IPL, however, will require careful methodological exploration to allow differentiation between the memory and attention effects of neuromodulation. Methods, such as the tactile cued recall task and the IPA task (which could be easily adapted to a memory paradigm) developed in this research provide a suitable direction for this important work.

Further investigations are required to better understand the distinction between memory and attention in order to provide the neuromodulatory experiments, discussed above, with the ability to target specific neural mechanisms. Some evidence supporting this dissociation has been provided in the left hemisphere (Hutchinson et al., 2009), however the same analysis has not been performed in the right hemisphere. The research in this thesis has shown that hemispheric specialisation of the IPL is similar and comparable across memory and attention (semantic/conceptual processing - left IPL; perceptual/experiential processing - right IPL). This observation will allow for a better classification of attention and memory tasks and better assessment of when shared or distinct processing would be expected. For example, an attention task that focuses on perceptual allocation of attention across visual space is potentially less likely to elicit shared activity with semantic/conceptual memory processing than with perceptual/experiential memory systems. A meta-analysis of right parietal activity, similar to that conducted by Hutchinson et al., (2009), is required. Similarly, better within-subjects comparisons targeting similar aspects of attention and memory processing should also be conducted.

The mechanism that was revealed for the first time in *Chapter 5* also warrants additional investigation. The research reported in this chapter revealed that specialised retrieval of perceptual features of episodic memories in the right hemisphere is associated with better memory for items originally encountered on the left side of visual space. I propose in *Chapter 5* that this advantage is a result of interaction between the IPL and SPL. Retrieval of perceptually-defined memories induces greater activity in the right IPL than the left, subsequently driving greater activation in the right, than the left, SPL. A dual role for attention and memory has been identified for the SPL and the strong contralateral guidance of attention to perceptual space also seems to characterise spatially-defined memories. Our understanding of semantic processing in both perception and memory has been further developed in this thesis, and more closely linked with processing in the IPL. The potential behavioural advantage that could be conferred by induction of left IPL activity by semantic/conceptual memory retrieval and a subsequent interaction with the SPL has yet to be investigated. The findings of this thesis, along with other previous work, suggest that the specialisation of semantic/conceptual memory retrieval in the left hemisphere could confer a memory advantage to items originally encountered on the right side of perceptual space. A within-subjects comparison of the effect of these different types of

memory on behaviour would provide the strongest evidence yet in support of the mechanistic model of LPC function and memory that is proposed here. Neuromodulation of the LPC could also provide informative insight into these systems and provide an even stronger causal link between the LPC and episodic memory retrieval.

Despite the need for further focused investigation, this research has established a set of novel developments that are central to our understanding of the functions of the IPLs, LPCs, and the contribution made by these regions to behaviourally significant networks. These include the novel association between semantic processing in the left hemisphere VAN and a bias in attention allocation to the right side of perceptual space; a better characterisation of the right VAN; a novel link between the line length, and the target-observer proximity effects that is underpinned by forced choice misperception; the hemispheric specialisation of the IPL that reflects semantic/conceptually-driven memory processing in the left hemisphere, and perceptually driven memory processing in the right hemisphere; and the behavioural advantage in memory for the left side of remembered space that is conveyed by the specialisation of the right but not the left IPL for perceptual memory. These developments will help guide and accelerate new discovery in this field and contribute to the development of strategies that improve the lives of healthy individuals, patients with brain damage (e.g. from a stroke or tumour), and those with a neurodegenerative disorder (such as Alzheimer's, or Parkinson's disease).

References

- Agosta, S., Herpich, F., Miceli, G., Ferraro, F., & Battelli, L. (2014). Contralesional rTMS relieves visual extinction in chronic stroke. *Neuropsychologia*, 62(1), 269-276. <http://doi.org/10.1016/j.neuropsychologia.2014.07.026>
- Benwell, C. S. Y., Harvey, M., & Thut, G. (2014). On the neural origin of pseudoneglect: EEG-correlates of shifts in line bisection performance with manipulation of line length. *NeuroImage*, 86, 370-80. <http://doi.org/10.1016/j.neuroimage.2013.10.014>
- Berryhill, M. E., Phuong, L., Picasso, L., Cabeza, R., & Olson, I. R. (2007). Parietal lobe and episodic memory: bilateral damage causes impaired free recall of autobiographical memory. *The Journal of Neuroscience*, 27(52), 14415-23. <http://doi.org/10.1523/JNEUROSCI.4163-07.2007>
- Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: an attentional account. *Nature Reviews Neuroscience*, 9(8), 613-625. <http://doi.org/10.1038/nrn2459>
- Cabeza, R., Mazuz, Y. S., Stokes, J., Kragel, J. E., Woldorff, M. G., Ciaramelli, E., ... Moscovitch, M. (2011). Overlapping Parietal Activity in Memory and Perception: Evidence for the Attention to Memory Model. *Journal of Cognitive Neuroscience*, 22(11), 3209-3217. <http://doi.org/10.1162/jocn>
- Chambers, C. D., & Heinen, K. (2010). TMS and the functional neuroanatomy of attention. *Cortex*, 46(1), 114-117. <http://doi.org/10.1016/j.cortex.2009.03.002>
- Chambers, C. D., Payne, J. M., & Mattingley, J. B. (2007). Parietal disruption impairs reflexive spatial attention within and between sensory modalities. *Neuropsychologia*, 45(8), 1715-1724. <http://doi.org/10.1016/j.neuropsychologia.2007.01.001>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201-15. <http://doi.org/10.1038/nrn755>
- Corbetta, M., & Shulman, G. L. (2011). Spatial Neglect and Attention Networks. *Annual Reviews Neuroscience*, 34, 569-99. <http://doi.org/10.1146/annurev-neuro-061010-113731>
- Davey, J., Cornelissen, P. L., Thompson, H. E., Sonkusare, S., Hallam, G., Smallwood, J., & Jefferies, E. (2015). Automatic and Controlled Semantic Retrieval: TMS Reveals Distinct Contributions of Posterior Middle Temporal Gyrus and Angular Gyrus. *Journal of Neuroscience*, 35(46), 15230-15239. <http://doi.org/10.1523/JNEUROSCI.4705-14.2015>
- Della Sala, S., Darling, S., & Logie, R. H. (2010). Items on the left are better remembered. *Quarterly Journal of Experimental Psychology*, 63(5), 848-55. <http://doi.org/10.1080/17470211003690672>
- Duecker, F., & Sack, A. T. (2015). The hybrid model of attentional control: New insights into hemispheric asymmetries inferred from TMS research. *Neuropsychologia*, 74, 21-29. <http://doi.org/10.1016/j.neuropsychologia.2014.11.023>
- Gigliotta, O., Malkinson, T. S., Miglino, O., & Bartolomeo, P. (2017). Pseudoneglect in Visual Search: Behavioral Evidence and Connectional Constraints in Simulated Neural Circuitry. *eNeuro*, 4(December), 1-14. <http://doi.org/10.1523/ENEURO.0154-17.2017>
- Göbel, S. M., Calabria, M., Farnè, A., & Rossetti, Y. (2006). Parietal rTMS distorts the mental number line: simulating "spatial" neglect in healthy subjects. *Neuropsychologia*, 44, 860-8. <http://doi.org/10.1016/j.neuropsychologia.2005.09.007>

- Hutchinson, J. B., Uncapher, M. R., & Wagner, A. D. (2009). Posterior parietal cortex and episodic retrieval: convergent and divergent effects of attention and memory. *Learning & Memory*, (650), 343-356. <http://doi.org/10.1101/lm.919109.16>
- Hutchinson, J. B., Uncapher, M. R., Weiner, K. S., Bressler, D. W., Silver, M. A., Preston, A. R., & Wagner, A. D. (2014). Functional heterogeneity in posterior parietal cortex across attention and episodic memory retrieval. *Cerebral Cortex*, 24(1), 49-66. <http://doi.org/10.1093/cercor/bhs278>
- Lane, A. R., Ball, K., & Ellison, A. (2015). Dissociating the neural mechanisms of distance and spatial reference frames. *Neuropsychologia*, 74. <http://doi.org/10.1016/j.neuropsychologia.2014.12.019>
- Longo, M. R., Trippier, S., Vagnoni, E., & Lourenco, S. F. (2015). Right hemisphere control of visuospatial attention in near space. *Neuropsychologia*, 70, 350-357. <http://doi.org/10.1016/j.neuropsychologia.2014.10.035>
- McGeorge, P., Beschin, N., Colnaghi, A., Rusconi, M. L., & Della Sala, S. (2007). A lateralized bias in mental imagery: evidence for representational pseudoneglect. *Neuroscience Letters*, 421(3), 259-63. <http://doi.org/10.1016/j.neulet.2007.05.050>
- Newman, D. P., O'Connell, R. G., & Bellgrove, M. A. (2013). Linking time-on-task, spatial bias and hemispheric activation asymmetry: a neural correlate of rightward attention drift. *Neuropsychologia*, 51(7), 1215-23. <http://doi.org/10.1016/j.neuropsychologia.2013.03.027>
- Price, A. R., Peelle, J. E., Bonner, M. F., Grossman, M., & Hamilton, R. H. (2016). Causal Evidence for a Mechanism of Semantic Integration in the Angular Gyrus as Revealed by High-Definition Transcranial Direct Current Stimulation. *Journal of Neuroscience*, 36(13), 3829-3838. <http://doi.org/10.1523/JNEUROSCI.3120-15.2016>
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2010). Attention to Memory and the Environment: Functional Specialization and Dynamic Competition in Human Posterior Parietal Cortex. *Journal of Neuroscience*, 30(25), 8445-8456. <http://doi.org/10.1523/JNEUROSCI.4719-09.2010>
- Shimamura, A. P. (2011). Episodic retrieval and the cortical binding of relational activity. *Cognitive, Affective and Behavioral Neuroscience*, 11(3), 277-291. <http://doi.org/10.3758/s13415-011-0031-4>
- Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2010). Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cerebral Cortex*, 20(2), 479-85. <http://doi.org/10.1093/cercor/bhp116>
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, 9(9), 445-53. <http://doi.org/10.1016/j.tics.2005.07.001>

Appendix 1 - Supplementary Materials of Chapter 2

Supplementary Materials 2.1 - Abstract Shapes Interpretability

Methods

Participants

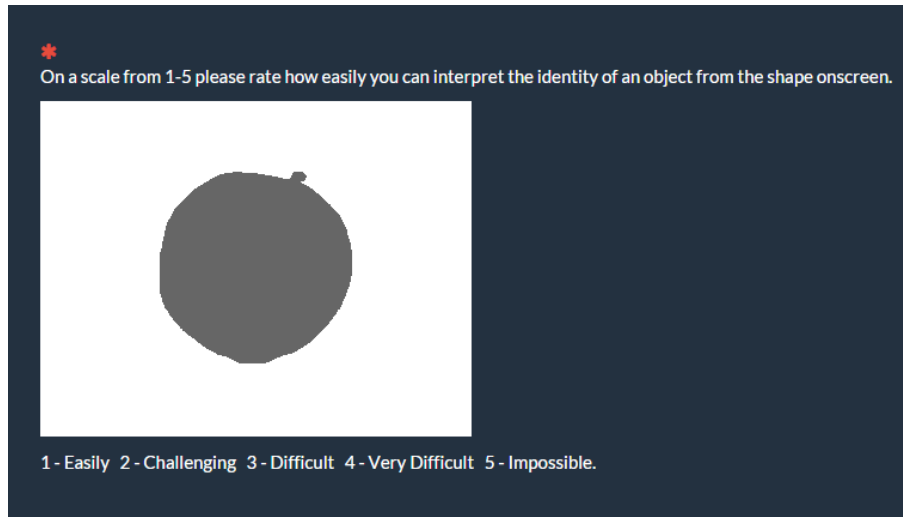
Data were collected for 22 (10 males, 21-55 years, Mean = 28.41 years old) individuals took part in the online interpretability rating procedure. All participants read the participant information and confirmed their informed consent before at the start of the experimental session. All procedures were approved by the University of Manchester Research Ethics Committee.

Images

The online interpretability rating procedure was performed on all abstract shape images (72) used in Experiment 2.2.

Procedure

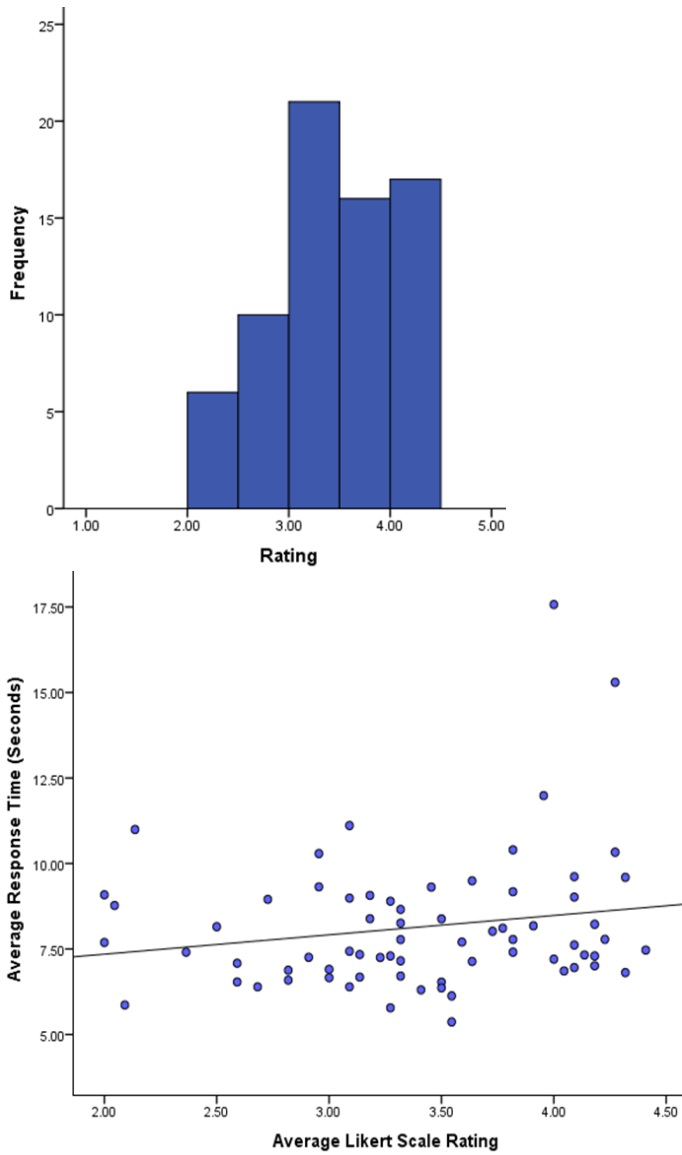
Participants were presented with each abstract shape and instructed to rate the ease with which they could infer the identity of an object from the image on a 1-5 Likert Scale: 1 - Easy, 2 - Challenging, 3 - Difficult, 4 - Very Difficult, 5 - Impossible. Participants could take as long as they needed to respond and response time was automatically recorded. The order in which shapes were presented was randomised. An example presentation is provided in *Supplementary Figure 2.1*.



Supplementary Figure 2.1: A representative example of the format of the online abstract shape image interpretability rating procedure.

Results

On average, abstract shape images were given a rating of 3.40 (SD = 0.63, CI = [3.24 - 3.55]). This means that on average participants found the shapes ‘Difficult’/‘Very Difficult’ to interpret as objects. The distribution of abstract shape interpretability ratings is provided in *Supplementary Figure 2.2*. A Pearson’s correlation assessed the relationship between the average time taken for participants to rate each shape (Mean = 8.14, SD = 1.98, CI = [7.67 - 8.61]) and the average interpretability rating assigned to each image. We observed no association between image interpretability ratings and time taken for participants to provide a rating ($r = 0.181$, $p = 0.134$).



Supplementary Figure 2.2: **A)** A histogram depicting the distribution of abstract shape image interpretability ratings. **B)** We observed no significant association between abstract shape image interpretability ratings and average response times ($r = 0.181$, $p = 0.134$).

Supplementary Materials 2.2 - IPA task (Experiment 2.3)

Eye-Tracking

Preprocessing

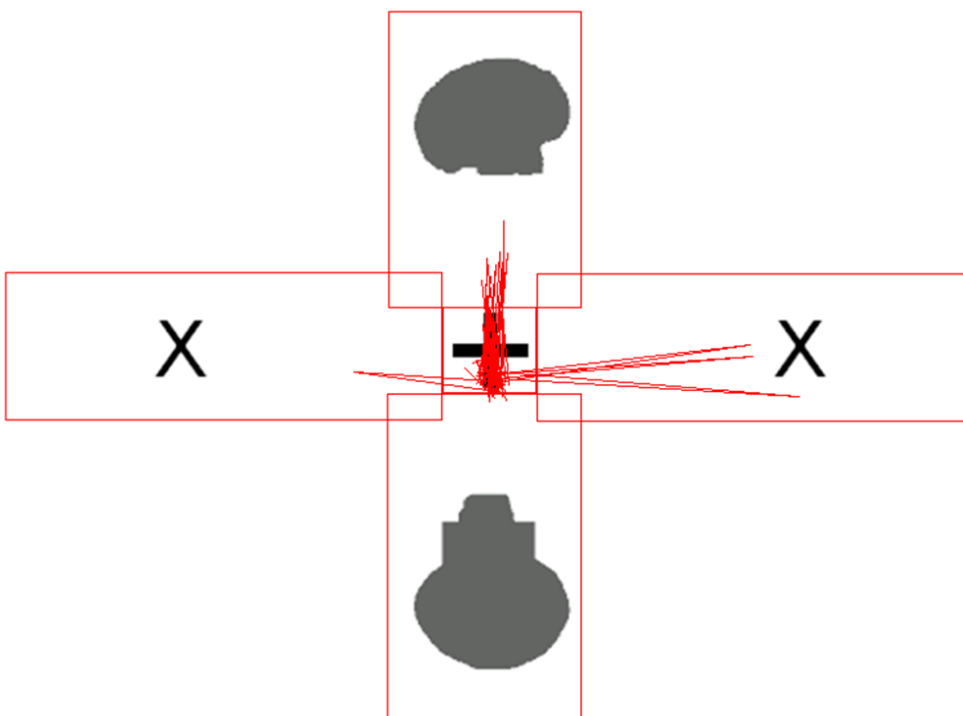
Blinks and other losses in the raw eye tracking signal were identified and removed from the analysis by the eye tracking software. Trials without valid recordings during the critical fixation periods (during prime or target presentation epochs) were excluded. In addition, trials where participants were not fixating centrally during the critical fixation periods were also removed from the analysis. Participants with more than 75% of excluded data were removed from the eye tracking analyses (8 participants without data, 1 participant without 75% of data after removal of erroneous fixations).

Results

Data from 13 participants were included in this analysis. Only trials where central fixation could be confirmed were examined. The same repeated measures 2x2x2 ANOVA investigated differences in reaction times for laterally presented X-Targets. Image Type (Abstract Shape/Object) x Image Vertical Position (LoVF/UpVF) x X-Target Horizontal Position (Right/Left) were included as independent variables. We replicated the findings of the unconstricted (no eye tracking confirmation of central fixation) IPA task analysis presented in the Results section of the principle manuscript. Right visual field identification of X-Targets was significantly faster than in the left visual field ($F(1,12) = 11.88$, $p = 0.005$, $\eta^2 = 0.497$). There were no other significant main effects of the independent variables on reaction times to the X-Target. Image Type (Abstract Shape/Objects) - $F(1,12) = 0.56$, $p = 0.469$, $\eta^2 = 0.045$. Image Vertical Position (LoVF/UpVF) - $F(1,12) = 0.81$, $p = 0.385$, $\eta^2 = 0.063$. There were no significant interactions between the independent variables. Image Type*Image Vertical Position - $F(1,12) = 1.94$, $p = 0.189$, $\eta^2 = 0.139$. Image Type*X-Target Horizontal Position - $F(1,12) = 0.16$, $p = 0.699$, $\eta^2 = 0.013$. Image Vertical Position*X-Target Horizontal Position - $F(1,12) = 3.59$, $p = 0.083$, $\eta^2 = 0.23$. Image Type*Image Vertical Position*X-Target Horizontal Position - $F(1,12) = 1.65$, $p = 0.223$, $\eta^2 = 0.121$.

We also replicated the findings of the primary analysis with respect to the object versus abstract shape identification decision times. A two-way mixed ANOVA investigated the effects of Image

Vertical Position (LoVF/ UpVF) and Response Type (respond only to Abstract Shapes/respond only to Objects) on response time during correct trials (objects identified as objects/abstract shapes identified as abstract shapes). Response times were significantly faster for images presented to the LoVF than for those in the UpVF ($F(1,11) = 6.65, p = 0.026, \eta^2 = 0.377$). We observed no interaction between response type (respond to abstract shapes but not objects and vice versa) and reaction time to the object/abstract shape identification decision ($F(1,11) = 0.007, p = 0.935, \eta^2 = 0.001$). We did not observe enough errors on confirmed fixation trials to enable investigation in the same way as the unconstricted analysis.



Supplementary Figure 2.3: A representative example of the eye positions of a participant during the IPA task. Trials with fixations extending outside of the central area of interest were excluded from the eye tracking restricted analysis presented in Supplementary Material 2.2.

Appendix 2 - Supplementary Materials of Chapter 3

Landmark Task

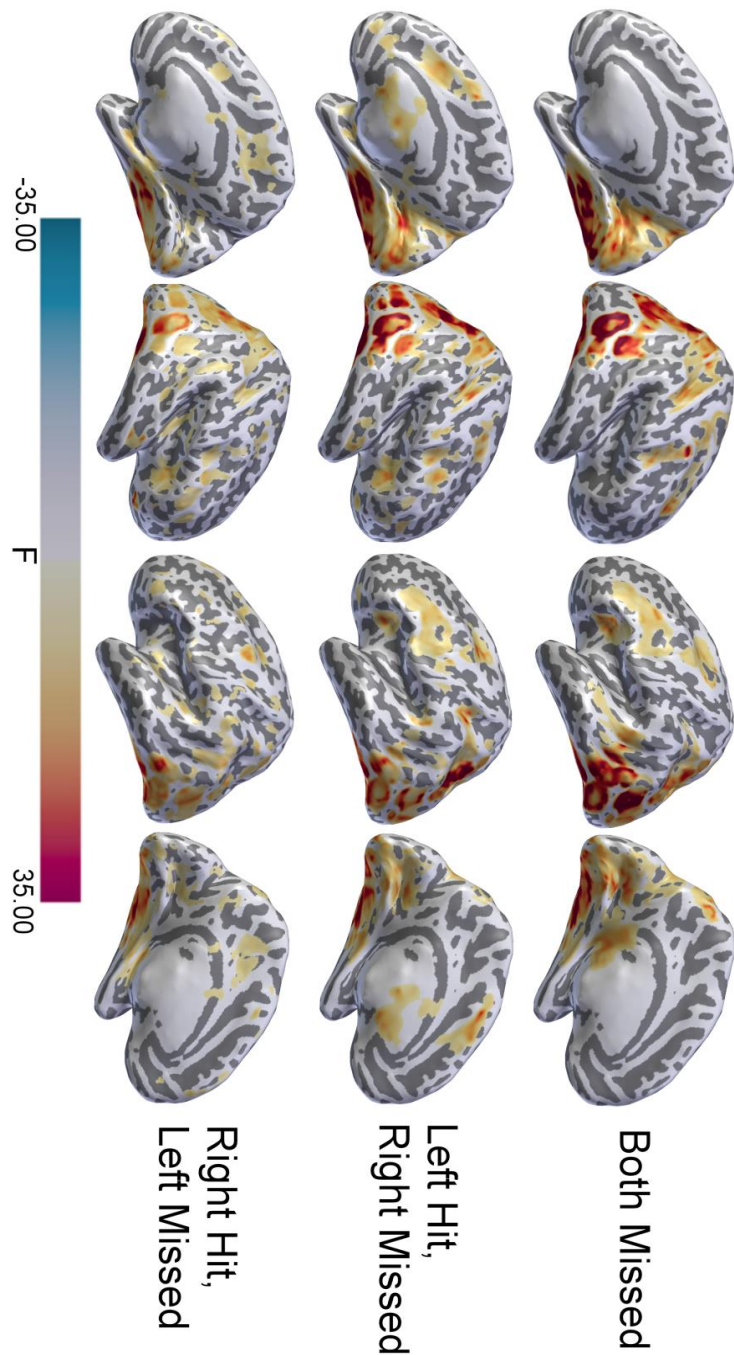
Cluster	Location (aal)	BA	Voxels	MNI $x y z$	Z-value
$k_E = 1586$ $q < 0.001$	Cerebellum 4-5 (R)	NA	176	18 -50 -21	6.01
	Cerebellum 6 (R)	NA	295	23 -52 -21	5.93
	Inferior Occipital Cortex (R)	37	63	43 -62 -14	5.58
	Fusiform Gyrus (R)	37	132	41 -50 -18	5.11
	Calcarine (L)	19	132	-25 -67 4	5.05
	Inferior Temporal Cortex (R)	37	160	41 -57 -7	4.92
	Vermis 4-5	NA	75	6 -55 -4	4.74
	Lingual Gyrus (L)	19	129	-15 -55 -4	4.65
	Lingual Gyrus (R)	18	103	8 -65 4	4.55
$k_E = 316$ $q < 0.001$	Intraparietal Sulcus/Angular Gyrus (R)	7/39	24	36 -47 42	4.88
	Superior Parietal Cortex (R)	7	49	23 -62 49	4.19
	Supramarginal Gyrus (R)	40	33	56 -35 49	3.53
$k_E = 322$ $q < 0.001$	Angular Gyrus (L)	39	148	-47 -67 32	4.76
	Middle Occipital Cortex (L)	39	87	-42 -77 35	4.74
	Middle Temporal Gyrus (L)	39	61	-45 -62 18	4.62
$k_E = 211$ $q < 0.001$	Insula Cortex (R)	13	72	38 23 -7	4.60
	Inferior Frontal Operculum (R)	44	41	53 13 4	4.12
	Inferior Frontal Cortex (R)	46	30	46 36 14	8.82
$k_E = 186$ $q < 0.001$	Middle Cingulum (L)	23	71	-5 -47 35	4.55
	Middle Cingulum (R)	23	37	6 -45 35	4.55
$k_E = 81$ $q < 0.001$	Rolandic Operculum (L)	40	28	-47 -22 14	4.52
	Superior Temporal Cortex (L)	40	33	-57 -20 11	3.99
$k_E = 59$ $q = 0.001$	Precuneus (R)	23	25	16 -55 21	4.42
	Precuneus (L)	31	24	-2 -67 28	3.90
$k_E = 35$ $q = 0.011$	Inferior Frontal Cortex (L)	45	34	-57 21 18	4.06
$k_E = 80$ $q < 0.001$	Postcentral Gyrus (R)	1	37	41 -22 49	3.86
	Precentral Gyrus (R)	4	28	41 -25 60	3.79

Supplementary Table 3.1: Brain regions with significant activation ($q < 0.05$, cluster uncorrected) associated with the responses in the landmark task.

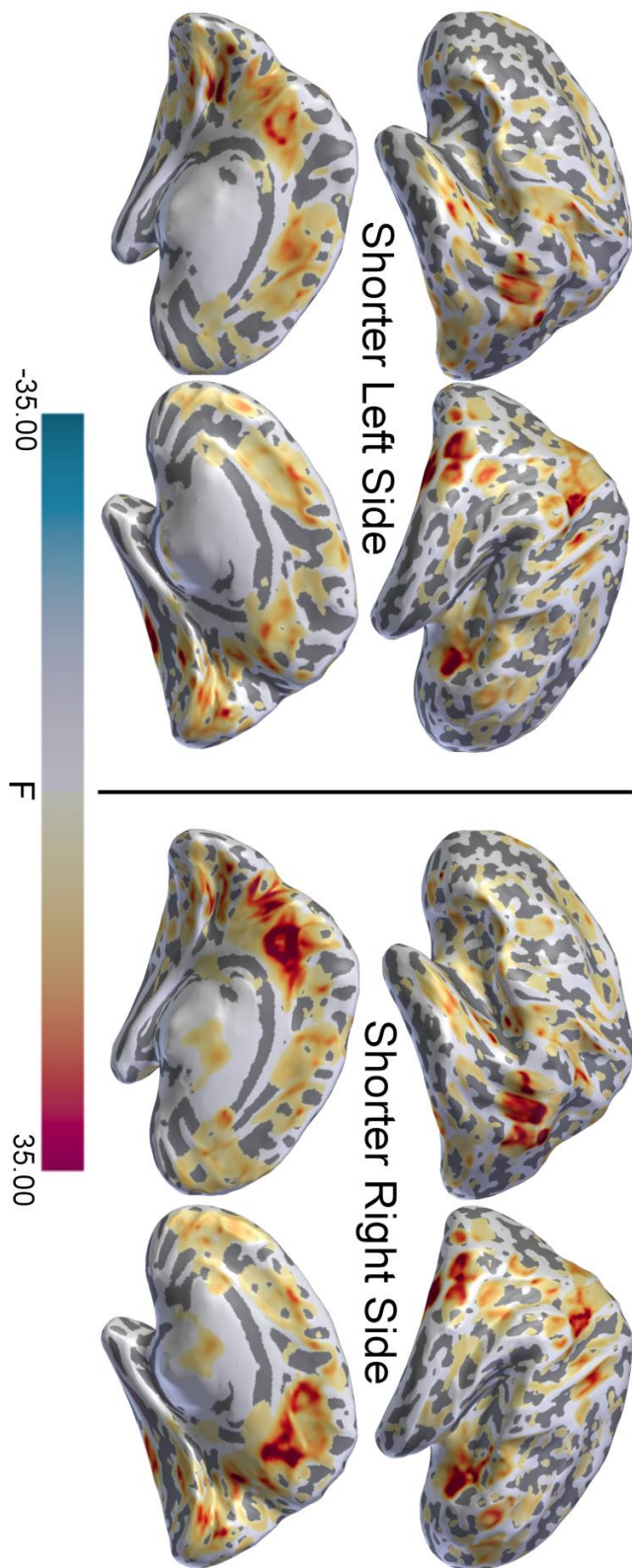
Object Perception Task

Cluster	Location (aal)	BA	Voxels	MNI $x y z$	Z-value
$k_E = 861$ $q < 0.001$	Fusiform Gyrus (R)	37	227	31 -42 -18	5.35
	Lingual Gyrus (R)	18	88	11 -85 -7	4.61
	Cerebellum 6 (R)	NA	139	38 -67 -21	4.05
	Inferior Temporal Cortex (R)	37	88	43 -60 -11	3.99
	Middle Occipital Cortex (R)	39	68	33 -70 28	3.75
$k_E = 514$ $q < 0.001$	Inferior Occipital Cortex (L)	19	83	-42 -70 -11	4.24
	Cerebellum 6 (L)	NA	78	-35 -57 -21	4.13
	Cerebellum Crus 1 (L)	NA	65	-25 -82 -21	4.13
	Middle Occipital Cortex (L)	19	85	-42 -85 11	4.09
	Fusiform Gyrus (L)	19	87	-40 -70 -18	3.90
$k_E = 15$ $q = 0.033$ uncorrected	Insula Cortex (R)	45	15	33 31 0	3.87
$k_E = 16$ $q = 0.029$ uncorrected	Angular Gyrus (L)	39	16	-47 -70 42	3.77
$k_E = 24$ $q = 0.010$ uncorrected	Middle Occipital Gyrus (R)	18	24	28 -90 7	3.72

Supplementary Table 3.2: Brain regions with significant activation ($q < 0.05$, cluster uncorrected) associated with the successful perception and encoding of items from both sides of space.



Supplementary Figure 3.1: Comparison of brain activity associated with (A) the successful encoding of objects on the left, but not the right side, (B) the successful encoding of objects on the right, but not the right side, (C) and unsuccessful encoding of objects on both sides of space with null events was performed. These comparisons revealed similar regions of activation as the condition (both items successfully encoded - Figure 3.4A) condition used for the conjunction analysis in Figure 3.4C.

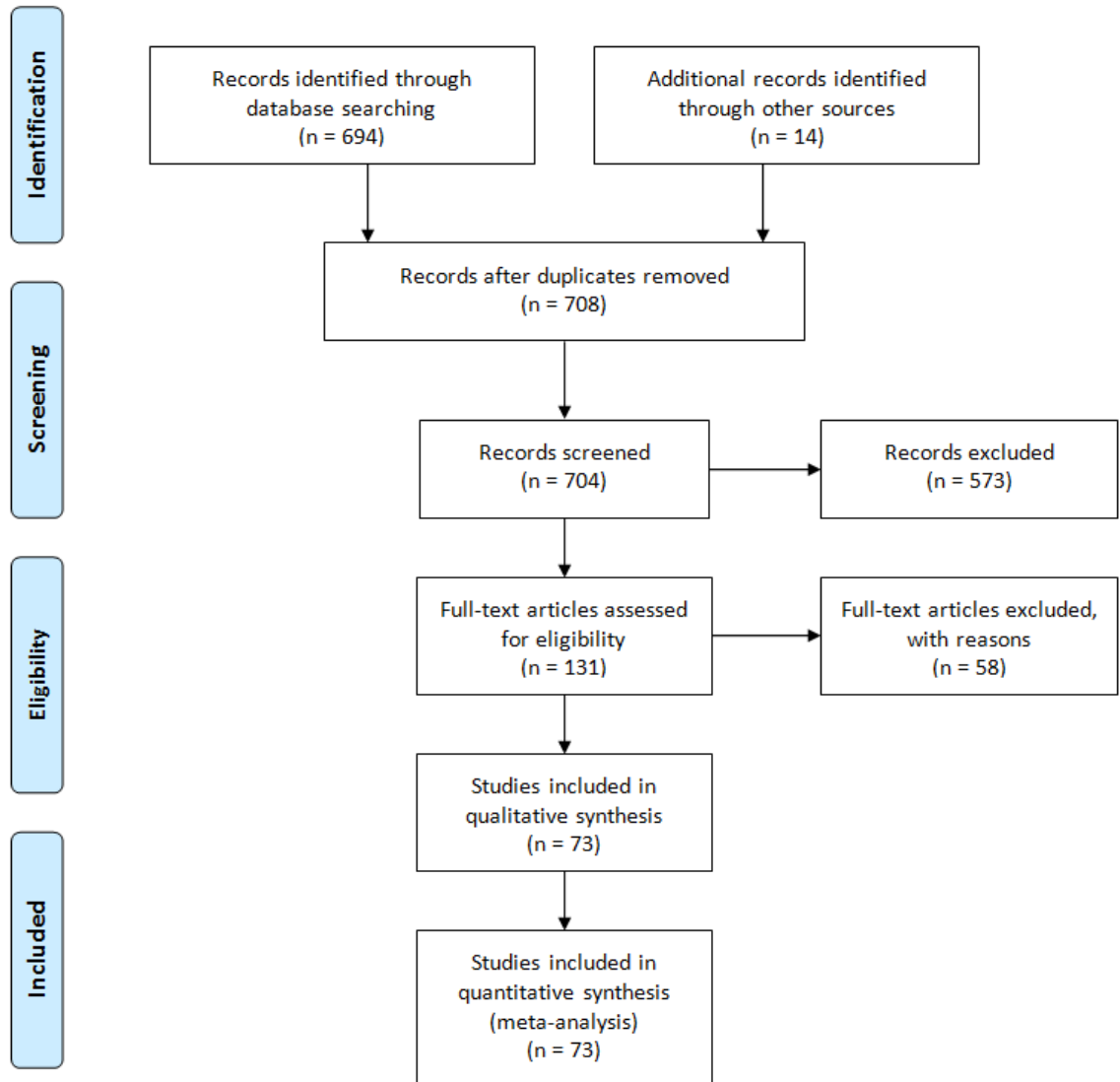


Supplementary Figure 3.2: Contrasting the different responses ((A) Shorter Left Side; (B) - Shorter Right Side) on the landmark task with null events revealed very similar regions of activation as when landmark trials were averaged across response type.

Appendix 3 - Supplementary Materials of Chapter 4



PRISMA 2009 Flow Diagram



Supplementary Figure 5.1: A schematic representation of the process of identification, screening, and classification of eligible studies for the review of IPL activations associated with the perceptual and semantic aspects of episodic memory retrieval.

Supplementary Table 4.1: Neuroimaging contrasts focussed on perceptually-defined memory experiences.

Study reference	Type of memory retrieval	Imaging contrast	Left IPL	Right IPL
Angel et al., 2016	<p>Encoding – Black and white line drawings of common objects. Half of drawings were presented twice, the other half were shown once. Relative size judgement made for each object.</p> <p>Retrieval – Remember/know recognition memory task.</p>	Old > New	✓ BA 39/40	✓ BA 40
Brown, Rissman, Chow, Uncapher, & Wagner, 2018	<p>Wearable cameras captured snapshots of subjects' lives. Subjects encoded naturally in their daily lives.</p> <p>Retrieval – the autobiographical memory test challenged recognition of a short time series (4 images) that was provided by these snapshots. New items were presented from others' cameras.</p>	<p>Recollection > CR</p> <p>Familiarity > CR</p> <p>Know > CR</p> <p>Recollection > (F,K,CR)</p> <p>Memory (R,F) > No Memory (K,CR)</p>	<p>✓ BA 39/40</p> <p>✓ BA 39/40</p> <p>✓ BA 39/40</p> <p>✓ BA 39</p> <p>✓ BA 40</p>	<p>✓ BA 39/40</p> <p>✓ BA 39/40</p> <p>✓ BA 39/40</p> <p>✓ BA 39</p> <p>✓ BA 40</p>
Cansino, Maquet, Dolan, & Rugg, 2002	<p>Encoding – images of objects were presented in various spatial locations.</p> <p>Retrieval – In an old/new recognition memory paradigm, subjects were asked to identify which images (no similar lures were used) had been presented before, and to retrieve the spatial location of original encounter with the image (if they thought the image was old). This location assessment provided an indication of source memory.</p>	Correct source memory vs incorrect source memory	X	✓ BA 40

Chen, Gilmore, Nelson, & McDermott, 2017	<p>Encoding - Subjects incidentally encoded a series of scene images whilst making indoor/outdoor judgements.</p> <p>Retrieval - Memory was assessed in two ways. Subjects were presented with scene images.</p> <ul style="list-style-type: none"> - In the autobiographical memory retrieval task, participants were asked to use the scene image as a prompt to vividly recall a specific event from their life. - Participants also completed a picture recognition judgement. 	<p>Autobiographical hit > CR</p> <p>Autobiographical hit > Picture only hit</p>	<p>✓ BA 40</p> <p>✓ BA 40</p>	<p>✓ BA 40</p> <p>✓ BA 40</p>
Cooper et al., 2017	<p>Encoding – Background scenes were overlaid with common objects and presented at encoding. Objects varied in colour, orientation, and location. Participants explicitly encoded the appearance of the objects relative to the background.</p> <p>Retrieval – Subjects were presented with the background scene image and rated the vividness of their memory of the associated objects. Each object was then represented and participants manipulated the colour, orientation, and location of the object to match their memory representation.</p>	<p>Successful > Unsuccessful Retrieval</p> <p>Precision</p>	<p>X</p> <p>✓ BA 39</p>	<p>✓ BA 39</p> <p>✓ BA 39</p>
DeMaster, Pathman, & Ghetti, 2013	<p>Encoding – Object images were presented on either the left or right side of visual space. Subjects were required to make a connection between the object and the side of presentation.</p> <p>Retrieval – Old and new images of objects were presented. Subjects were required to identify whether item was old or new, and recall which side of space the item was presented.</p>	Correct spatial source > CR	✓ BA 39/40	✓ BA 40
Dennis, Bowman, & Vandekar, 2012	<p>Encoding – 8 different images of objects of a single given category were presented and incidentally encoded alongside judgements of pleasantness.</p> <p>Retrieval – A remember/know/new recognition memory paradigm utilising related lure images was performed.</p>	<p>Remember FAs > Know FA</p> <p>Recollection accuracy effects on connectivity: True > False - Left MTL connectivity</p> <p>False > True - Right MTL connectivity</p>	<p>X</p> <p>X</p> <p>X</p>	<p>✓ BA 39</p> <p>✓ BA 39</p> <p>✓ BA 40</p>

Dobbins & Wagner, 2005	<p>Encoding – subjects provided judgements of object images that were either perceptual (bigger/smaller than previous image) or non-perceptual (pleasant/unpleasant or living/non-living) in nature.</p> <p>Retrieval – participants completed a perceptual (size) or conceptual (which question) source memory task.</p>	<p>Domain-sensitive contrast:</p> <p>Recollecting perceptual details</p>	✓ BA 40	✓ BA 40
Elman, Cohn-Sheehy, & Shimamura, 2013	<p>Encoding – Previously photographs of unfamiliar buildings were shown to participants twice.</p> <p>Retrieval – Subjects were subsequently presented with images from the study phase, along with unseen images, and images of highly familiar buildings as part of a recognition memory paradigm. Participants indicated whether they had seen the building before with an indication of confidence.</p>	<p>Studied images: Hits > CR</p> <p>Both high confidence: Studied > Familiar</p>	<p>✓ BA 40</p> <p>✓ BA 39/BA 40</p>	<p>✓ BA 40</p> <p>✓ BA 39/BA 40</p>
Gimbel & Brewer, 2014	<p>Encoding – Pairs of object images were presented to, and intentionally encoded as image pairs by participants.</p> <p>Retrieval - One image from each pair was presented (no lures were presented) and subjects were instructed to either suppress recall, recall, or recall specific details about the other item in the pair.</p>	<p>Task-positive activity:</p> <p>Elaborative cued recall > failed elaborative cued recall</p> <p>Cued recall > failed cued recall</p>	<p>✓ BA 39 & 40</p> <p>✓ BA 39 & 40</p>	<p>✓ BA 39 & 40</p> <p>✓ BA 39 & 40</p>

<p>Herweg, Sommer, & Bunzeck, 2017</p>	<p>Prefamiliarization – Subjects were presented with all 160 scenes (indoor or outdoor) to be used in the study. Two images (that were not used in subsequent tasks) served as target images and subjects responded when they saw these images.</p> <p>Further encoding – Re-presentation of images from prefamiliarization along with new images. Subjects made an indoor/outdoor decision regarding all scenes.</p> <p>Test #1 – Participants performed an old/new recognition memory paradigm with confidence judgements.</p>	<p>Hits > CR</p>	<p>✓ IPL</p>	<p>✓ IPL</p>
<p>Hirshhorn, Grady, Rosenbaum, Winocur, & Moscovitch, 2012</p>	<p>Retrieval – Participants performed an autobiographical assessment of which of two well-known landmarks the subjects had visited most recently.</p> <p>The experimenters compared personal episodic memory with allocentric judgements about the spatial relationship between the two landmarks (furthest north?/furthest east?)</p>	<p>Experiential episodic memory > spatial allocentric judgement</p>	<p>✓ BA 39</p>	<p>✓ BA 39</p>
<p>Hutchinson et al., 2014</p>	<p>Encoding – An adjective word was presented to subjects accompanied by a cue to internally generate 1 of 4 encoding experiences: an indoor (1) or outdoor (2) scene, or the name of a female (3), or male (4) celebrity.</p> <p>Retrieval – Subjects performed an old/new recognition memory task with visually presented adjective words. Participants were encouraged to make source judgements about the task and the contents of their memory for Old items.</p>	<p>Specific source hit > item only</p> <p>Item only > specific source</p>	<p>✓ BA 39</p> <p>✓ BA 40</p>	<p>✓ BA 39</p> <p>✓ BA 40</p>
<p>Hutchinson, Uncapher, & Wagner, 2015</p>	<p>Encoding - An adjective word was presented to participants accompanied by a cue to internally generate 1 of 4 encoding experiences: an indoor (1) or outdoor (2) scene, or the name of a female (3), or male (4) celebrity.</p> <p>Retrieval – Participants performed an old/new recognition memory task with judgements about their memory confidence.</p>	<p>Linear relationship with memory strength</p> <p>Uncertain memory decisions</p> <p>Certain memory decisions</p>	<p>✓ BA 39/40</p> <p>✓ BA 40</p> <p>✓ BA 39</p>	<p>X</p> <p>✓ BA 39</p> <p>✓ BA 40</p>

King & Miller, 2014	<p>Encoding – Concrete nouns were presented accompanied by either a matching object image (percieved trials) or a prompt for the participant to imagine (imagine trials) an object matching the word. Subjects then made relative size judgements about these objects.</p> <p>Retrieval – An old/new recognition memory paradigm presented subjects with the words presented in the encoding phase alongside unstudied words. Participants made source judgements about whether items they judged to be old were perceived or imagined at encoding.</p>	ROI: Perceived > imagined trials	✓ BA 40	✓ BA 39
King & Miller, 2017	<p>Encoding – Concrete nouns were presented to participants alongside either a matching object image or a prompt to imagine an image of the noun. Subjects made a relative size judgement regarding the perceived or imagined object.</p> <p>Retrieval – An old/new recognition memory task presented subjects withvisually presented nouns. The experimenters manipulated the ratio of old to new items (high/low probability of being old).</p>	Low probability of being old: Perceived hits > CR	✓ BA 39 & 40	✓ BA 39 & 40
King, Schubert, & Miller, 2015	<p>Encoding – Nouns presented in one of five encoding conditions: High vividness perceive object image (1), low vividness perceive object image (2), imagine object image (3), perceive sentence (4), low vividness imagine sentence (abstract noun cue) (5).</p> <p>Retrieval – Subjects completed an old/new recognition memory paradigm using with source memory for whether item was perceived, imagined, or new.</p>	<p>Highly vivid photo perception > CR</p> <p>Low vividness (blurry) photo perceived > CR</p>	<p>✓ BA 39</p> <p>✓ BA 39 & 40</p>	<p>✓ BA 39</p> <p>✓ BA 39</p>
Lundstrom et al., 2003	<p>Encoding – Concrete nouns were presented to subjects, followed by either a pictoral representation of the noun (viewed) or a blank screen. On seeing a blank screen, participants imagined a representation of the noun word (imagined).</p> <p>Retrieval – Participants completed an old/new recognition memory paradigm with source memory judgements. Source task options: viewed, imagined, or new.</p>	Source memory task: hit (imagined) > correct rejection	✓ BA 39,40	✓ BA 40 (& BA 7, BA 19)

Lundstrom, Ingvar, & Petersson, 2005	<p>Encoding – Concrete nouns were presented accompanied by either a matching image or a blank screen that prompted subjects to imagine an image that matched the noun.</p> <p>Retrieval – Participants completed an old/new recognition task with source memory judgements of whether the noun word was accompanied by a visible or imagined picture. No comparison was made between retrieval activations elicited by viewed and imagined trials.</p>	Correct source memory > CR	✓ BA 39/40	X
Marie St-Laurent, Moscovitch, & McAndrews, 2016	<p>Encoding - Subjects encoded either video clips with minimal or no dialog, or narrations of a video clip. These events were paired with a relevant cue word.</p> <p>Retrieval - The relevant cue words were presented and participants were asked to recall the event in as much detail as possible.</p>	Video clips > Narrative laboratory events	X	✓ BA 39
Meusel, Grady, Ebert, & Anderson, 2017	<p>Encoding – Subjects deliberately encoded word pairs that were either visually or audibly presented. Participants were instructed to remember the modality of exposure for each pair.</p> <p>Retrieval – Subjects completed a source memory-only recognition task. Participants indicated whether they had seen or heard the visually presented word pair.</p>	Source memory > control task	X	✓ BA 40
Sestieri, Shulman, & Corbetta, 2010	<p>Encoding – Participants watched two episodes of an English language TV sitcom.</p> <p>Retrieval – Subjects judged the accuracy of statements about factual details of the programme.</p>	Memory search-related activity	✓ BA 39	✓ BA 39
Sharot, Delgado, & Phelps, 2004	<p>Encoding – Participants provided judgements regarding the visual complexity of photos.</p> <p>Retrieval – Subjects completed a remember/know recognition memory paradigm.</p>	<p>Remember>New judgements</p> <p>Know>New</p>	<p>X</p> <p>✓ BA 40</p>	<p>✓ BA 39</p> <p>✓ BA 40</p>

<p>St. Jacques, Carpenter, Szpunar, & Schacter, 2018</p>	<p>Autobiographical memory paradigm – Participants provided details of previous life events.</p> <p>Retrieval – Subjects were asked to adopt either their own perspective or that of another person in order to mentally experience either their events from memory or a similar counterfactual alternative of their event.</p>	<p>Autobiographical memory retrieval > counterfactual simulation</p> <p>Counterfactual simulation > autobiographical retrieval</p> <p>Autobiographical repetition suppression</p>	<p>✓ BA 40</p> <p>✓ BA 39</p> <p>✓ BA 39</p>	<p>✓ BA 40</p> <p>✓ BA 39</p> <p>✓ BA 39</p>
<p>St-Laurent, Abdi, Bondad, & Buchsbaum, 2014</p>	<p>Encoding – Participants observed naturalistic video clips accompanied by appropriate labels.</p> <p>Retrieval – When cued with the label, participants were asked to mentally replay the appropriate video clip.</p>	<p>Mental replay</p>	<p>✓ BA 40</p>	<p>✓ BA 40</p>
<p>Thakral, Wang, & Rugg, 2015</p>	<p>Encoding – Subjects were presented with images of objects that were accompanied by either a concrete noun that either matched, or was incongruent with the image. Participants judged whether the image-word pair was congruent. Nouns were presented either visually or auditorily.</p> <p>Retrieval – An old/new recognition memory paradigm was performed. Subjects indicated whether the object image that was presented was old or new. For items believed to be old, subjects indicated the accompanying word was presented visually or audibly.</p>	<p>Modality-independent source effects</p>	<p>✓ BA 40</p>	<p>✓ BA 40</p>
<p>van Buuren et al., 2014</p>	<p>Encoding – Subjects learned associations between objects and locations within a visually presented spatial arena.</p> <p>Retrieval – Objects were presented as cues, and subjects were asked to recall the location of each object in the spatial arena.</p>	<p>Correct > Incorrect</p> <p>Greater > lesser memory accuracy</p>	<p>✓ BA 39</p> <p>X</p>	<p>✓ BA 39</p> <p>✓ BA 39</p>

Wais, Jahanikia, Steiner, Stark, & Gazzaley, 2017	<p>Encoding – Subjects made either a weight, or relative size judgement about visually presented object images.</p> <p>Retrieval - Participants completed an old/new recognition paradigm that utilised similar lures.</p>	<p>Similar Lures Data:</p> <p>CR (perceptually discriminate memory + novelty detection) > FA (perceptually indiscriminate memory + no novelty detection)</p>	✓ BA 39	✓ BA 39
Weis, Klaver, Reul, Elger, & Fernández, 2004	<p>Encoding – Colour photographs of buildings or natural landscapes without buildings were visually presented. Subjects intentionally encoded the images and indicated the presence or absence of a building in the scene.</p> <p>Retrieval – Participants completed an old/new recognition memory task and provided confidence ratings of their judgements.</p>	<p>Hits > CR</p> <p>Positive Recognition Effect</p>	<p>✓ BA 40</p> <p>X</p>	<p>✓ BA 40</p> <p>✓ BA 39</p>
Weymar, Bradley, Sege, & Lang, 2018	<p>Encoding - Images of emotionally positive, negative, or neutral scenes were intentionally encoded by participants.</p> <p>Retrieval - Subjects provided either an old/new recognition judgement or a judgement about the number of people in the scene (1 person or >1 person).</p>	Hit > CR	✓ BA 39	✓ BA 39
Xiao et al., 2017	<p>Familiarisation – Subjects learned associations between cue words and scene images. They then categorised the scene images according to their content (e.g. foreign architecture/water landscape).</p> <p>Encoding – Participants restudied the word – image associations and tried to encode as many perceptual details of the image as possible.</p> <p>Retrieval – The cue word was presented and subjects were asked to recall the visual details of the associated picture.</p>	Item specific memory	✓ BA 40	✓ BA 40
Activation Consistency			80.00%	96.00%

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Supplementary Table 4.2: Neuroimaging contrasts focussed on semantic/conceptually-defined memory experiences.

Study reference	Type of memory retrieval	Imaging contrast	Left IPL	Right IPL
Cabeza, Dolcos, Graham, & Nyberg, 2002	<p>Encoding – Participants made judgements of whether visually presented words represented living/non-living things. Subjects were aware that their memory for the items would be subsequently tested.</p> <p>Retrieval – Participants completed a remember/know recognition memory paradigm. This was compared with a working memory test. Working memory task presented four words simultaneously and required subjects to subsequently match a test word with this presentation.</p>	Episodic > Working Memory	✓ BA 39	✓ BA 39
Clemens Von Zerssen, Mecklinger, Opitz, & Yves Von Cramon, 2001	<p>Encoding – Subjects intentionally encoded audibly presented words. Words were presented in batches of 5 words that all conformed to a single category.</p> <p>Retrieval – An old/new recognition memory task using visually presented words was performed. Three word types were used: Old, New-categorically related, New-unrelated.</p>	Hits > CR	✓ BA 40	X
Compère et al., 2016	<p>Autobiographical cued recall task - Subjects reported their interests and details of their memory prior to scanning. Participants were instructed to remember the details (episodic - time, location, perceptions, feelings, scenery, and people present in the scene; semantic - generic memories of repeated events) of the appropriate memory.</p> <p>Autobiographical memories were classified as either episodic or semantic. Episodic memories were infrequent occurrences e.g. a specific family holiday. Semantic memories were frequent occurrences e.g. a weekly chess club.</p>	<p>Episodic + Semantic Memory > Control</p> <p>Semantic Memory > Control</p> <p>Women - Episodic Memory</p>	<p>✓ BA 39</p> <p>✓ BA 39</p> <p>✓ BA 39</p>	<p>X</p> <p>X</p> <p>✓ BA 39</p>
Daselaar, Fleck, & Cabeza, 2006	<p>Encoding – Participants were presented with a list of words. Subjects judged whether each list item was an English word.</p> <p>Retrieval – Subjects completed a recognition memory paradigm. This consisted of an old/new recognition memory judgement followed by a confidence rating.</p>	<p>Word recollection</p> <p>Word familiarity</p>	<p>✓ BA 39,40</p> <p>✓ BA 39,40</p>	<p>X</p> <p>X</p>

Dobbins & Wagner, 2005*	<p>Encoding – Subjects provided a perceptual judgement (bigger/smaller than previous image) or semantic rating (pleasant/unpleasant or living/non-living) of visually presented images.</p> <p>Retrieval – Participants provided source memory judgements of whether the item was encoded perceptually (relative size judgement) or conceptually (pleasantness/living).</p>	<p>Domain-sensitive contrast:</p> <p>Recollecting conceptual semantic details</p>	✓ BA 40	✓ BA 40
Dobbins, Foley, Schacter, & Wagner, 2002	<p>Encoding - Subjects made a pleasant/unpleasant or concrete/abstract decision regarding visually presented noun words.</p> <p>Retrieval - An old/new recognition memory paradigm was conducted. Subjects also judged which task they performed during encoding of items they believed to be old.</p>	Source memory > item recognition	✓ BA 40	X
Dobbins, Rice, Wagner, & Schacter, 2003	<p>Encoding – Participants made either pleasant/unpleasant or abstract/concrete judgements about visually presented words.</p> <p>Retrieval – Subjects completed a forced choice recognition and source memory task. Source memory – which question was asked at encoding? This was compared with a recency judgement - which item was encoded more recently.</p>	Source > recency memory	✓ BA 40	X
Donaldson, Petersen, & Buckner, 2001	<p>Encoding – Subjects were instructed to mentally generate a sentence from a visually presented word pair.</p> <p>Retrieval – Words were subsequently presented in an old/new recognition memory task.</p>	Hit > CR	✓ BA 39 & 40	✓ BA 40
Donaldson, Petersen, Ollinger, & Buckner, 2001	<p>Encoding – same encoding as Donaldson et al., 2001. The retrieval phase of Donaldson et al., (2001) served to re-encode these items.</p> <p>Retrieval – Participants completed an old/new recognition memory task.</p>	<p>Increases relative to baseline</p> <p>Decreases relative to baseline</p>	<p>✓ BA 40</p> <p>X</p>	<p>X</p> <p>✓ BA 40 (borders 19)</p>

Duarte, Henson, & Graham, 2011	<p>Encoding – Subjects made a pleasantness or commonness judgement on unrelated nouns, object images, or scenes.</p> <p>Retrieval – An old/new recognition memory task with source memory judgements was performed. Subjects judged whether items they considered old had been judged for pleasantness or commonness.</p>	Material independent source memory	✓ BA 39	X
Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000	<p>Encoding – Subjects deliberately encoded a visually presented list of noun words.</p> <p>Retrieval – Subjects responded indicating a remember (recollection) or know (familiarity) memory experience (remember/know recognition memory task).</p>	Remember > know	✓ BA 39	✓ BA 39
Flegal, Marín-Gutiérrez, Ragland, & Ranganath 2014	<p>Encoding - In an incidental encoding task, subjects judged the pleasantness of visually presented sentences.</p> <p>Retrieval - Subjects were presented with congruent or incongruent combinations of words from the encoding task, or new words. Participants judged which of the test words had been seen previously.</p>	Confident Old > Misses	✓ BA 39	X
Frithsen & Miller, 2014	<p>Encoding – Participants made pleasant/unpleasant or abstract/concrete judgements regarding nouns presented during study.</p> <p>Retrieval – Subjects performed an old/new recognition memory task. A source memory task asked which question had been asked at encoding for half of the targets at test. The other 50% of stimuli were assessed using a remember/know paradigm.</p>	<p>Recollection</p> <p>Familiarity</p> <p>Hits: Remember > Know</p> <p>Source > No Source</p> <p>Know Hits > CR</p>	<p>✓ BA 39</p> <p>✓ BA 39</p> <p>✓ BA 39/40</p> <p>✓ BA 39</p> <p>✓ BA 40</p>	<p>X</p> <p>✓ BA 39</p> <p>✓ BA 39</p> <p>X</p> <p>✓ BA 39/40</p>

Hall, Rubin, Miles, Davis, & Wing, 2015	<p>Encoding - Subjects were presented with either unpaired sounds or sounds that were paired with images of simple scenes. Both sounds and scenes were easily recognisable and easily described with a label e.g. heartbeat.</p> <p>Retrieval - Participants were presented with sounds and asked to recall which picture was associated with the sound (if there had been one).</p>	Image recalled (averaging across voluntary (detailed perception) and involuntary (no detailed perception)) > unpaired sounds	✓ BA 39	X
Hayes, Buchler, Stokes, Kragel, & Cabeza, 2011	<p>Encoding - Subjects made a relative size, or pleasant/unpleasant judgement about visually presented concrete nouns.</p> <p>Retrieval – Old/New recognition memory paradigm with source judgements regarding the encoding task performed on all old items.</p>	<p>Memory confidence: High > low</p> <p>High confidence item memory > high confidence source memory</p>	<p>✓ BA 40</p> <p>✓ BA 40</p>	<p>X</p> <p>X</p>
Henson, Hornberger, & Rugg, 2005	<p>Encoding – Participants encoded visually presented words with either a 'deep' (living/non-living decision) or a 'shallow' judgement (whether first and last letter of word in alphabetical order?)</p> <p>Retrieval – Memory for the words was subsequently assessed using an old/new recognition paradigm.</p>	Hits > CR	✓ BA 39 & 40	✓ BA 40
Herron, Henson, & Rugg, 2004	<p>Encoding – A concrete noun word list was presented. On each trial, subjects made a animate/inanimate object decision.</p> <p>Retrieval – Participants completed an old/new recognition memory task. The ratio of targets to foils varied between blocks.</p>	Hits > CR	✓ BA 39	✓ BA 39

<p>Hutchinson et al., 2014*</p>	<p>Encoding – On each trial, an adjective was presented accompanied by a cue to internally generate 1 of 4 encoding experiences: an indoor (1) or outdoor (2) scene, or the name of a female (3), or male (4) celebrity.</p> <p>Retrieval – Subjects completed an old/new recognition task that tested memory for visually presented adjective words. Participants were encouraged to make source judgements about the task and the contents of their memory for items they considered old.</p>	<p>Item hits (no source) > CR</p>	<p>✓ BA 40</p>	<p>X</p>
<p>Kafkas & Montaldi, (2012)</p>	<p>Encoding - Subjects completed a matching-to-sample task in which subjects were asked to identify which of two different object images was an identical match to a third object image.</p> <p>Retrieval - Subjects completed the Familiarity-only remember/know recognition task that tested memory for the object images observed in the study phase and new images (no similar lures used). This task encouraged participants to judge the stimuli based on feelings of familiarity rather than attempting to recollect. This gives an index of recollection, along with both strong and weak familiarity.</p>	<p>Remember > Miss</p> <p>Strong Familiarity (F3) > Miss</p>	<p>✓ BA 39 & 40</p> <p>✓ BA 40</p>	<p>✓ BA 39</p> <p>X</p>
<p>Kahn, Davachi, & Wagner, 2004</p>	<p>Encoding – Concrete nouns were visually presented and subjects encoded them under one of two conditions: image (mentally picture the word described), or read (covertly pronounce the word backwards).</p> <p>Retrieval – Subjects completed an old/new recognition task with source memory (whether item was read or imaged).</p>	<p>Word Hits>CR</p>	<p>✓ BA 40</p>	<p>X</p>
<p>King, Schubert, & Miller, 2015</p>	<p>Encoding – Nouns were presented in one of five encoding conditions: High vividness perceive object image (1), low vividness perceive object image (2), imagine object image (3), perceive sentence (4), low vividness imagine sentence (abstract noun cue) (5).</p> <p>Retrieval – Subjects completed an old/new recognition memory paradigm and subsequently provided source memory judgements for whether item was perceived, imagined, or new.</p>	<p>Low vividness perceived sentence > CR</p> <p>Low vividness sentence imagined > CR</p>	<p>✓ BA 39</p> <p>✓ BA 40</p>	<p>X</p> <p>X</p>

Kragel & Polyn, 2016	<p>Encoding – Subjects made an animate/inanimate or size judgement regarding concrete nouns.</p> <p>Retrieval - Memory was assessed in two ways:</p> <ul style="list-style-type: none"> - Subjects freely recalled as many nouns as possible. - Source recognition – probed with studied nouns, participants were asked to remember whether an animacy or size judgement was required at encoding. 	<p>Item memory > CR</p> <p>Overlapping activation in free recall and item familiarity</p>	<p>✓ BA 40</p> <p>✓ BA 40</p>	<p>✓ BA 40</p> <p>✓ BA 40</p>
Leiker & Johnson, 2015	<p>Encoding – Subjects considered each noun in a word list in 1 of 3 ways. <i>Artist</i>: The way the object would be drawn. <i>Function</i>: Mentally generate as many functions for the object as possible. <i>Cost</i>: How expensive the object would be.</p> <p>Retrieval – An old/new recognition task assessed subjects' memory for the encoded words. Participants were also asked about which encoding task was used to encode the target word (source memory).</p>	Source Memory confidence: High > low	✓ BA 39	✓ BA 39
Leiker & Johnson, 2014	<p>Encoding – Subjects considered each noun in a word list in 1 of 3 ways. <i>Artist</i>: The way the object would be drawn. <i>Function</i>: Mentally generate as many functions for the object as possible. <i>Cost</i>: How expensive the object would be.</p> <p>Retrieval – An remember/know recognition task assessed subjects' memory for the encoded words. Participants also provided confidence judgements regarding their know responses.</p>	Remember>Know	✓ BA 39	X
Maratos, Dolan, Moscovitch, Henson, & Rugg, 2001	<p>Encoding – Subjects read and encoded emotionally negative, neutral or positive sentences. On each trial, the key word in the sentence was subsequently presented.</p> <p>Retrieval – The key sentence words were presented in an old/new recognition memory task.</p>	Hits > CR	✓ BA 39 & 40	✓ BA 40

McDermott, Jones, Petersen, Lageman, & Roediger, III, 2000	<p>Encoding – Subjects intentionally encoded a list of compound noun words.</p> <p>Retrieval – Participants completed an old/new recognition memory paradigm. Stimuli were ‘studied’ (identical to encoding), ‘recombined’ (nosebleed and skydive recombined to nosedive), or new.</p>	Hits > CR	✓ BA 40	✓ BA 40
Montaldi, Spencer, Roberts, & Mayes, 2006	<p>Encoding – Subjects judged which of two scenes perceptually matched the target image. No similar lures were used and scenes were easily identified with a label (e.g. a beach).</p> <p>Retrieval – Participants completed a familiarity sensitive old/new recognition memory paradigm.</p>	Remember > Familiar	✓ BA 40	X
Mugikura et al., 2016	<p>Encoding – Subjects read statements aloud whilst observing images of either a male or a female face. They were instructed to memorize the statement and gender of the face.</p> <p>Retrieval – Participants completed an old/new recognition memory test. They were also asked which gender characterised the face that was observed whilst encoding the statement.</p>	<p>Source hit confidence: High > low</p> <p>CR > low confidence item hits</p>	<p>✓ BA 39</p> <p>X</p>	<p>X</p> <p>✓ BA 40</p>
Ragland et al., 2004	<p>Encoding – A list of nouns was visually presented and participants were asked to intentionally encoding each word.</p> <p>Retrieval – Subjects completed an old/new recognition memory task.</p>	Hits > CR	✓ BA 40	✓ BA 40
Ragland, Valdez, Loughhead, Gur, & Gur, 2006	<p>Encoding – Noun words were presented visually to participants. Subjects were questioned on whether word was abstract/concrete, or upper/lower case.</p> <p>Retrieval – Subjects completed an old/new recognition memory paradigm and provided source memory judgements about the question they were asked during each word's encoding.</p>	<p>Item hit > CR</p> <p>Source hit > CR</p>	<p>✓ BA 40</p> <p>✓ BA 40</p>	<p>X</p> <p>X</p>

<p>Raposo, Frade, & Alves, 2016</p>	<p>Encoding – Subjects judged whether visually presented words were pleasant/unpleasant (semantic task) or had more than 6 letters (perceptual task).</p> <p>Retrieval – Participants completed an old/new recognition memory paradigm with source judgements regarding the task performed during the encoding of old items. For example, did you perform the semantic task with this item? (semantic query). Did you perform the perceptual task with this item? (perceptual query).</p>	<p>Semantic query > perceptual query</p>	<p>✓ BA 39 & 40</p>	<p>X</p>
<p>Shannon & Buckner, 2004</p>	<p>Encoding – Subjects made preference judgments on a mixed list of cartoon pictures and natural sounds.</p> <p>Retrieval – An old/new recognition task assessed memory for the encoded stimuli against new images and sounds.</p>	<p>Hits > CR</p>	<p>✓ BA 40</p>	<p>X</p>
<p>Takashima, Bakker, van Hell, Janzen, & McQueen, 2017</p>	<p>Encoding – Novel and pre-known words were presented to participants in either unaccompanied, or with a matching image or description. These were repeated multiple times and subject to a free recall task as part of training.</p> <p>Retrieval – At the end of the session, participants completed an old/new recognition memory paradigm in the scanner. Subjects returned 7 days later and completed another recognition memory paradigm also in the scanner.</p>	<p>Meaningful > non-meaningful</p> <p>Picture group: Meaningful > non-meaningful</p> <p>Day 8: Meaningful > non-meaningful</p>	<p>✓ BA 39/40</p> <p>✓ BA 39</p> <p>✓ BA 39/40</p>	<p>X</p> <p>X</p> <p>X</p>
<p>Tsukiura, Mochizuki-Kawai, & Fujii, 2005</p>	<p>Encoding – Subjects completed three types of encoding: 1) Subjects wrote down a sentence using 12 presented words and read it aloud. 2) Subjects transcribed a premade sentence with the 12 keywords highlighted. 3) Subjects copied the 12 keywords without a sentence. Subjects told to refrain for alternative strategies and just copy in 2nd and 3rd variants.</p> <p>Retrieval – Subjects subsequently completed an old/new recognition memory task.</p>	<p>Words encoded via a self-generated sentence > CR</p>	<p>✓ BA 39 & 40</p>	<p>X</p>

Vilberg & Rugg, 2014	<p>Encoding – Stimulus pairs consisting of concrete nouns and unrelated object images were visually presented. Subjects identified which item of the pair would likely be largest.</p> <p>Retrieval – Object images were subject to an old/new recognition memory test. For images thought to be old, subjects attempted to recall the word that accompanied the image at encoding.</p>	Sustained recollection: Associative hits > item hits	✓ BA 39/40	✓ BA 39/40
Vogelsang, Bonnici, Bergström, Ranganath, & Simons, 2016	<p>Encoding – Subjects made a semantic (pleasantness) or non-semantic (are the letters O or U in the word) judgement on each presentation of a noun from a list of words.</p> <p>Retrieval - An old/new recognition test was conducted to assess memory for the word list.</p>	<p>Retrieval success</p> <p>Words encoded semantically</p> <p>Words encoded “non-semantic”</p>	<p>✓ BA 39/ 40</p> <p>✓ BA 39/ 40</p>	<p>✓ BA 39/40</p> <p>✓ BA 39/ 40</p>
W. Wang, Brashier, Wing, Marsh, & Cabeza, 2018	<p>Encoding - Subjects incidentally encoded true, false , or unknown (nonsensicle relationship between different aspects of the statement) statements using an 'interestingness' rating task.</p> <p>Retrieval - Statements were presented to subjects and subjected to an old/new recognition memory judgement.</p>	<p>Hit > CR</p> <p>Unknown statements: Hit > CR</p>	<p>X</p> <p>✓ BA 39</p>	<p>✓ BA 40</p> <p>✓ BA 39</p>
Wang, Johnson, De Chastelaine, Donley, & Rugg, 2016	<p>Encoding – Subjects were required to make either relative size judgements regarding pictures of objects, or an inside/outside function decision regarding visually presented concrete noun words.</p> <p>Retrieval – An old/new recognition paradigm tested memory retrieval. The words from the encoding phase were represented, and the pictures of objects were replaced with word labels for the test phase.</p>	Material-independent age-invariant recollection	✓ BA 39	X
Westphal, Reggente, Ito, & Rissman, 2016	<p>Encoding – Subjects intentionally encoded visually presented word nouns whilst forming a mental image of either themselves or another individual interacting with the word.</p> <p>Retrieval – Target words were presented in a 4 choice forced choice paradigm with source judgements regarding whether “self” or “other” was presented with word.</p>	Memory > perception	✓ BA 40	X

Wheeler & Buckner, 2003	<p>Encoding – Concrete nouns were presented as congruent word-image or word-sound pairs.</p> <p>Retrieval – Subjects were presented with concrete noun words as part of an old/new recognition memory task.</p>	Hits > CR	✓ BA 40	✓ BA 40
Yaoi, Osaka, Osaka, & Salomon, 2015	<p>Encoding - Subjects judged the degree to which single, visually presented adjective words applied to either themselves or a celebrity.</p> <p>Retrieval - Participants completed an old/new recognition memory paradigm.</p>	Self-related hits > others-related hits	✓ BA 40	✓ BA 40
Yonelinas, Otten, Shaw, & Rugg, 2005	<p>Encoding – Participants were presented with a list of concrete and abstract noun words. Subjects provided a speeded abstract/concrete decision.</p> <p>Retrieval – Subjects completed a remember/know recognition memory task. Know memories (referred to as familiarity in the article) were rated for confidence.</p>	<p>Remember > highly confident familiarity</p> <p>Increasing with familiarity confidence</p>	<p>✓ BA 40</p> <p>✓ BA 39</p>	<p>✓ BA 40</p> <p>✓ BA 40</p>
			95.08%	45.90%

References

- Angel, L., Bastin, C., Genon, S., Salmon, E., Fay, S., Balteau, E., ... Collette, F. (2016). Neural correlates of successful memory retrieval in aging: Do executive functioning and task difficulty matter? *Brain Research*, 1631, 53-71.
<http://doi.org/10.1016/j.brainres.2015.10.009>
- Brown, T. I., Rissman, J., Chow, T. E., Uncapher, M. R., & Wagner, A. D. (2018). Differential Medial Temporal Lobe and Parietal Cortical Contributions to Real-world Autobiographical Episodic and Autobiographical Semantic Memory. *Scientific Reports*, (April), 1-14.
<http://doi.org/10.1038/s41598-018-24549-y>
- Cabeza, R., Dolcos, F., Graham, R., & Nyberg, L. (2002). Similarities and differences in the neural correlates of episodic memory retrieval and working memory. *NeuroImage*, 16(2), 317-330. <http://doi.org/10.1006/nimg.2002.1063>
- Cansino, S., Maquet, P., Dolan, R. J., & Rugg, M. D. (2002). Brain Activity Underlying Encoding and Retrieval of Source Memory. *Cerebral Cortex*, 12(10), 1048-1056.
<http://doi.org/10.1093/cercor/12.10.1048>
- Chen, H.-Y., Gilmore, A. W., Nelson, S. M., & McDermott, K. B. (2017). Are There Multiple Kinds of Episodic Memory? An fMRI Investigation Comparing Autobiographical and Recognition Memory Tasks. *The Journal of Neuroscience*, 37(10), 2764-2775.
<http://doi.org/10.1523/JNEUROSCI.1534-16.2017>
- Clemens Von Zerssen, G., Mecklinger, A., Opitz, B., & Yves Von Cramon, D. (2001). Conscious recollection and illusory recognition: An event-related fMRI study. *European Journal of Neuroscience*, 13(11), 2148-2156. <http://doi.org/10.1046/j.0953-816X.2001.01589.x>
- Compère, L., Sperduti, M., Gallarda, T., Anssens, A., Lion, S., Delhommeau, M., ... Piolino, P. (2016). Sex Differences in the Neural Correlates of Specific and General Autobiographical Memory. *Frontiers in Human Neuroscience*, 10(June), 1-16.
<http://doi.org/10.3389/fnhum.2016.00285>
- Cooper, R. A., Richter, F. R., Bays, P. M., Plaisted-Grant, K. C., Baron-Cohen, S., & Simons, J. S. (2017). Reduced Hippocampal Functional Connectivity During Episodic Memory Retrieval in Autism. *Cerebral Cortex*, (February 2017), 888-902. <http://doi.org/10.1093/cercor/bhw417>
- Daselaar, S. M., Fleck, M. S., & Cabeza, R. (2006). Triple Dissociation in the Medial Temporal Lobes: Recollection, Familiarity, and Novelty. *Journal of Neurophysiology*, 96(4), 1902-1911.
<http://doi.org/10.1152/jn.01029.2005>

- DeMaster, D., Pathman, T., & Ghetti, S. (2013). Development of memory for spatial context: Hippocampal and cortical contributions. *Neuropsychologia*, 51(12), 2415-2426.
<http://doi.org/10.1016/j.neuropsychologia.2013.05.026>
- Dennis, N. A., Bowman, C. R., & Vandekar, S. N. (2012). True and phantom recollection: An fMRI investigation of similar and distinct neural correlates and connectivity. *NeuroImage*, 59(3), 2982-2993. <http://doi.org/10.1016/j.neuroimage.2011.09.079>
- Dobbins, I. G., Foley, H., Schacter, D. L., & Wagner, A. D. (2002). Executive Control during Episodic Retrieval. *Neuron*, 35(5), 989-996. [http://doi.org/10.1016/S0896-6273\(02\)00858-9](http://doi.org/10.1016/S0896-6273(02)00858-9)
- Dobbins, I. G., Rice, H. J., Wagner, A. D., & Schacter, D. L. (2003). Memory orientation and success: separable neurocognitive components underlying episodic recognition. *Neuropsychologia*, 41(3), 318-333. [http://doi.org/10.1016/S0028-3932\(02\)00164-1](http://doi.org/10.1016/S0028-3932(02)00164-1)
- Dobbins, I. G., & Wagner, A. D. (2005). Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. *Cerebral Cortex*, 15(11), 1768-1778. <http://doi.org/10.1093/cercor/bhi054>
- Donaldson, D. I., Petersen, S. E., & Buckner, R. L. (2001). Dissociating Memory Retrieval Processes Using fMRI: Evidence that Priming Does Not Support Recognition Memory. *Neuron*, 31(6), 1047-1059. [http://doi.org/10.1016/S0896-6273\(01\)00429-9](http://doi.org/10.1016/S0896-6273(01)00429-9)
- Donaldson, D. I., Petersen, S. E., Ollinger, J. M., & Buckner, R. L. (2001). Dissociating state and item components of recognition memory using fMRI. *NeuroImage*, 13(1), 129-142.
<http://doi.org/10.1006/nimg.2000.0664>
- Duarte, A., Henson, R. N. A., & Graham, K. S. (2011). Stimulus content and the neural correlates of source memory. *Brain Research*, 1373, 110-123.
<http://doi.org/10.1016/j.brainres.2010.11.086>
- Eldridge, L. L., Knowlton, B. J., Furmanski, C. S., Bookheimer, S. Y., & Engel, S. A. (2000). Remembering episodes: a selective role for the hippocampus during retrieval. *Nature Neuroscience*, 3(11), 1149-1152. <http://doi.org/10.1038/80671>
- Elman, J. A., Cohn-Sheehy, B. I., & Shimamura, A. P. (2013). Dissociable parietal regions facilitate successful retrieval of recently learned and personally familiar information. *Neuropsychologia*, 51(4), 573-583. <http://doi.org/10.1016/j.neuropsychologia.2012.12.013>
- Flegal, K. E., Marín-Gutiérrez, A., Ragland, J. D., & Ranganath, C. (2014). Brain Mechanisms of Successful Recognition through Retrieval of Semantic Context. *Journal of Cognitive Neuroscience*, 26(8), 1694-1704. http://doi.org/10.1162/jocn_a_00587

- Frithsen, A., & Miller, M. B. (2014). The posterior parietal cortex: Comparing remember/know and source memory tests of recollection and familiarity. *Neuropsychologia*, 61(1).
<http://doi.org/10.1016/j.neuropsychologia.2014.06.011>
- Gimbel, S. I., & Brewer, J. B. (2014). Elaboration versus suppression of cued memories: Influence of memory recall instruction and success on parietal lobe, default network, and hippocampal activity. *PLoS ONE*, 9(2), 7-11. <http://doi.org/10.1371/journal.pone.0089037>
- Hall, S. A., Rubin, D. C., Miles, A., Davis, S. W., & Wing, E. A. (2015). The neural basis of involuntary episodic memories. *Journal of Cognitive Neuroscience*, 26(10), 2385-2399.
- Hayes, S. M., Buchler, N., Stokes, J., Kragel, J. E., & Cabeza, R. (2011). Neural Correlates of Confidence during Item Recognition and Source Memory Retrieval: Evidence for Both Dual-process and Strength Memory Theories. *Journal of Cognitive Neuroscience*, 23(12), 3959-3971.
http://doi.org/10.1162/jocn_a_00086
- Henson, R. N. A., Hornberger, M., & Rugg, M. D. (2005). Further Dissociating the Processes Involved in Recognition Memory: An fMRI Study. *Journal of Cognitive Neuroscience*, 17(7), 1058-1073. <http://doi.org/10.1162/0898929054475208>
- Herron, J. E., Henson, R. N. A., & Rugg, M. D. (2004). Probability effects on the neural correlates of retrieval success: An fMRI study. *NeuroImage*, 21(1), 302-310.
<http://doi.org/10.1016/j.neuroimage.2003.09.039>
- Herweg, N. A., Sommer, T., & Bunzeck, N. (2017). Retrieval demands adaptively change striatal old/new signals and boost subsequent long-term memory. *The Journal of Neuroscience*, 1315-17. <http://doi.org/10.1523/JNEUROSCI.1315-17.2017>
- Hirshhorn, M., Grady, C. L., Rosenbaum, R. S., Winocur, G., & Moscovitch, M. (2012). Brain regions involved in the retrieval of spatial and episodic details associated with a familiar environment: An fMRI study. *Neuropsychologia*, 50(13), 3094-3106.
<http://doi.org/10.1016/j.neuropsychologia.2012.08.008>
- Hutchinson, J. B., Uncapher, M. R., & Wagner, A. D. (2015). Increased functional connectivity between dorsal posterior parietal and ventral occipitotemporal cortex during uncertain memory decisions. *Neurobiology of Learning and Memory*, 117(18), 71-83.
<http://doi.org/10.1016/j.nlm.2014.04.015>
- Hutchinson, J. B., Uncapher, M. R., Weiner, K. S., Bressler, D. W., Silver, M. A., Preston, A. R., & Wagner, A. D. (2014). Functional heterogeneity in posterior parietal cortex across attention

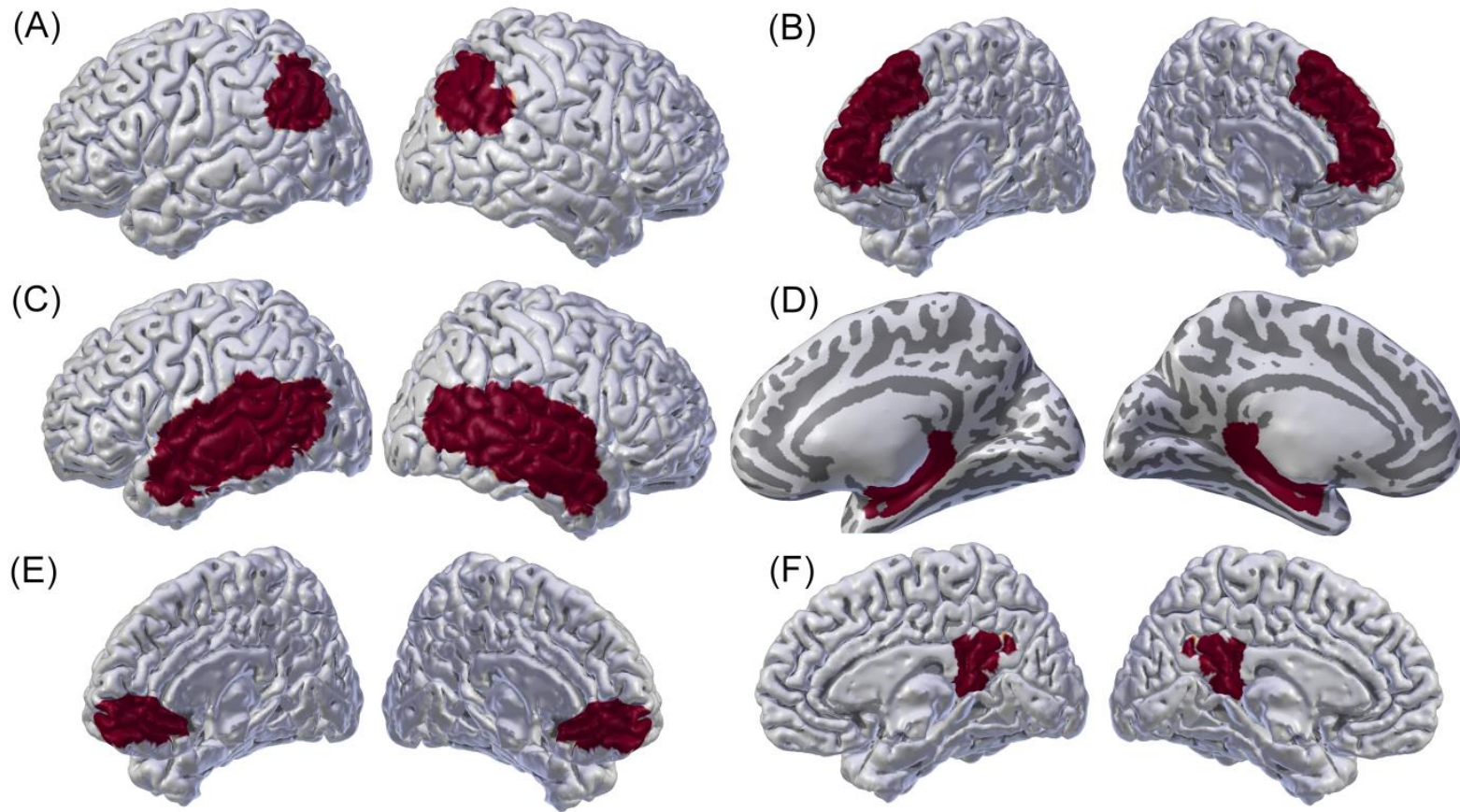
- and episodic memory retrieval. *Cerebral Cortex*, 24(1), 49-66.
<http://doi.org/10.1093/cercor/bhs278>
- Kafkas, A., & Montaldi, D. (2012). Familiarity and recollection produce distinct eye movement, pupil and medial temporal lobe responses when memory strength is matched. *Neuropsychologia*, 50(13), 3080-93. <http://doi.org/10.1016/j.neuropsychologia.2012.08.001>
- Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional-neuroanatomic correlates of recollection: implications for models of recognition memory. *The Journal of Neuroscience*, 24(17), 4172-80. <http://doi.org/10.1523/JNEUROSCI.0624-04.2004>
- King, D. R., & Miller, M. B. (2014). Lateral posterior parietal activity during source memory judgments of perceived and imagined events. *Neuropsychologia*, 53(1), 122-136.
<http://doi.org/10.1016/j.neuropsychologia.2013.11.006>
- King, D. R., & Miller, M. B. (2017). Influence of response bias and internal/external source on lateral posterior parietal successful retrieval activity. *Cortex*, 91, 126-141.
<http://doi.org/10.1016/j.cortex.2017.04.002>
- King, D. R., Schubert, M. L., & Miller, M. B. (2015). Lateral posterior parietal activity during reality monitoring discriminations of memories of high and low perceptual vividness. *Cognitive, Affective & Behavioral Neuroscience*, 15(3), 662-679.
<http://doi.org/10.3758/s13415-015-0357-4>
- Kragel, J. E., & Polyn, S. M. (2016). Decoding Episodic Retrieval Processes: Frontoparietal and Medial Temporal Lobe Contributions to Free Recall. *Journal of Cognitive Neuroscience*, 28(1), 125-139. http://doi.org/10.1162/jocn_a_00881
- Leiker, E. K., & Johnson, J. D. (2014). Neural reinstatement and the amount of information recollected. *Brain Research*, 1582, 125-138. <http://doi.org/10.1016/j.brainres.2014.07.026>
- Leiker, E. K., & Johnson, J. D. (2015). Pattern reactivation co-varies with activity in the core recollection network during source memory. *Neuropsychologia*, 75, 88-98.
<http://doi.org/10.1016/j.neuropsychologia.2015.05.021>
- Lundstrom, B. N., Ingvar, M., & Petersson, K. M. (2005). The role of precuneus and left inferior frontal cortex during source memory episodic retrieval. *NeuroImage*, 27(4), 824-834.
<http://doi.org/10.1016/j.neuroimage.2005.05.008>
- Lundstrom, B. N., Petersson, K. M., Andersson, J., Johansson, M., Fransson, P., & Ingvar, M. (2003). Isolating the retrieval of imagined pictures during episodic memory: Activation of the

- left precuneus and left prefrontal cortex. *NeuroImage*, 20(4), 1934-1943.
<http://doi.org/10.1016/j.neuroimage.2003.07.017>
- Maratos, E. J. J., Dolan, R. J., Morris, J. S., Henson, R. N. A., Rugg, M. D., Moscovitch, M., ... Rugg, M. D. (2001). Neural activity associated with episodic memory for emotional context. *Neuropsychologia*, 39(9), 910-920. [http://doi.org/10.1016/S0028-3932\(01\)00025-2](http://doi.org/10.1016/S0028-3932(01)00025-2)
- McDermott, K. B., Jones, T. C., Petersen, S. E., Lageman, S. K., & Roediger, III, H. L. (2000). Retrieval success is accompanied by enhanced activation in anterior prefrontal cortex during recognition memory: an event-related fMRI study. *Journal of Cognitive Neuroscience*, 12(6), 965-976. <http://doi.org/10.1162/08989290051137503>
- Meusel, L. A., Grady, C. L., Ebert, P. E., & Anderson, N. D. (2017). Brain-behavior relationships in source memory: Effects of age and memory ability. *Cortex*, 91, 221-233.
<http://doi.org/10.1016/j.cortex.2016.12.023>
- Montaldi, D., Spencer, T. J., Roberts, N., & Mayes, A. R. (2006). The neural system that mediates familiarity memory. *Hippocampus*, 16(5), 504-520.
<http://doi.org/10.1002/hipo.20178>
- Mugikura, S., Abe, N., Ito, A., Kawasaki, I., Ueno, A., Takahashi, S., & Fujii, T. (2016). Medial temporal lobe activity associated with the successful retrieval of destination memory. *Experimental Brain Research*, 234(1), 95-104. <http://doi.org/10.1007/s00221-015-4415-5>
- Ragland, J. D., Gur, R. C., Valdez, J. N., Turetsky, B. I., Elliott, M., Kohler, C., ... Gur, R. E. (2004). Event-Related fMRI of Frontotemporal Activity During Word Encoding and Recognition in Schizophrenia. *American Journal of Psychiatry*, 161(6), 1004-1015.
<http://doi.org/10.1176/appi.ajp.161.6.1004>
- Ragland, J. D., Valdez, J. N., Loughhead, J., Gur, R. C., & Gur, R. E. (2006). Functional magnetic resonance imaging of internal source monitoring in schizophrenia: Recognition with and without recollection. *Schizophrenia Research*, 87(1-3), 160-171.
<http://doi.org/10.1016/j.schres.2006.05.008>
- Raposo, A., Frade, S., & Alves, M. (2016). Framing memories: How the retrieval query format shapes the neural bases of remembering. *Neuropsychologia*, 89, 309-319.
<http://doi.org/10.1016/j.neuropsychologia.2016.06.036>
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2010). Attention to Memory and the Environment: Functional Specialization and Dynamic Competition in Human Posterior Parietal Cortex.

- Journal of Neuroscience, 30(25), 8445-8456. <http://doi.org/10.1523/JNEUROSCI.4719-09.2010>
- Shannon, B. J., & Buckner, R. L. (2004). Functional-Anatomic Correlates of Memory Retrieval That Suggest Nontraditional Processing Roles for Multiple Distinct Regions within Posterior Parietal Cortex. *The Journal of Neuroscience*, 24(45), 10084-10092. <http://doi.org/10.1523/JNEUROSCI.2625-04.2004>
- Sharot, T., Delgado, M. R., & Phelps, E. A. (2004). How emotion enhances the feeling of remembering. *Nature Neuroscience*, 7(12), 1376-1380. <http://doi.org/10.1038/nn1353>
- St-Laurent, M., Abdi, H., Bondad, A., & Buchsbaum, B. R. (2014). Memory Reactivation in Healthy Aging: Evidence of Stimulus-Specific Dedifferentiation. *The Journal of Neuroscience*, 34(12), 4175-4186. <http://doi.org/10.1523/JNEUROSCI.3054-13.2014>
- St-Laurent, M., Moscovitch, M., & McAndrews, M. P. (2016). The retrieval of perceptual memory details depends on right hippocampal integrity and activation. *Cortex*, 84, 15-33. <http://doi.org/10.1016/j.cortex.2016.08.010>
- St. Jacques, P. L., Carpenter, A. C., Szpunar, K. K., & Schacter, D. L. (2018). Remembering and imagining alternative versions of the personal past. *Neuropsychologia*, 110(February 2017), 170-179. <http://doi.org/10.1016/j.neuropsychologia.2017.06.015>
- Takashima, A., Bakker, I., van Hell, J. G., Janzen, G., & McQueen, J. M. (2017). Interaction between episodic and semantic memory networks in the acquisition and consolidation of novel spoken words. *Brain and Language*, 167, 44-60. <http://doi.org/10.1016/j.bandl.2016.05.009>
- Thakral, P. P., Wang, T. H., & Rugg, M. D. (2015). Cortical reinstatement and the confidence and accuracy of source memory. *NeuroImage*, 109(2), 118-129. <http://doi.org/10.1016/j.neuroimage.2015.01.003>
- Tsukiura, T., Mochizuki-Kawai, H., & Fujii, T. (2005). The effect of encoding strategies on medial temporal lobe activations during the recognition of words: An event-related fMRI study. *NeuroImage*, 25(2), 452-461. <http://doi.org/10.1016/j.neuroimage.2005.01.003>
- van Buuren, M., Kroes, M. C. W., Wagner, I. C., Genzel, L., Morris, R. G. M., & Fernandez, G. (2014). Initial Investigation of the Effects of an Experimentally Learned Schema on Spatial Associative Memory in Humans. *Journal of Neuroscience*, 34(50), 16662-16670. <http://doi.org/10.1523/JNEUROSCI.2365-14.2014>

- Vilberg, K. L., & Rugg, M. D. (2014). Temporal dissociations within the core recollection network. *Cognitive Neuroscience*, 5(2), 77-84. <http://doi.org/10.1080/17588928.2013.860088>
- Vogelsang, D. A., Bonnici, H. M., Bergström, Z. M., Ranganath, C., & Simons, J. S. (2016). Goal-directed mechanisms that constrain retrieval predict subsequent memory for new “foil” information. *Neuropsychologia*, 89, 356-363. <http://doi.org/10.1016/j.neuropsychologia.2016.07.016>
- Wais, P. E., Jahanikia, S., Steiner, D., Stark, C. E. L., & Gazzaley, A. (2017). Retrieval of high-fidelity memory arises from distributed cortical networks. *NeuroImage*, 149(January), 178-189. <http://doi.org/10.1016/j.neuroimage.2017.01.062>
- Wang, T. H., Johnson, J. D., De Chastelaine, M., Donley, B. E., & Rugg, M. D. (2016). The Effects of Age on the Neural Correlates of Recollection Success, Recollection-Related Cortical Reinstatement, and Post-Retrieval Monitoring. *Cerebral Cortex*, 26(4), 1698-1714. <http://doi.org/10.1093/cercor/bhu333>
- Wang, W., Brashier, N. M., Wing, E. A., Marsh, E. J., & Cabeza, R. (2018). Knowledge supports memory retrieval through familiarity, not recollection. *Neuropsychologia*, 113(August 2017), 14-21. <http://doi.org/10.1016/j.neuropsychologia.2018.01.019>
- Weis, S., Klaver, P., Reul, J., Elger, C. E., & Fernández, G. (2004). Temporal and Cerebellar Brain Regions that Support both Declarative Memory Formation and Retrieval. *Cerebral Cortex*, 14(3), 256-267. <http://doi.org/10.1093/cercor/bhg125>
- Westphal, A. J., Reggente, N., Ito, K. L., & Rissman, J. (2016). Shared and distinct contributions of rostrolateral prefrontal cortex to analogical reasoning and episodic memory retrieval. *Human Brain Mapping*, 37(3), 896-912. <http://doi.org/10.1002/hbm.23074>
- Weymar, M., Bradley, M. M., Sege, C. T., & Lang, P. J. (2018). Neural activation and memory for natural scenes : Explicit and spontaneous retrieval. *Psychophysiology*, (March 2017), 1-12. <http://doi.org/10.1111/psyp.13197>
- Wheeler, M. E., & Buckner, R. L. (2003). Functional dissociation among components of remembering: control, perceived oldness, and content. *Journal of Neuroscience*, 23(9), 3869-3880. Retrieved from <http://www.jneurosci.org/content/23/9/3869.short>
- Xiao, X., Dong, Q., Gao, J., Men, W., Poldrack, R. A., & Xue, G. (2017). Transformed Neural Pattern Reinstatement during Episodic Memory Retrieval. *Journal of Neuroscience*, 37(11), 2986-2998. <http://doi.org/10.1523/JNEUROSCI.2324-16.2017>

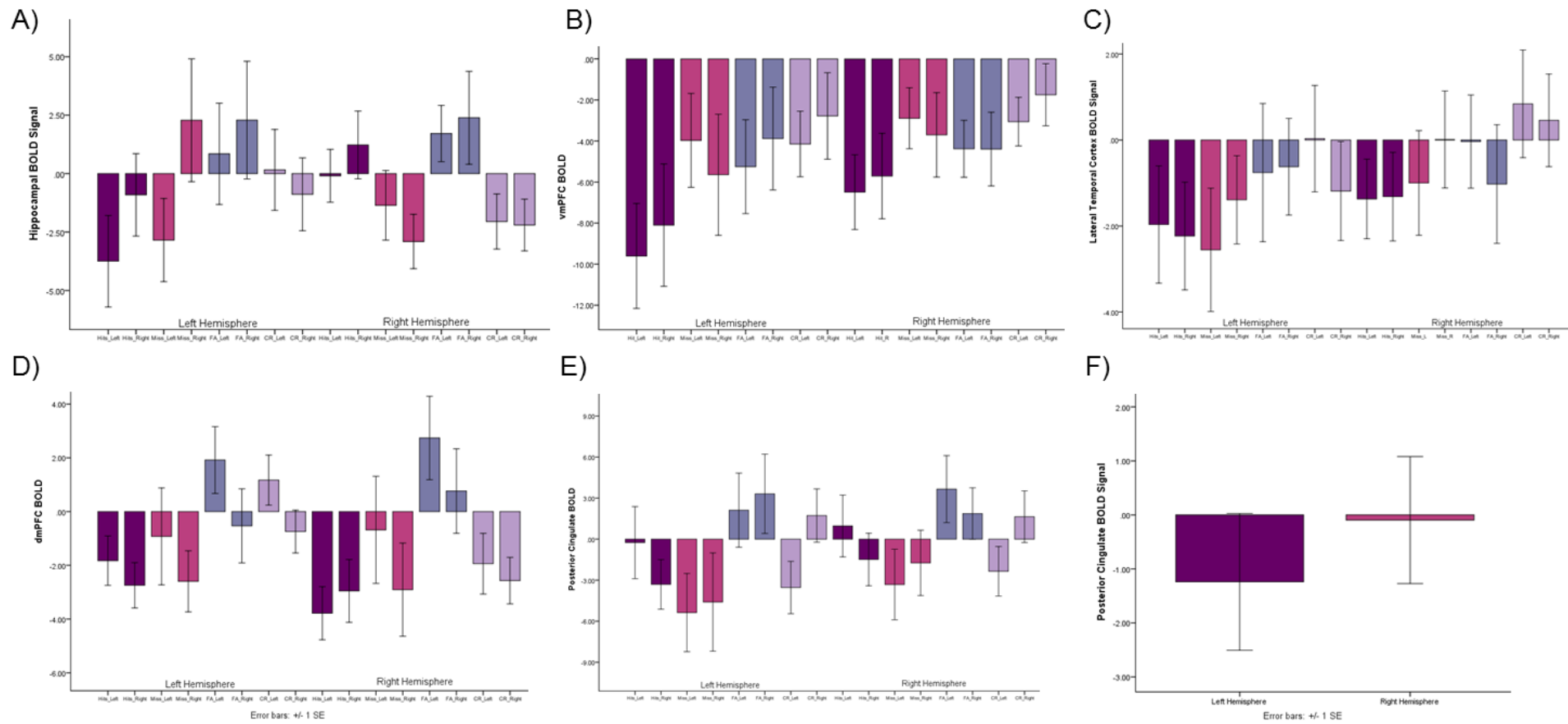
- Yaoi, K., Osaka, M., & Osaka, N. (2015). Neural correlates of the self-reference effect: evidence from evaluation and recognition processes. *Frontiers in Human Neuroscience*, 9(June), 1-9. <http://doi.org/10.3389/fnhum.2015.00383>
- Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the Brain Regions Involved in Recollection and Familiarity in Recognition Memory. *The Journal of Neuroscience*, 25(11), 3002-3008. <http://doi.org/10.1523/JNEUROSCI.5295-04.2005>



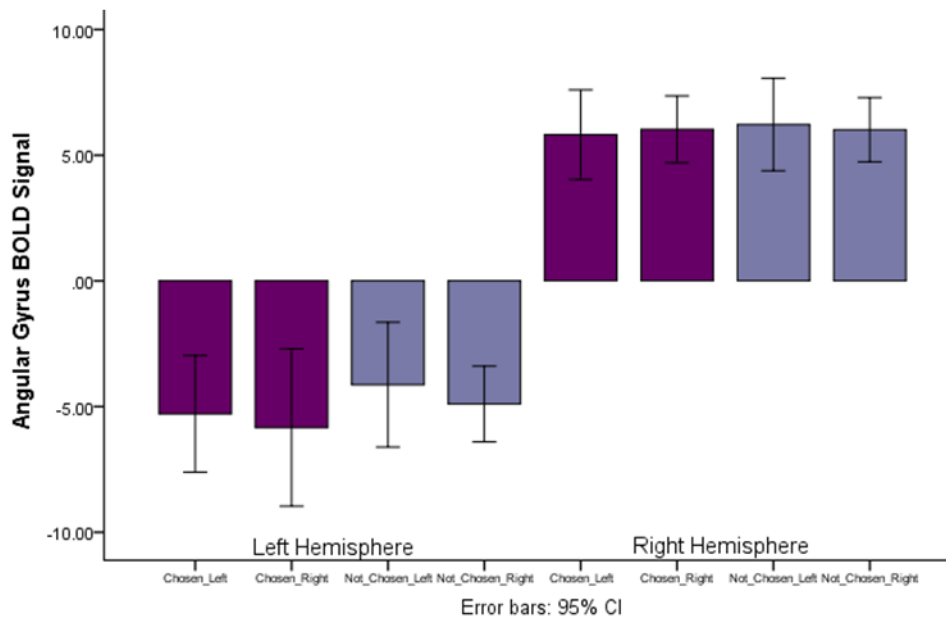
Supplementary Figure 4.2: An illustration of the ROIs used for the comparison of brain activity across the hemisphere (A) Angular Gyrus (B) Dorsomedial Prefrontal Cortex (C) Lateral Temporal Cortex (D) Hippocampus (E) Ventromedial Prefrontal Cortex (F) Posterior Cingulate Cortex.

Brain Region	Main Effect	Statistics				Brain Region	Main Effect	Statistics			
		F	DF	p	η_p^2			F	DF	p	η_p^2
Angular Gyrus	Memory Type	0.64	1.69 28.68	0.510	0.036	dmPFC	Memory Type	3.80	1.68 28.56	0.041	0.183
	Side	2.26	1.00 17.00	0.151	0.117		Side	7.62	1.00 17.00	0.014	0.307
	Hemisphere	98.05	1.00 17.00	<0.001	0.852		Hemisphere	1.71	1.00 17.00	0.208	0.092
	Memory Type * Side	1.08	3.00 51.00	0.36	0.060		Memory Type * Side	0.53	3.00 51.00	0.67	0.030
	Memory Type * Hemisphere	4.09	3.00 51.00	0.01	0.194		Memory Type * Hemisphere	1.78	1.27 21.54	0.16	0.095
	Side * Hemisphere	1.55	1.00 17.00	0.23	0.083		Side * Hemisphere	1.11	1.00 17.00	0.31	0.061
	Memory Type * Hemisphere	0.67	3.00 51.00	0.57	0.038		Memory Type * Hemisphere	1.78	1.50 25.51	0.16	0.095
Hippocampus	Memory Type	2.72	3.00 51.00	0.054	0.138	vmPFC	Memory Type	1.96	3.00 51.00	0.131	0.104
	Side	3.39	1.00 17.00	0.083	0.166		Side	0.47	1.00 17.00	0.500	0.027
	Hemisphere	<0.01	1.00 17.00	0.950	<0.001		Hemisphere	4.24	1.00 17.00	0.055	0.200
	Memory Type * Side	0.47	3.00 51.00	0.71	0.027		Memory Type * Side	0.19	3.00 51.00	0.91	0.011
	Memory Type * Hemisphere	1.20	2.04 34.73	0.31	0.066		Memory Type * Hemisphere	1.08	3.00 51.00	0.37	0.059
	Side * Hemisphere	2.88	1.00 17.00	0.11	0.145		Side * Hemisphere	0.33	1.00 17.00	0.57	0.019
	Memory Type * Hemisphere	1.05	3.00 51.00	0.38	0.058		Memory Type * Hemisphere	0.76	2.14 36.43	0.76	0.017
Posterior Cingulate	Memory Type	2.18	1.86 31.64	0.132	0.144	Lateral Temporal	Memory Type	1.04	3.00 51.00	0.383	0.058
	Side	0.30	1.00 17.00	0.591	0.017		Side	0.04	1.00 17.00	0.846	0.002
	Hemisphere	4.99	1.00 17.00	0.039	0.227		Hemisphere	2.20	1.00 17.00	0.156	0.115
	Memory Type * Side	1.58	3.00 51.00	0.207	0.085		Memory Type * Side	0.49	3.00 51.00	0.689	0.028
	Memory Type * Hemisphere	1.65	2.05 34.80	0.207	0.088		Memory Type * Hemisphere	0.37	3.00 51.00	0.775	0.021
	Side * Hemisphere	1.453	1.00 17.00	0.25	0.079		Side * Hemisphere	0.003	1.00 17.00	0.96	<0.001
	Memory Type * Hemisphere	1.02	1.54 26.22	0.36	0.057		Memory Type * Hemisphere	0.60	3.00 51.00	0.62	0.034

Supplementary Table 4.3: The results of six 4x2x2 repeated measures ANOVAs are displayed. Each analysis compares activity in a default mode network region for each memory condition (hit, miss, false alarm, and correct rejection), side of original presentation (left visual field, right visual field), and hemisphere (left hemisphere, right hemisphere). Interactions between these factors are also listed.



Supplementary Figure 4.3: Activity in other default mode network regions did not exhibit a similar pattern of activity as the angular gyrus during recognition memory judgements ((A) hippocampus, (B) ventromedial prefrontal cortex, (C) lateral temporal cortex, (D) dmPFC, (E) Posterior cingulate cortex, (F) A summary of the very small difference in BOLD signal between the posterior cingulate cortex in the left and right hemisphere ($p = 0.039$).



Supplementary Figure 4.4: The Old/Old test format was also strongly associated with greater activity in the right than left hemisphere for during recognition memory judgements ($p < 0.001$).