

The neural correlates of Human Spatial Memory and Representation

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PhD Thesis



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*“Stand in the place where you live, think about direction and
wonder why you haven’t before”*

- Michael Stipe

This thesis is dedicated to my Family and Friends

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Abstract

The importance of object-location memory for our everyday survival is now well accepted. This behaviour relies on spatial representation and memory within the brain. With these representations, we are able to construct what has been described as a “cognitive map” (Tolman, 1948) that allows us to accurately direct ourselves within our environment, be it throughout a city or within a building, in an automobile or on foot. However, how these representations interact remains poorly understood. In particular, the temporal dynamics involved in the recruitment of and retrieval from different spatial representations has received little attention. Likewise, the use of spatial information for object-location binding is another largely unexplored area.

As virtual reality begins to gain a solid foothold in psychology laboratories, we describe a novel and flexible small-scale test of spatial memory which we coined ‘The Spatial Grid Task’. With variants of this array task we investigated human spatial memory in an attempt to test the relationship between elements of the cognitive map and between spatial and object memory. This investigation has involved a number of experiments studying the efficacy of different information-types on performance and analysis of performance from shifted-viewpoints as well as an examination of the neural correlates of spatial memory.

We report behavioural and electrophysiological differences in ego- and allocentric strategies and provide the first temporal markers identifying the divergence between representations. Amplitude differences in a parietal P300 component are found to emerge after 300ms with evidence that early translational processes precede location categorisation processes. These differences were found to be consistent after controlling for task difficulty, mental rotation, scene recognition and other ecological confounds. In

addition to interactions within the cognitive map, we assessed how, when and where in the brain spatial information is integrated with object information. Our investigations used implicit and explicit measures, both of which revealed a locational bias in information-processing. Electrophysiological differences suggest that spatial evaluation can exhibit an early (and implicit) influence on object recognition. Explicitly, the primacy of spatial processing was accompanied by earlier peaking frontal P2 components and centro-parietal P300s when participants were evaluating locations compared to objects. The results are discussed alongside models of brain activation; these models suggest structures that are dissociable along the ventral and dorsal streams as well as highlighting areas of convergence. The parahippocampal gyrus of the MTL is posited to play a crucial role in spatial coding while more dorsal regions and the posterior cingulate cortex are suggested to underlie integration and translation.

This thesis details experiments which are amongst the first to use EEG to probe spatial memory in such detail as to expose electrophysiological differences between representations. As well as showing viewpoint-related differences, the work suggests areas that are engaged for translation between representations and provides temporal markers for their involvement. It also gives an insight into the processing speeds along the visual streams suggesting a contextual dominance in object-location (and episodic) memory. Finally, this thesis provides clear electrophysiological markers of spatial memory which can be used in further research with normals and in the assessment of brain damage.

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1

Chapter I Introduction

1.1 Overview: Human memory

How do we learn and remember? How do we store information in our brains and where is this ‘information’ stored? The concept of memory has captivated human interest to such an extent that we’ve come up with more metaphors for it than for any other mental phenomenon. Characterising memory can be traced back to Plato who distinguished between two aspects of memory: the power to retain information, and the power of recollection. These are defined, in modern terms, as encoding and retrieval respectively. Since then distinctions have been made between short-term vs. long-term memory (e.g. Baddeley, 1966; Atkinson & Schiffman, 1968); declarative vs. procedural memory (e.g. Anderson, 1976; Tulving & Schacter, 1990; Squire *et al.*, 1992); episodic vs. semantic memory (e.g. Tulving, 1972; Jacoby & Dallas, 1981) and explicit vs. implicit memory (Tulving & Schacter, 1990). Descriptions of memory and the types of encoding, storage and retrieval involved led to the formulation of many memory theories over the last century. Most of these theories have suggested an important role for the medial temporal lobe structure – the hippocampus – in memory formation.

A dissemination of the semantic memory theories is best reserved for a discussion on language, thus a review of theories of episodic memory and more specific spatial memory theories will be discussed. Marr’s (1971) *simple memory theory* has influenced most computational models of memory which proffer the hippocampus with an automatic ‘snap-shot’ role in memory formation (Muir, 1996; Nadel *et al.*, 2000), many of which point to the auto-associative features of the recurrent CA3¹ network (McNaughton & Nadel, 1990; Burgess *et al.*, 1994; McClelland and O’Reilly, 1995; Rolls and Treves,

¹ Area CA3 is one of the four *Cornu Ammonis* sub-regions of the hippocampus proper. Area CA3 (and CA1) consist of densely packed pyramidal cells. CA3 receives input from the entorhinal cortex via axons in the perforant pathway and transmits to other CA fields via the Schaffer collaterals. It is also the termination point for many hippocampal connections, hence the network here is known as recurrent.

1998; Kali and Dayan, 2000). Both the *auto-association theory (AAT)* of Rolls & Treves (1998) and the earlier *configural association theory (CAT)* proposed by Sutherland & Rudy (1989) posited that the hippocampus was important for the binding of information during memory formation. These theories differ about the degree of involvement of the hippocampus with CAT positing a permanent role for the hippocampus in the memory process i.e. encoding, storage, and retrieval. The temporary role proposed by Rolls & Treves (1998) is more consistent with other theories (e.g. McClelland and O'Reilly, 1995; Rolls, 1996; Baddeley, 2000). These models all share features with the standard model of memory known as *classic consolidation theory (CCT)* (Squire *et al.*, 1984; 1992) which sees the neocortex as the permanent repository of memory. While the other theories might view the hippocampus as the initial storage point, the temporary role attributed by CCT allows the hippocampal representation to be just detailed enough to unconsciously re-activate and strengthen the memory in the neocortex. The idea that the hippocampus stores 'sufficient' information for activation of the neocortical trace is a shared concept of the *representational flexibility theory (RFT)* of Eichenbaum & Cohen (2001). Nadel & Moscovitch's (1997) *multiple trace theory (MTT)* was compiled to address evidence (mostly from amnesic patients) against the CCT viewpoint of consolidated neocortical memory storage. Here a hippocampal-neocortical ensemble constitutes the memory trace and multiple traces are formed through re-activation leading to a greater number of associations for older, more remote memories.

In reviewing the aforementioned theories of hippocampal involvement in episodic memory, Good (2002), noted a common organising principle i.e. that the hippocampus contributes to the binding together of memories for events and their spatiotemporal

context. Shared components of the theories include a hippocampal storage role, a transition from hippocampus to neocortex and a consolidation of memory in the cortex. At the most basic level, all the theories agree on one point - we remember because the connections between our brains' neurons change.

It was believed that neuron *production* was involved in memory formation (i.e. that there was an increase in the number of neurons with memory) until Ribot (1882) and later Cajal (1894) suggested a mechanism for forming memories that involved strengthening the connections between neurons. Hebb (1949, p. 63) supported this suggestion saying, *"When one cell repeatedly assists in firing another, the axon of the first cell develops synaptic knobs (or enlarges them if they already exist) in contact with the soma of the second cell."* Hebbian theory (commonly paraphrased as 'cells that fire together, wire together') concerns how neurons might connect themselves to become engrams. Since the initial 'search for the engram' (Semon, 1921; Lashley, 1929; Hebb, 1949), conceptions of the memory trace have changed from the cognitive and systems domain to the chemical and molecular. An example of a modern neuroscientific description of short-term to long-term memory formation is illustrated in Figure 1.1.



Figure 1.1 A molecular account of the late stages of long-term potentiation. Second messengers, such as Calcium²⁺ act on protein kinases, such as PKA which in turn activates the transcription factor CREB. This then binds to DNA leading to protein synthesis and synaptic changes.

Long-term potentiation (LTP) along with long-term depression (LTD), are widely considered the major cellular mechanisms that underlie learning and memory (Cooke and Bliss, 2006). More specifically, LTP is the rapidly induced and relatively enduring increase in synaptic strength following an electrophysiological event such as high-frequency stimulation. LTD is the opposing process which results in synaptic weakening. The model in Figure 1.1 illustrates the late stages of LTP but is just one of many, and as our knowledge of the effects of neurotransmitters, enzymes, genes and proteins increases, these models will undoubtedly become more accurate, (see Lomo (2003) for a review of LTP). As elaborating on the molecular mechanisms of memory is beyond the remit of this overview, a discussion of one specific aspect of memory, namely spatial memory, will follow.

1.2 Spatial Memory and the Cognitive Map

A number of general memory theories have a spatial component and there are some others which hypothesise about spatial memory specifically. As mentioned in the overview above, CAT (Sutherland & Rudy, 1989) shares similarities with AAT (Rolls and Treves, 1998). AAT, however, specifies a role for the hippocampus in spatial as well as non-spatial memory, suggesting it acts to bind spatial contexts to the semantic and episodic elements of events. Both theories assume a degree of associative learning within the hippocampus, as did Marr (1971). The associative approach is one of two prominent theoretical perspectives guiding current research on place learning and spatial memory. As one moves through an environment, associations are built between stimuli, such as objects in the environment, and responses, such as moving towards an object; spatial learning follows conventions of classical and instrumental conditioning (Kelly & Gibson, 2007). In contrast, the cognitive map theory, proposed by O'Keefe and Nadel (1978), argues that a topographical representation of one's environment is constructed in the hippocampus and that these spatial representations allow for flexible navigation to a goal location from familiar or novel positions with equal capacity. The 'cognitive map' has been used to describe the mental representations of space, whereby one's location within an environment is updated through the relative associations of distal cues in addition to, yet distinct from, any proximal information available. The concept of such a map provides an alternative to a rigid viewpoint storage system, for example Cartwright and Collett's (1983) 'snapshot' model of spatial memory, which would need to be constantly and accurately updated to compensate for the subject's movements. Purely sensory forms of representation and navigation (Restle, 1957) would be inefficient due to this constant re-calculation of position and heading as well as the storage of unnecessary information

(Hartley *et al.*, 2003). A theory relating the cognitive map to episodic memory was proposed by Burgess and colleagues (2001a) where the hippocampus holds the spatiotemporal context of episodic memory (see also Burgess, 2002; Burgess and O'Keefe, 2002; Hartley and Burgess, 2002). This role for the hippocampus is similar to that proposed by Redish (1999) and the *hippocampal reinstatement theory (HRT)*.

The cognitive mapping theory has been widely accepted as a means for long-term spatial representation and memory mainly due to its underlying premise: coding of location and goal direction occurs in a universal manner, irrespective of a person's body-centred orientation, therefore yielding a less redundant and more flexible representation. This satisfies many problems such as memory capacity, detour and novel route behaviour, competency in novel environments and performance after viewpoint-change (Hartley *et al.*, 2003). Although the basic premise of a cognitive map is shared by most researchers, the qualities, capacity, anatomy and nature of such a map are topics of debate, and the interaction of representations within the brain is poorly understood (Roche *et al.*, 2005). The main issue for those taking an associative approach to spatial memory is not the concept of a cognitive map *per se*, but the mechanism through which place learning occurs. In fact, the idea of mental maps dates back to the earliest research on human spatial memory at the start of the twentieth century when Trowbridge (1913) investigated the use of "imaginary maps" by humans in orientation tasks. It was Tolman who coined the term "cognitive map" to describe internal mental representations of physical space that animals and humans use to find their way, especially to find novel shortcuts, when navigating in real-world situations (Tolman, 1948). Since then, this term has been used widely in the literature and has inspired a number of groups to explore the concept behind it.

Location is inherently relative. It has to be defined with respect to something, and the something is a spatial reference system. In psychology, many spatial reference systems have been proposed. There have been distinctions between intrinsic reference systems and deictic, object and scene-centered vs. viewer centered, absolute vs. relative, orientation-independent versus orientation-dependent. Several of these terms can be grouped as characteristics of allocentric representations: intrinsic, object/scene-centered, absolute, and orientation-independent. In this reference system, location is represented independently of the orientation of the observer and relative to objects or features within the environment. Other terms can be grouped as characteristics of an egocentric system: deictic, viewer-centered, relative, and orientation-dependent. Here location is represented in terms of the observer's location or orientation in space at the time in which it is learned. These *egocentric* and *allocentric* representations are the two main reference systems believed to underlie human spatial memory and the cognitive map (O'Keefe & Nadel, 1978; Klatzky, 1998; Maguire *et al.*, 1999). Their properties will be described in detail below along with a possible third *functional* reference system which receives its information from haptic sources, movement through an environment and knowledge of body position. Before this however, a description of the types of information available in the environment is given. This is the information we garner as we negotiate a map, view a scene or traverse a route.

1.2.1 Spatial knowledge

Spatial knowledge is acquired through the use of strategies which are implemented selectively depending on the information available within the environment. A distinction has been made between information sources, defined as *route* and *survey* (Siegel and White, 1975; Perrig and Kintsch, 1985; Tversky, 1991; Mellet *et al.*, 2000; Shelton and Gabrieli, 2002, Roche *et al.*, 2005). Route-based knowledge is perhaps the most available source of spatial information used by humans (MacEachren, 1992). It is characterized as knowledge of spatial layout from the perspective of a ground-level observer navigating the environment (Shelton & McNamara, 2001; Shelton & Gabrieli, 2002). Roche and colleagues (2005) define this knowledge as any information pertaining to the environment that is acquired as a result of physical navigation through the environment. This includes information from all the senses, with vestibular and proprioceptive inputs contributing to *path integration* (Tversky, 2000). The term path integration (PI) refers to the updating of position on the basis of velocity, temporal and acceleration information (Gibson, 1950; Loomis *et al.*, 1999; Etienne, 1992; Mittelstaedt and Mittelstaedt, 2001). Although PI is based on route information, the internal representation underlying it is very different from what is referred to as route knowledge (Loomis *et al.*, 1999) and it has been categorised as a parallel process to the egocentric strategy by Roche *et al.* (2005).

Survey knowledge is characterized by an external perspective, such as an aerial or map-like view, allowing direct access to the global spatial layout. In addition to learning a spatial layout through navigation and direct experience which can involve some or all of our senses, we can learn from secondary sources of information. Humans have evolved mechanisms to represent spatial information symbolically with maps, diagrams and

verbal descriptions (Gattis, 2001; Gauvain, 2001; Glasgow, Narayanan, & Chandrasekaran, 1995; Plumert, Ewert, & Spear, 1995; Taylor & Tversky, 1992; Uttal, 2000). It has been shown that cognitive maps constructed from these indirect, symbolic sources differ from those derived from direct, navigational experience in some ways (e.g., Thorndyke & Hayes-Roth, 1982; Streeter *et al.*, 1985) and yet are similar in other ways (e.g., Taylor *et al.*, 1999).

These distinctive knowledge sources are processed by dichotomous egocentric (i.e., ego-centered; body-centered) and allocentric (also referred to as exocentric, exocentered, or environment-centered) spatial strategies (O'Keefe and Nadel, 1978). An egocentric strategy refers to the discrimination of a spatial locus with reference to the body midline, vertical visual meridian, or relative self-movement whereas an allocentric strategy involves object-to-object relational processing, a much greater memory component, and use of a wider range of both perceived and non-visible cues (Hartley, Trinkler, & Burgess, 2004; Burgess, Spiers, & Paleologou, 2004; Roche *et al.*, 2005). Travel requires humans to activate both egocentric and allocentric processes to facilitate spatial knowledge acquisition: person-to-object relations that dynamically alter as movement takes place (egocentric referencing) and a more stable object-to-object allocentric strategy that anchors their cognitive map (Sholl, 1996). The result of the convergence of route-based and survey-based information gathered via egocentric and allocentric strategies (and PI) is a composite mental representation of the environment containing both types of knowledge, i.e. the cognitive map.

1.2.2 Mental representations

Gallistel (1990) suggested that allocentric (in his terms, geocentric) maps of a spatial environment are constructed from two lower-level processes. One is the construction of an egocentric representation, which he assumed to result from early perceptual processes. The second is PI, the process by which velocity or acceleration signals are integrated to keep track of a navigator's position in allocentric coordinates. Knowing their allocentric position in space and having the egocentric coordinates to other objects, navigators can build a map that allows the object-to-object relations to be represented allocentrically. Klatzky (1998) makes some core assumptions about the representations in the cognitive map, suggesting that allocentric and egocentric representations convey the layout of points in space by means of an internal equivalent of a coordinate system (which may be distorted or incomplete). The locational information provided by an allocentric representation is referenced to space external to the perceiver; the information provided by an egocentric representation is referenced to the perceiver (ego) with a definable axis of orientation. Specifically, the allocentric representation conveys the positions of points in the internal equivalent of Cartesian or Polar coordinates (Klatzky, 1998). The egocentric representation makes use of a special polar coordinate system in which the perceiver is at the origin and the reference axis is their axis of orientation; it conveys the location of a point by egocentric distance and the egocentric bearing. Roche *et al.* (2005) published a model of neurocognitive mapping which contained independent but interacting representational systems. They describe the characteristics of such a model from the anatomical (see section 1.4.1) to the cognitive level. Figure 1.2 is a reproduction of their model at the systems and processing level.

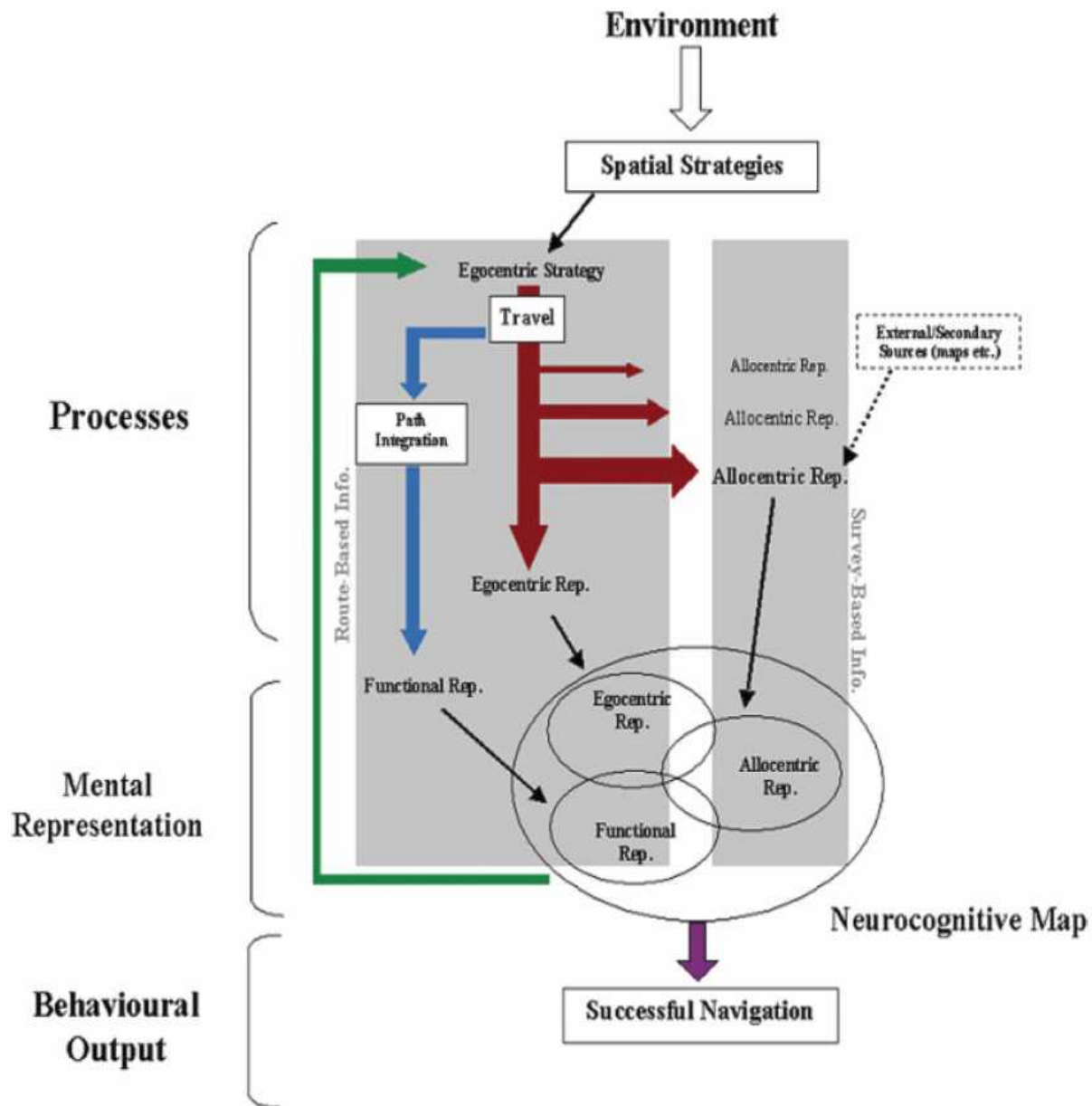


Figure 1.2 Flow diagram of the neurocognitive map showing the processing pathways that lead to mental representational development. Reproduced from Roche et al. (2005)

Their proposal - that there is a spatial representation system that consists of multiple parallel processes (pertaining to visual and motoric information) resulting in an integrated model - bears similarities to certain influential models within the animal literature, particularly O'Keefe and Nadel's locale and taxon representations (1978), Jacobs and Schenk's bearing, sketch and integrated maps (2003) and Whishaw's (1998) conception of path integration. The idea that an allocentric representation is constructed through

increased egocentric experience is consistent with Gallistel (1990) but the role of PI in the neurocognitive map is formalised by the conception of a separate but interacting functional representation rather than a direct role in allocentric representation. The validity for a separate functional representation has been verified in previous real-world experiments which tested the functional contribution from proprioception and vestibular input (e.g. Berthoz *et al.*, 1995; Israel *et al.*, 1997; Loomis *et al.*, 1993; Rieser *et al.*, 1989). Both parietal and temporal areas are posited to contribute to spatial location processing, engaging both an egocentric and allocentric frame of reference, respectively (with the functional reference playing a supporting role). All types of reference contribute to object-location memory, although in a summary of the literature, Postma *et al.* (2004) state that an emphasis is placed on the allocentric representation.

Spatial memory is schematic (Montello *et al.*, 2004) – shapes become more symmetric and regular over time, remembered as being more like familiar or typical shapes. Turns and angles are remembered as being straighter or more like right angles, an orthogonality bias that holds for both survey- and route-knowledge (Sadalla & Montello, 1989; Tversky, 1981). Spatial memory is most usually based on multiple learning sources (Tversky, 1993) and therefore requires an integration of representations in the cognitive map but just how these multiple sources are integrated is a critical issue (Montello *et al.*, 2004). The next section will introduce the concept of translation as a mechanism of interaction between representations which could reconcile differences in multiple source information.

1.2.3 Combining information for way-finding and object-location

The presence of multiple representations raises the question of how they interact (Roche *et al.*, 2005). Waller and Hodgson (2006) manipulated angular change for participants who were required to view and point to object locations. An increase in pointing error variation occurred after 135° but not after 90° or less, indicating a switch from one system to the other, rather than a compromise. Burgess (2006) however notes that:

Whereas egocentric systems can be used alone, the egocentric nature of perception and imagery require that input to and output from allocentric systems are mediated by transient egocentric representations. Conversely, action-oriented egocentric representations must be derived from enduring allocentric representations following long or complicated self-motion. (Burgess, 2006, p. 555)

This suggests a cooperative relationship with an implied process of translation between the systems (e.g. between environmentally defined north and south and body-referenced left and right). Roche *et al.* (2005) describe in detail the parallel paths of egocentric and allocentric processing, specify a role for functional information and propose experimental manipulations to test relationships between these systems but actual interaction between representations (i.e. the egocentric → allocentric translations suggested by Burgess, 2006) are unfortunately absent from their descriptions. This process of translation, as a mechanism for interaction between representations, is highlighted in the model of spatial encoding and retrieval shown in Figure 1.3. This model by Burgess *et al.* (2001) suggests this mediating role is subserved by posterior parietal areas in mental representation.

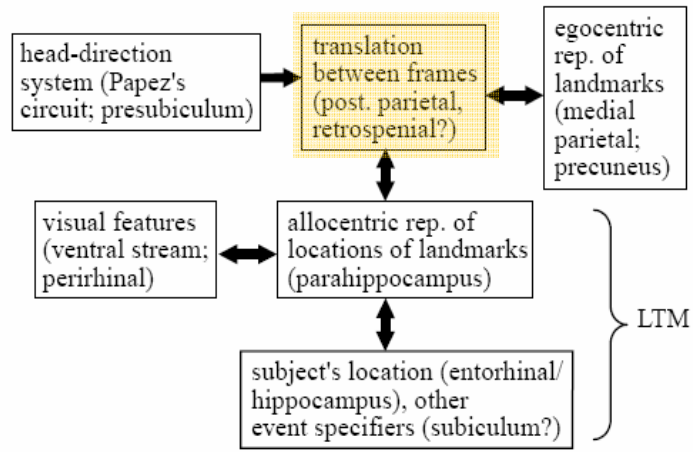


Figure 1.3 *The functional architecture of another model of spatial memory specifying a role for translational processes between representations and suggesting a location within the brain where these translations occur (highlighted box). Adapted from Burgess, Becker, King and O'Keefe (2001). LTM, long-term memory; post., posterior; rep., representation*

The concept of translations between representations has in recent years received growing interest in studies of spatial updating (Sholl and Nolin, 1997; Wang and Brockmole, 2003; Mou *et al.*, 2004; Waller and Hodgson, 2006; Cheng, 2005; Byrne *et al.*, 2007). Egocentric movement-related spatial updating is believed to maintain the percept of a stable world from moment to moment but reliance over long distances on such egocentric representations is shown to result in increased error (Etienne *et al.*, 1996; Waller *et al.*, 2003; Wang and Brockmole, 2003). Burgess (2006) echoes the opinions of many researchers by suggesting that over time people can negotiate large-scale environments with high accuracy through the construction of an enduring allocentric representation (from temporary egocentric representations). This highlights a time-sensitivity in how we combine information through the ego/allocentric relationship.

A number of methods have been employed in order to better understand how we integrate and use spatial information. The next section reviews techniques used throughout the spatial research literature and reports findings from a wide range of studies which inform us of the processes underlying spatial memory and help answer the question, 'How do we find our way and remember where things are?'.

1.3 Spatial Research: Paradigms and Methodologies

1.3.1 *Clinical and lesion studies*

Although most contemporary theories of memory accept that memory is most likely distributed throughout the cortex (see the overview of human memory), there remains a debate over the structures involved in the initial memory formation and those involved in retrieval; Early studies of brain pathology and memory disorders revealed the importance of the hippocampus in the process of consolidation. Korsakoff syndrome (Korsakoff, 1887-1891; Gudden, 1896), caused by alcoholism, malnutrition and the consequential thiamine deficiency, leads to anterograde amnesia due to hippocampal decay. Bekhterev (1900) was the first to attribute this memory function to the hippocampus but its importance in memory was not fully realised until patient HM.

HM suffered from intractable epilepsy and, after several *grand mal* fits following his 16th birthday, he was referred to Hartford Hospital for treatment. In 1953 (11 years later) he underwent a surgical resection of his medial temporal lobes and as a result he suffered from severe anterograde amnesia: although his short-term memory was intact, he could not commit new events to long-term memory. However, his ability to form long-term procedural memories was still intact (Scoville & Milner, 1957). This dissociation between short-term and long-term memory and declarative and non-declarative memory were not the only discoveries about memory and the brain thanks to HM. Corkin and colleagues (2002) present a review of the studies carried out on HM and the major findings are shown in the timeline in Figure 1.4 (Reproduced with permission from Corkin *et al.*, 2002). But what specifically has the study of HM told us about the role of the hippocampus in spatial memory?

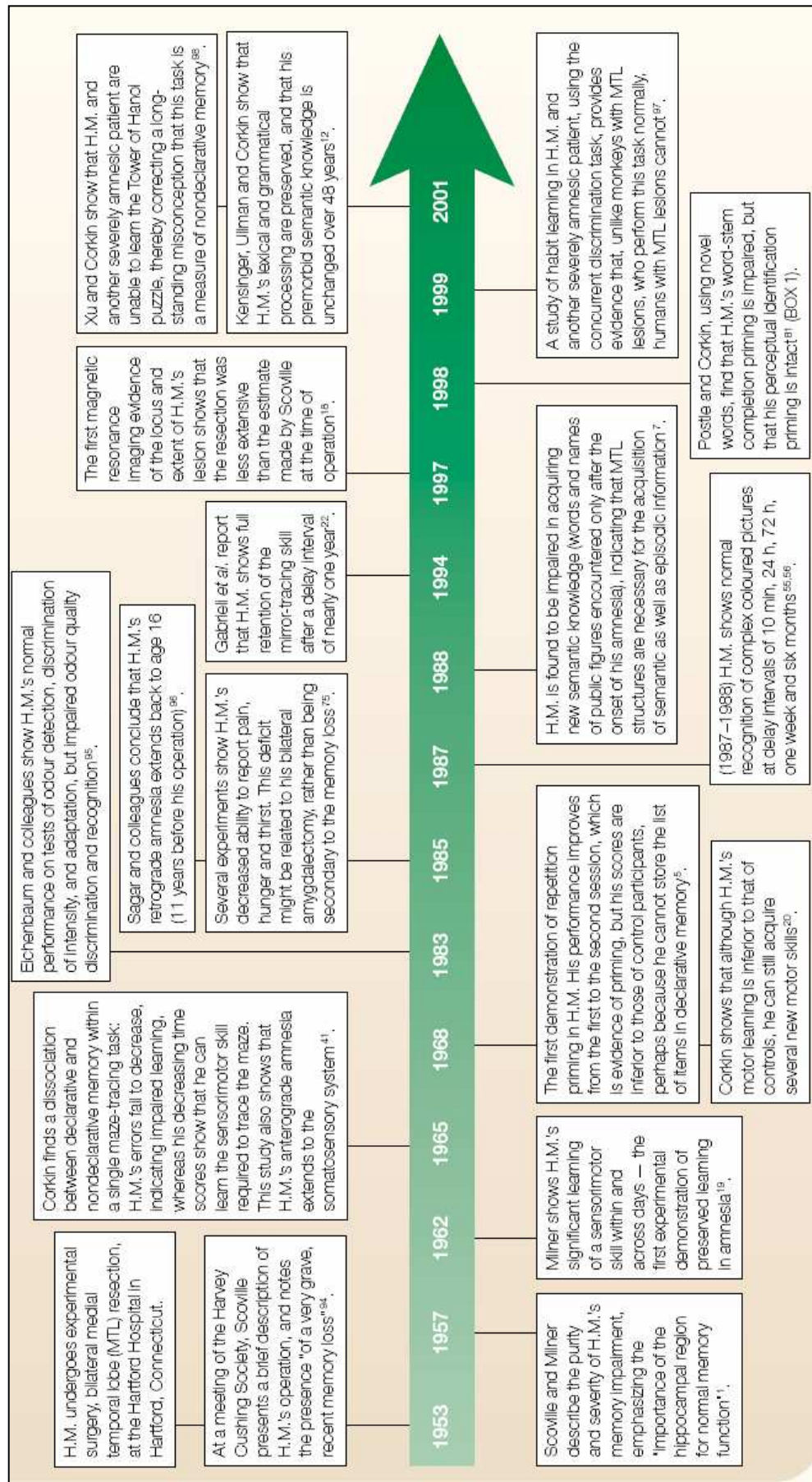


Figure 1.4 A timeline summary of experimental findings related to the study of H.M. Reproduced with permission from Corkin *et al.* (2002)

Examining spatial memory performance in patients with medial temporal lesions, Ploner *et al.* (1999, 2000) downplay the role of the hippocampus for spatial memory and highlight a parahippocampal involvement. Spatial memory function in extrahippocampal MTL sub-regions has previously been suggested (Smith & Milner, 1989; Rains & Milner, 1994). HM was in fact able to draw the layout of an apartment which his family had moved into after his operation, meaning he had preserved topographical memory (McClelland *et al.*, 1995). This knowledge is in marked contrast to HM's striking inability to incorporate other new information into declarative memory. Other hippocampally-damaged patients (Teng & Squire, 1999; Rosenbaum *et al.*, 2000) have shown an inability to form new topographical memories after the onset of amnesia. It was posited that through his repeated exposure to the house (over years) and his locomotion between the rooms, HM built an allocentric representation of his house enabling his topographic recall (Corkin *et al.*, 2002). However, his lesioned MTL caused severe impairments on other spatial tasks which included learning the correct sequence of turns in a visual (Milner, 1965) and a tactile (Corkin, 1965) stylus maze.

It has been suggested that HM could learn and store topographical information due to the sparing of certain brain structures: namely the medial parietal lobule, posterior cingulate gyrus, occipitotemporal areas and the spared posterior 2cm of his parahippocampal gyrus (Corkin *et al.*, 2002). These areas along with the right hippocampus have been identified elsewhere for their role in topographical learning and memory (Habib & Sirigu, 1987; McNaughton *et al.*, 1994; Aguirre *et al.*, 1996; Maguire *et al.*, 1996; Maguire, 1997; Maguire *et al.*, 1997; Epstein & Kanwisher 1998; Maguire *et al.*, 1998 Epstein *et al.*, 1999; Barrash *et al.*, 2000). In a review of lesion studies by Maguire (2001), the posterior cingulate (also referred to as the retrosplenial cortex in rats)

was concluded to be a crucial structure for topographical memory and human navigation. Another human lesion study reported the right parahippocampus as a necessary structure for spatial memory (Bohbot *et al.*, 1998). The connectivity of the parahippocampal, posterior parietal and retrosplenial cortices has been demonstrated (at least in monkeys) by Suzuki and Amaral (1994), evidence this region could be a part of a spatial circuit.

The case of 'Jon' is another example of a hippocampally-damaged patient who has been studied by various researchers assessing the effect of hippocampal pathology on spatial memory (Bird, Vargha-Khadem & Burgess, 2007; Hartley *et al.*, 2007; King *et al.*, 2002, King *et al.*, 2004, Kumaran *et al.*, 2007). Jon has bilateral hippocampal pathology due to perinatal anoxia, resulting in what has been termed developmental amnesia (Gadian *et al.*, 2000; see also Baddeley *et al.*, 2001; Maguire *et al.*, 2001, and Vargha-Khadem *et al.*, 2003). The study by King and colleagues (2002) is of particular interest for spatial research. Jon was found to have grossly impaired object-location recognition for shifted viewpoints in a virtual reality environment. The authors suggested that the shifted-view condition required a viewpoint independent representation or an equivalent mechanism for translating or rotating viewpoints in memory and based on Jon's performance they concluded that the hippocampus supports viewpoint independence in spatial memory by providing a mechanism for viewpoint manipulation. Possible difficulty confounds between the same- and shifted-viewpoints was accounted for by King *et al.* (2004), where all views were made equally difficult. A similar impairment was reported by Burgess *et al.* (2006) for patient CF, believed to be in the early stages of Alzheimer's disease (AD) and showing topographical disorientation. The authors observed a dissociation between her spared verbal and recognition memory for unknown buildings, landmarks and scenes and her severely impaired navigational ability

in a virtual reality task. In addition, they observed an impairment in her allocentric processing as her object-location memory was severely affected when tested from a shifted viewpoint compared to when tested from the same viewpoint as presentation (similar to King *et al.*, 2002). Burgess *et al.* (2006) suggest that the deficit in allocentric memory for object-location results in patient CF's navigational impairment. They speculate that damage to the hippocampus or entorhinal cortex, consistent with AD (Braak & Braak, 1991), may underlie the patient's impairment, though no such damage was evident on the MRI scans. Therefore, it may be that shifted-viewpoint tests are sensitive indicators of early stage neurodegeneration, flagging cases even before the pathological signs present themselves.

Hartley *et al.* (2007) examined the hippocampal contribution to perception and short-term memory for topographical and non-spatial information in scenes. They tested patients with focal hippocampal lesions, namely Jon and patients KC3, VC, RH and MH. All five patients showed impaired topographical memory and spared non-spatial processing in both memory and perception. Topographical perception was profoundly impaired in the patient MH whose damage was more extensive including the parahippocampal cortex. These results again support the role of the hippocampus (and parahippocampus) in allocentric topographical processing and mental representation.

Finally, in a recently published study on spatial learning and memory in schizophrenia patients, Weniger and Irle (2008) used virtual reality environments to assess allocentric (virtual park) and egocentric (virtual maze) memory. Compared to controls, the schizophrenia patients were only significantly impaired at learning and navigating the park. They suggest that the underlying declarative hippocampal memory system, affected in schizophrenia, is responsible for allocentric impairments.

1.3.2 Human navigation studies

In addition to the migratory and wayfinding behaviour in animals (not talked about here), navigational research in humans has contributed valuable information to our overall understanding of spatial processing and memory. Differences and similarities have emerged in the strategies we use to navigate compared to other species, the strategies available to us due to our use of language, symbols, abstractions and technology, and those unavailable to us due to our biological make up (e.g., perceiving the polarization of sunlight in the atmosphere). Navigation is described as coordinated and goal-directed movement through an environment and is comprised of two behaviours, locomotion and wayfinding (Montello, 2005). Locomotion here refers to the actual movement through the environment and it can be observed in many forms, from the various methods of self propulsion to the use of motorized aides. This is underpinned by non-declarative or procedural knowledge. Wayfinding is the more interesting behaviour in terms of spatial cognition in that it encapsulates the goal-directed element of navigation. This is the behaviour which relies on declarative knowledge, stored internally in the brain or externally in maps. These knowledge systems interact with various cognitive processes, which in turn interact with the various forms of incoming sensory information to produce outgoing motor commands and locomotion to the desired goal.

Some of these ‘cognitive processes’ have been identified for humans and have been discussed in detail earlier in this chapter in relation to cognitive maps (section 1.2). Like animals, but in a far lesser capacity than some, we have the ability to use path integration or dead reckoning, an ability incorporated into our putative functional representation of the environment. Locomotion through an environment also feeds into our egocentric and allocentric representations with proximal and distal cues informing us

of our position. Familiarity with a space and salient landmarks also improve our navigational abilities (Siegel & White, 1975; Acredolo & Evans, 1980; Kirasic, 1989; Ark *et al.*, 1998; Roche *et al.*, 2005). Researchers from numerous fields (e.g., psychology, neuroscience, geography, cartography) have approached the study of human navigation in a variety of ways (e.g., real-world and virtual reality navigation, blind navigation, map reading and distance estimate tasks) with a variety of goals. The studies outlined here all share the goal of understanding the brain areas and activity underlying navigation.

The medial temporal lobe structures have been implicated in navigation, and there has been a special focus on the hippocampus since publication of the Cognitive Map Theory proposed by O'Keefe and Nadel (1978). Navigation in virtual environments has offered an insight into the role of the hippocampus, with studies suggesting the left HF has a more verbal role in navigation while the right HF computes a vector that continuously points to the goal direction (Burgess & O'Keefe, 1996, Maguire *et al.*, 1998). Virtual environments have also been used to study passive navigation (e.g. Harris *et al.*, 2000; Gaunet *et al.*, 2001). Gaunet and colleagues (2001) examined spatial memory of a virtual city using active, passive and snapshot exploration methods. They found that the reproduction of the path shape was affected by the exploration method, with greater total distance and angle reproduction error scores following snapshot exploration than active and passive explorations. They suggested that the disadvantage of snapshot information was the difficulty of mentally updating the route between shots.

Blind navigation studies allow the investigation of path integration and the functional representation without the primary input to the egocentric strategy (i.e. vision). Information about step length, derived from proprioceptive or motor efferents, as well as

from vestibular signals can contribute to the updating of the mental representation of the subject's location in space and allow for path integration (Mittelstaedt & Glasauer, 1991; Glasauer *et al.*, 1994). A study by Israel and colleagues (1997) used a clever method of passive transport to investigate non-visual linear distance memory (used for path integration). Blindfolded participants used a joystick-controlled robot to move themselves along linear trajectories. They were asked to reproduce specific, previously-experienced distances in the dark. Subjects were able to accurately reproduce stimulus distances, durations, peak velocities and velocity profiles. Accurate distance estimation was attributed to the integration of the otolith signal (a structure in the vestibular labyrinth of the inner ear). The results of this study showed that vestibular and somatosensory cues provided during passive transport contribute to static and dynamic representations of a travelled path.

Neurological measures of real-world navigation are difficult to achieve and usually involve before and after the fact comparisons with some form of recall or rehearsal task (e.g., Burgess *et al.*, 2002; Ghaem *et al.*, 1997; Maguire *et al.*, 1996, 1997). Increases in hippocampal activity have been reported when subjects learned how to navigate through a real town. A study involving London taxi drivers with sophisticated knowledge of the city showed increased activations of the right hippocampus (Maguire *et al.*, 1997). Similar to the animal research showing hippocampal volume differences in food storing species, navigation-related structural change has been found in humans, namely taxi drivers (Maguire *et al.*, 2000). The 'London Taxi-driver study' showed that the posterior hippocampi of taxi drivers were significantly larger relative to those of control subjects. This finding is in accordance with the idea that the posterior hippocampus stores a spatial representation of the environment and can expand

regionally to accommodate elaboration of this representation in people with a high dependence on navigational skills. A PET study by Ghaem *et al.* (1997) using a Mental Simulation of Routes task corroborated these findings. Engaging in mental navigation along a learned, real-world route activated the right middle hippocampal areas, as well as the posterior hippocampal areas bilaterally.

However, Teng and Squire (1999) found unimpaired spatial and topographic memory in patient EP who had extensive damage to his medial and anterior temporal lobes concluding that the medial temporal lobes were not the repository of remote spatial memories. Recent findings also offer an alternative role for the hippocampus in navigation, maintaining its involvement in the process but reducing its importance. Maguire *et al.* (2006) tested the navigation ability of a London taxi driver (TT) who had sustained bilateral hippocampal damage. They found that the hippocampus was not required for general orientation in the city either in first person or survey perspectives, or for topographical knowledge of landmarks and their spatial relationships, or even for active navigation along some routes. They concluded that it was necessary only for ‘facilitating’ navigation in places learned long ago, particularly where complex large-scale spaces are concerned, and successful navigation requires access to detailed spatial representations. Many researchers have postulated a time-sensitive, facilitating role for the hippocampus in memory formation (Squire & Alvarez, 1995; Squire *et al.*, 2001; Bayley *et al.*, 2003, 2005; Maviel *et al.*, 2004; Roche *et al.*, 2005) but continue to argue over the details of such involvement (see the overview of memory theories in section 1).

In contrast to hippocampally-subversed allocentric processing, egocentric encoding of space has been shown to recruit a fronto-parietal network along the dorsal stream (Committeri *et al.*, 2004; Galati *et al.*, 2000; Wilson, Woldorff, & Mangun, 2005).

The posterior parietal lobe (Andersen, 1997) and dorsal striatum (Wiener, 1993; Devan *et al.*, 1996; Potegal, 1982) have been implicated as possible elements of a navigation system, providing complementary egocentric representations. The role of the parietal lobes in egocentric processing was recently explored by Seubert *et al.* (2008), who implicated their importance (over the frontal elements of the system) in route negotiation.

Experiments investigating route-following and response learning in way-finding have highlighted the involvement of different brain structures outside of the temporal lobes (Cook & Kesner, 1988; Kesner *et al.*, 1993; Ghaem *et al.*, 1997). One such study by Hartley *et al.* (2003) used *fMRI* to measure brain activity in participants as they explored in or followed a well-learned route through a virtual town. They showed that wayfinding and route following involve different forms of representation with correspondingly distinct neural bases. Route-following was reported to engage the insula, caudate body, and lateral parietal/somatosensory cortex, premotor cortex and SMA with no involvement of the medial temporal lobes. The caudate is part of the basal ganglia which is known for its role in habit learning (Knowlton *et al.*, 1996; Packard & Knowlton, 2002). Poldrack *et al.* (2001) provided evidence for a competitive or interfering interaction between the caudate nucleus and the hippocampus for wayfinding. In an attempt to assess this interaction, Voermans *et al.* (2004) measured caudate and hippocampal activity with *fMRI* in patients with Huntington's disease (which detrimentally affects caudate functioning) and normal controls. A non-competitive interaction between the two systems was observed in the controls, an interaction which could be commandeered by the hippocampus to compensate for caudate damage in the patients with Huntington's disease.

1.3.3 Spatial arrays and table-top tasks

Small-scale spatial studies have the advantage of a stationary participant which simplifies administration (to large populations) as with paper-and-pencil tasks (e.g., the Mental Rotations test: Vandenberg & Kuse, 1978; and the Object Location Memory test: Eals & Silverman, 1994; Silverman & Eals, 1992) and more recently the use of neurophysiological and neuroimaging measures. These studies have moved from tests of mental rotation and visuo-spatial awareness in IQ testing to the exploration of viewpoint and movement changes in spatial memory and representation, as well as landmark salience and geometric cues for object-recognition. They have facilitated investigations into egocentric and allocentric processing differences and enabled the study of mental representation with and without the influence of vestibular information from the functional representation.

Wang and Simons (1999) showed that participants' recognition memory for a table top array of objects was better after they had moved around the table to a new viewpoint than after an equivalent rotation of the tabletop. This was interpreted as evidence for an egocentric automatic updating process driven by the active motion of the viewer. However, a replication of this result using purely visual virtual reality (Christou & Bulthoff, 1999) indicates that the important variable is movement of viewpoint relative to a participant's cognitive model of the world rather than actual movement and the concordant vestibular/proprioceptive feedback or movement of the objects relative to the subject. Wang and Spelke (2000) further explored how locations of objects in the environment may be represented. Participants studied locations of objects placed outside the test chamber. Then from inside the chamber they were required to specify where the now hidden objects might be (either when they were oriented or disorientation after

rotation). Absolute (i.e. heading) and relative (i.e. configurational) accuracy of responses was measured. Disorientation increased both heading and configurational errors whereas the presence of a light cue throughout the study produced the opposite effect. They concluded that object locations, including distances and directions, are represented egocentrically and are updated on a continual basis during movement. This conclusion supports a previous finding that participants' response latencies vary linearly with the angular difference between studied and novel views for scenes (Diwadkar & McNamara, 1997).

However it was proposed by Sholl (1987) that object arrays could be encoded in an orientation-free manner. Support for this comes from recent studies which have found that humans can represent objects on a table top array in an allocentric manner. Burgess, Spiers and Paleologou (2004) asked subjects to assess any changes in position of common objects within an array on a table after spending a period of time in the dark during which the objects, the table, the subject, and/or an externally placed fluorescent card could have been moved. Results suggested that, in addition to an egocentric representation, object locations can be represented relative to visual landmarks placed outside the array of interest (i.e. via allocentric representation). Other studies have shown that the location of objects might also be stored in representations oriented with respect to landmarks or intrinsic axes in the external environment (Mou & McNamara, 2002; McNamara *et al.*, 2003), again providing evidence for an allocentric representation of object location but suggesting an orientation-dependence. Burgess (2006) reviewed recent experiments on pointing errors (Waller & Hodgson, 2006) and reorientation (Mou *et al.*, 2006), and concluded that the effects attributed to an egocentric system by Wang

and Spelke (2000) could more readily be explained by a two-system model which included both ego- and allocentric representations.

Egocentric/allocentric dissociations have been studied in a litany of ‘shifted-viewpoint’ (or ‘viewpoint-dependant’) studies using stimulus arrays (Johnsrude *et al.*, 1999; King *et al.*, 2002, 2004; Burgess *et al.*, 2006). There is agreement amongst these studies that allocentric processing underlies performance on shifted-viewpoints rather than the use of simple mental rotation as proposed by Diwadkar and McNamara (1997). However there is still no consensus on the role of the hippocampus in these tasks. The studies by King *et al.* (2002, 2004) were replicated using hippocampally-damaged patients and controls, and it was reported that memory load adversely affected the hippocampal patients’ performance across all viewpoints, suggesting that damage to the hippocampus does not selectively impair viewpoint-independent spatial memory (Shrager *et al.*, 2007). The conclusions of Shrager and colleagues seem to be based solely on accuracy data. Alternative strategies may have been employed by the hippocampally damaged patients that levelled out their accuracies on trials from shifted viewpoints. And they may have taken longer on these trials to accomplish correct recognition. This, regrettably, is undeterminable as reaction times are not reported.

Another group of studies have employed virtual mazes to assess performances in small-scale local space. These have included the use of Virtual Morris Water Mazes (VMWM - e.g. Astur, Ortiz, & Sutherland, 1998; Hamilton, Driscoll & Sutherland, 2002; Hamilton & Sutherland, 1999) as well as Virtual Radial Arm Mazes (VRAM - e.g. Astur, Tropp, Sava, Constable & Markus, 2004; Levy *et al.*, 2005). An important study by Hamilton *et al.* (2002) attempted to replicate a study conducted by Sutherland *et al.* (1987) on rats, instead using the human virtual water maze task. The aim was to assess

the characteristics of human mental representations. Participants were trained in one half of a virtual pool to find a hidden goal. They either had access to the other half with a full range of distal cues available to them or were restricted to the goal half (region 1) during training. Participants were then tested to find a hidden goal in the other half of the pool (region 2). Accurate transfer, from region 1 to region 2, in locating the hidden goal was found to be dependent on prior exposure to the distal cues in region 2 while training in region 1. This result contradicts an earlier study which supported the idea of topographical representations in VMWM (Jacobs *et al.*, 1997) and disputes the automatic formation and modification of the cognitive map as proposed by O'Keefe and Nadel (1978). The results were instead explained by an associative effect similar to that proposed by CAT (Rudy & Sutherland, 1995; Sutherland & Rudy, 1989), where "accurate place navigation depends upon the establishment of associations between views of distal stimuli and the execution of specific trajectories to the goal" (Hamilton *et al.*, 2002, p. 169). A comparative review of human virtual and animal maze studies shows preliminary support for an associative learning role in spatial memory (Kelly & Gibson, 2007) but the authors stress that the evidence is not yet strong enough to refute cognitive mapping theory.

One point, however, is clear from this synopsis of small-scale spatial studies: orientation-dependence in spatial representation remains a hotly-debated issue. Based on five studies, Sholl and Nolin (1997), suggest that orientation-free performance is only evidenced under a certain set of conditions including a horizontal viewing angle during encoding, a room-sized test space, and "on-path" testing. There is indeed a growing body of evidence, mainly from Timothy McNamara's laboratory (e.g. Diwadkar & McNamara, 1997; Shelton & McNamara, 1997; Shelton & McNamara, 2001a, b; McNamara, Rump

& Werner, 2003) against the idea of the orientation-free representations proposed by Sholl (1987). Our cognitive map seems to take advantage of a variety of different reference frames (e.g., egocentric, intrinsic or environmental) to determine this orientation-dependence, but this evidence only implies the imposition of a 'preferred' viewpoint/orientation onto a more general allocentric representation. There is general agreement about the enduring allocentric representations incorporating numerous experienced viewpoints to allow flexible and adaptive spatial behaviours.

1.3.4 Electrophysiological studies

Electrophysiological research on spatial navigation can provide insight into the neural basis of way-finding within an environment. Many researchers have used this recording method to study brain oscillations relating to spatial memory and navigation. Specific oscillatory rates, such as the theta (θ) band (4 - 8 Hz range; Caplan *et al.*, 2003), are elicited during certain cognitive functions. Theta is usually associated with successful memory encoding, but it is also involved in navigation. A clinical study using intracranial electrodes tested the navigational ability of epilepsy patients on virtual T-mazes (Kahana *et al.*, 1999). The authors found increased theta activity associated with maze complexity during test rather than study phases, suggesting a role in spatial memory retrieval. A similar study by Caplan *et al.* (2001) also found theta activity related to maze complexity, and in addition found that lower and higher oscillations, delta and gamma (respectively), were related to memory processes such as encoding and retrieval. In a follow-up study, Caplan *et al.* (2003) also looked at theta rhythms during spatial navigation using a virtual town paradigm where the epileptic patients performed as virtual taxi drivers. They found a particularly strong increase in theta specifically during periods of integration between sensory information (such as optic flow during movement) and motor planning (such as finding a target location). The authors suggest that gamma (γ 20 - 30 Hz) activity underlies the memory related processing of sensory information and beta (β 13 - 20 Hz) underlies motor planning, while theta coordinates these oscillations.

Numerous studies using scalp electrodes have also examined the role of theta activity in spatial cognition. Nishiyama and Yamaguchi (2001) found theta activity in two distinct areas, the frontal region and the temporoparietal region, in subjects navigating a virtual maze. They propose that this theta activity is indicative of the

functional connections between the hippocampus, prefrontal cortex, and parietal cortex that may be involved in human spatial cognition. Also using scalp EEG and T-mazes (similar to Kahana *et al.*, 1999), Bischof and Boulanger (2003) found theta to increase when new spatial information is acquired. The strength of the evidence linking theta to spatial processing has led Buzsaki (2005) to refer to this frequency band as the ‘navigation rhythm’. The contribution of theta oscillations is reviewed by Kahana (2006).

Alpha (α 8 - 12 Hz) and theta phase locking occurs during the same epoch as the P1 and N1 waves (Klimesch *et al.*, 2004), and therefore these oscillations have a large effect on P1 and N1 amplitude. These components have been associated with early visual recognition, and are evoked by stimuli presented in different parts of the visual field (Townsend, Harris & Courchesne, 1996). A prominent late positive component (LPC) is normally seen after the appearance of the early visual response peaks (Makeig *et al.*, 1999). In event-related potential (ERP) studies, the P300 is considered an example of an LPC denoting attentional activity (Sutton *et al.*, 1965; Donchin & Coles, 1988; Duncan-Johnson & Donchin, 1977). Donchin and Coles (1988) have proposed a context-updating model in which stimuli that are more rare and task-relevant than other stimuli will produce a larger P300 component in the ERP waveform at electrode locations on the right parieto-occipital portion of the scalp. This old/new effect has been reported by many EEG studies using event-related potentials and has been linked to recognition memory in general (reviewed in [Johnson Jr., 1995; Rugg, 1995; Friedman & Johnson Jr., 2000; Mecklinger, 2000; Rugg & Allan, 2000]).

Mecklinger (1998) demonstrated functionally dissociable object and spatial visual working memory systems associated with spatiotemporally distinct event-related potential old/new effects (see also Mecklinger & Meinshausen, 1998). This dissociation

is manifested in parietal-occipital P300 differences for spatial processing as opposed to differences observed in early frontal negativity (FN400) as well as P300 for object and verbal stimuli. Mecklinger (1998) suggested that the frontal maximal N400 evoked by new objects is possibly associated with their integration into an already present conceptual-semantic context. In contrast, the P300 is associated with the accessibility of memory representations during recognition judgements. Other studies have reported topographic ERP differences in working memory dependent on information type (Bosch *et al.*, 2001; Lang *et al.*, 1987; Mecklinger & Pfeifer, 1996; Ruchkin *et al.*, 1992; Rugg *et al.*, 1987).

Single cell recording has also been used to study spatial processing. Ekstrom *et al.* (2003) found support for the role of the hippocampus in allocentric representation using single unit recording and also discovered human cells somewhat analogous to ‘place’ cells found in rodents (O’Keefe & Dostrovsky, 1971). Cells that responded at specific spatial locations were found primarily in the hippocampus while cells that responded to views of landmarks were found in the parahippocampal region (Ekstrom *et al.*, 2003). The authors suggest that the parahippocampal region collects local view information, regarding landmarks for example, and then outputs to the hippocampus which uses spatial and visual information to form a view-independent representation of space.

In summary, electrophysiological studies have helped define the brain regions involved in spatial memory and navigation as well as elucidating the temporal functioning of these regions. They have aided theory development from the cell to the systems level with the identification of spatially-mediated components (Bosch *et al.*, 2001; Lang *et al.*, 1987; Mecklinger, 1998; Mecklinger & Meinshausen, 1998; Mecklinger & Pfeifer, 1996; Ruchkin *et al.*, 1992; Rugg *et al.*, 1987). Consistent with the

other human and animal studies reviewed in this introduction, the medial temporal lobe structures as well as parietal areas are again implicated in spatial cognition. Medial temporal, parietal and frontal regions are posited to function together to enable route-following, construction of novel routes, planning and decision-making, and integration of sensorimotor information for egocentric-based and allocentric-based navigation (Kahana *et al.*, 1999; Caplan *et al.*, 2001; Caplan *et al.*, 2003; Nishiyama & Yamaguchi, 2001; Bischof and Boulanger, 2003). Electrophysiology is an invaluable method for exploring the properties of human “cognitive maps”, and a rich picture of brain dynamics has emerged from the research to date (Kahana, 2006).

1.4 Neuroanatomical bases of mental representation

1.4.1 Summary of the Neuroanatomical findings

The unenviable task of summarising the findings of spatial experiments going back three decades into discrete anatomical substrates and their proposed contributions is best attempted in a table and diagram format. The cortices identified in Figure 1.5 below have all been implicated in spatial processing and memory and Table 1.1 lists some of these structures, their roles and the studies reporting their involvement.

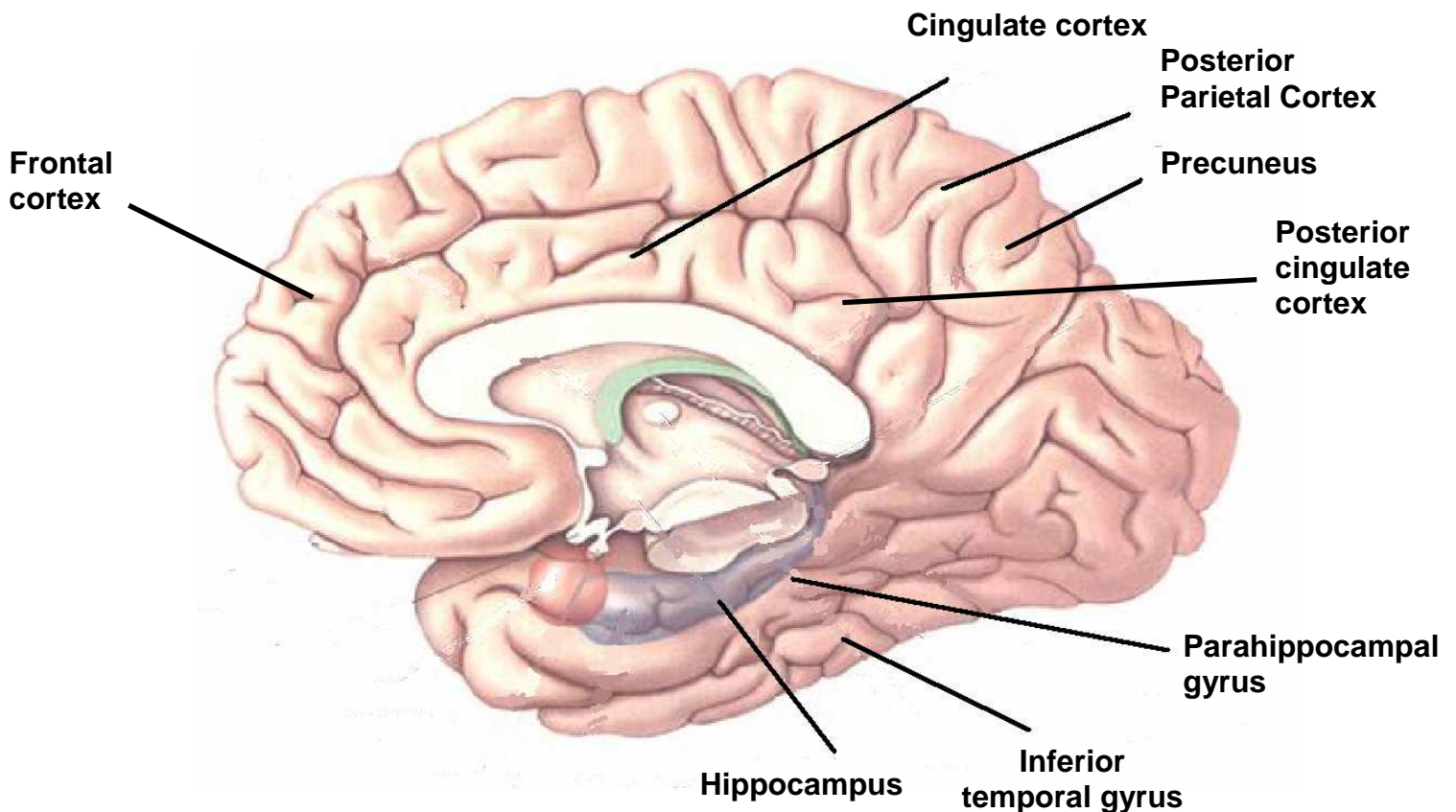


Figure 1.5 Illustration of a sagittal slice of human brain exposing the ventro-medial surface of the cortex with brain areas purported to be involved in spatial memory marked by arrows.

Table 1.1 Summary of structures implicated in spatial memory processes citing the studies that suggested their involvement

| | | Process / Role | | | | | | | | |
|-----------------|------------|---------------------------|----------------|----------------------------|---|-------------------|---------------------|-------------|-----------------|--|
| Lobe | Structure | Egocentric representation | | Allocentric representation | | | | Translation | Navigation | |
| | | Route knowledge | Ego-processing | Object-location | Topographical map | View manipulation | Spatial context | | Route following | Way-finding |
| Frontal | PreF | 6, 28, 31 | 6, 28, 31 | | 31, 32 | | | | 6, 28, 31 | 32 |
| Temporal | ITG/FUS | 25, 28 | 28 | | 28 | | | | 28 | 25 |
| Medial Temporal | HF | 6 | 6 | 10, 16 | 1, 2, 3, 8, 10, 16, 17, 19, 23, 30*, 32, 33 | 7, 8, 24 | 1, 2, 3, 10, 17, 19 | | 6, 7 | 1, 2, 3, 7, 8, 12, 22, 26, 28, 30*, 31, 32 |
| | PHG | | | 4, 9, 10, 11, 15 | 4, 5, 10, 15, 23, 32 | | 4, 5, 9, 10, 11 | | 9 | 5, 9, 11, 12, 28, 32 |
| | Sub/PreSub | 13, 14, 18 | 13, 14, 18 | | | | | 14 | | |
| Parietal | PPC/SPL | 25 | | | 23, 28, 31 | | | | 26 | 25 |
| | IPL | | | | 23, 31 | | | | 12, 26 | |
| | PreC | 6, 31 | 6, 31 | | 29 | | | | 6, 31 | 29 |
| | SMA | | | | | | | | 26 | |
| Occipital | OTC | | | | 31 | | | | 26 | 31 |
| Other | PCG | 6 | 6 | | 20, 23 | | | | 6, 20 | 20 |
| | INS | | 6 | | | | | | 6, 26 | |
| | CAU | | | | | | | | 26, 27 | 21, 27 |

PreF – Prefrontal cortex
ITG – Inferior temporal cortex
FUS – Fusiform gyrus
HF – Hippocampal formation
PHG – Parahippocampal gyrus
Sub – Subiculum
PPC – Posterior parietal cortex
SPL – Superior parietal lobule
IPL – Inferior parietal lobule
PreC – Precuneus
SMA – Supplementary motor area
OTC – Occipito-temporal cortex
PCG – Posterior cingulate gyrus
INS – Insula
CAU – Caudate

23. O’Keefe & Nadel (1978)
24. McNaughton et al. (1994)
25. Maguire et al. (1996)
26. Owen et al. (1996)
27. Warrington (1996)
28. Ghaem et al. (1997)
29. Rolls et al. (1997)
30. Vargha-Khadem et al. (1997)
31. Aguirre et al. (1998)
32. Bohbot et al. (1998)
33. Epstein & Kanwisher (1998)

12. Maguire et al. (1998)
13. Taube (1998)
14. Burgess et al. (1999)
15. Johnsrude et al. (1999)
16. Nunn et al. (1999)
17. Redish (1999)
18. Robertson et al. (1999)
19. Burgess et al. (2001)
20. Maguire (2001)
21. Poldrack et al. (2001)
22. Spiers et al. (2001)

1. Corkin et al. (2002)
2. King et al. (2002)
3. Shelton & Gabrieli (2002)
4. Hartley et al. (2003)
5. Voermans et al. (2004)
6. Roche et al. (2005)
7. Frings et al. (2006)
8. Maguire et al. (2006)
9. Zaehle et al. (2007)
10. Antonova et al. (2008)
11. Weniger & Irle (2008)

*Maguire *et al.* (2006) concluded HF involvement dependent on environmental complexity. This study in fact suggested the HF is not necessary for gross topographical mapping or general wayfinding

For the purpose of conciseness and clarity, anterior/posterior and left/right distinctions were not made when listing the relevant brain structures. Many of the studies listed are, in fact, more precise with their reported findings. Unfortunately the precision with which researchers identify brain activations is not shared in their description of the processes being tested. In tabularising the various spatial processes, a difficulty arose regarding nomenclature. The lack of clear definitions and distinctions between ego- and allocentric processes and representations and between processes involved during navigation and those employed while stationary means that any review undertaken faces problems integrating findings. For this reason the ‘process’ headings in Table 1.1 are broad and ill-defined. Roche *et al.* (2005) proposed a clarification of the terms by providing clearer distinctions between strategies and representations. The anatomical model they proposed is shown in Figure 1.6.

Combining this model with the summarised data above suggests that the processing of egocentric spatial relations is mediated by medial superior-posterior areas and a possible fronto-parietal network, whereas allocentric spatial coding requires the additional involvement of medial temporal regions with heavy reliance on the hippocampal formation. As mentioned earlier, the model of Roche and colleagues (2005) does not address any translational processes between representations. Table 1.1 also highlights the lack of investigation into the interaction of spatial representations. Burgess *et al.* (1999) was the only study reviewed which explicitly stated a role for translation, implicating the subiculum’s potential involvement. Zaehle *et al.* (2007) suggest that a hierarchically organized processing system exists in which egocentric spatial coding requires only a subsystem of the processing resources of the allocentric condition. A further clarification on representational interaction is in high demand.

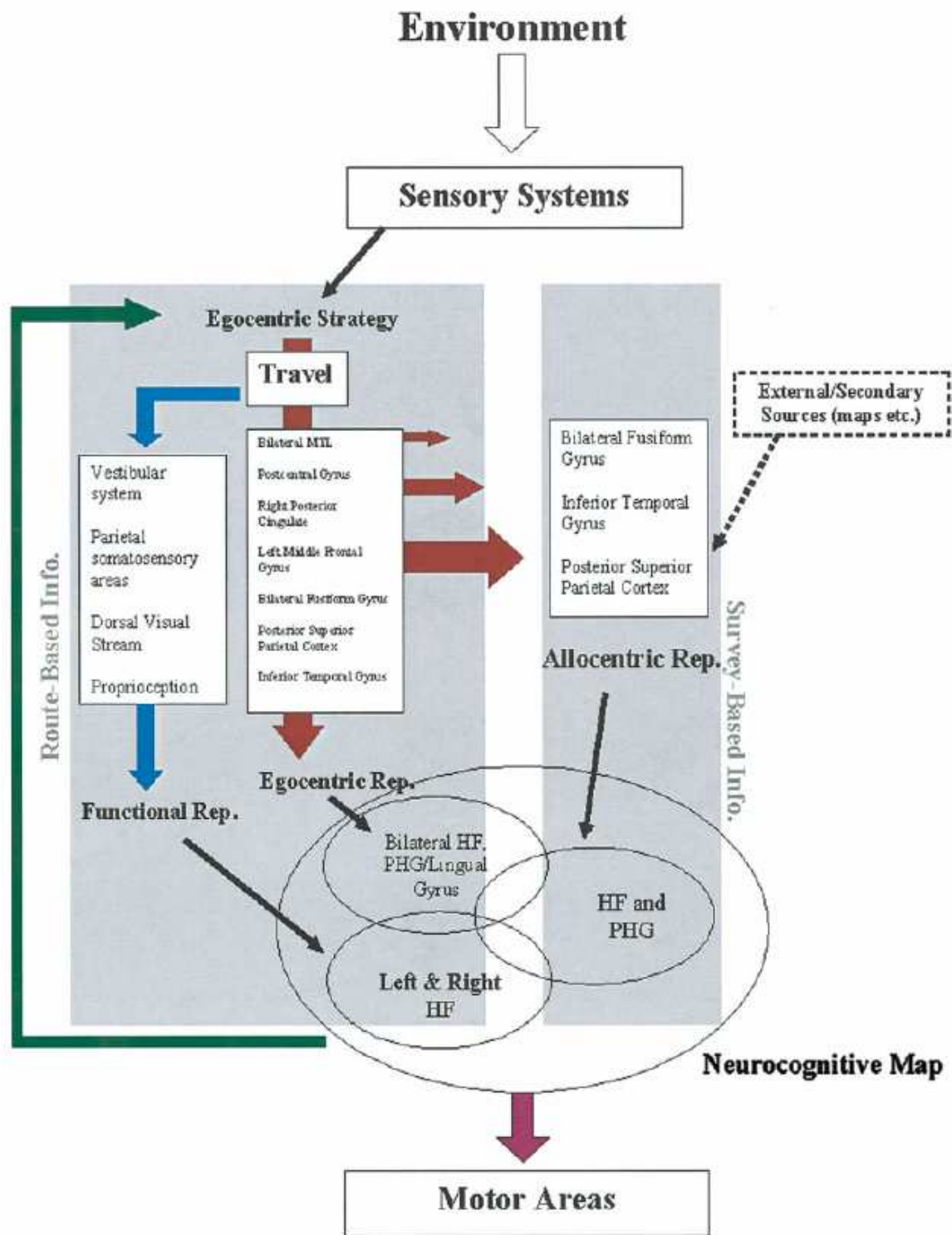


Figure 1.6 The anatomical model of neurocognitive mapping proposed by Roche et al. (2005) outlining the processing routes to distinct but overlapping mental representations and the brain structures involved in encoding and retrieval of spatial information. Reproduced with permission.

1.5 Objectives of thesis

A review of the literature reveals a consensus about many areas related to spatial cognition but many questions are still left unanswered; questions relating to the temporal sequence of activity underlying spatial abilities; questions relating to the process of translation between representations; questions relating to the issue of viewpoint dependence in spatial representations; and questions relating to object-location binding in the brain. The aim of this thesis is to explore the behavioural and neural correlates of human spatial representation and memory using high-density electroencephalography with a view to addressing these issues. To this end, the objectives are five-fold.

Firstly, in order to assess participants' spatial memory we aim to develop a simple and flexible measure which can be used to test object and/or location memory from numerous viewpoints, with the ability to distinguish egocentric and allocentric processes. Spatial cognition in spaces of different size, or scale, relies on qualitatively different information. Therefore it is appropriate to ask whether assessment on a small-scale test will capture a more general spatial ability or whether a disparate set of abilities underlies performance on spatial tasks of varying scale. Hegarty and colleagues (2006) have conducted experiments in an attempt to answer this question in particular and the general question of scale and spatial processing has been addressed extensively by Montello (Montello, 1993, 1998, 2001, 2005; Montello & Freundschuh, 1995; Montello & Golledge, 1999). Although Hegarty *et al.* (2006) highlight the importance of kinesthetics and vestibular feedback for large-scale spatial cognition, they report considerable shared variance between spatial abilities for large and small environments ($r=0.61$) which was also found in an earlier study (Richardson *et al.*, 1999). With this knowledge visual

media and virtual reality can be introduced as a safe and viable alternative in the laboratory.

Our second objective is to use this array alongside EEG to assess the temporal activation of engaged structures and identify areas involved in translations between ego- and allocentric representations. To my knowledge this will be the first electrophysiological investigation into how multiple representations interact. Following on from this, as a third objective we aim to study explicit and implicit spatial memory both behaviourally and electrophysiologically. This type of examination should highlight the influence of spatial memory on object recognition, and inform us as to the automaticity and prevalence of this involvement. After this interaction has been tentatively highlighted, our fourth objective will be to examine more thoroughly the processes, similar and divergent, underlying spatial and object memory.

Finally, a general discussion will attempt to bring the individual chapter findings together in a model of temporal activation encompassing the brain areas involved in spatial representation and memory. The individual chapter introductions will explicitly state the hypotheses being tested for the related experiments. It is hoped that this thesis will build on the current knowledge concerning spatial memory using a novel and easy to administer task that can also be adapted to suit future directions in spatial research. With the addition of electroencephalography, the temporal aspects of the complex processes involved in spatial memory can be investigated. Such electrophysiological indices will not only inform us with regard to interactions between spatial processes, but provide a baseline of activity in normal participants that may be used in both research and clinical settings to identify neurological deficits in the spatial domain.

2

Chapter II Methods

2.1 EEG Background & Theory

2.1.1 Electrophysiology

Electrophysiology is the study of the electrical properties of biological cells and tissues involving measurements of voltage change (electrical potential) or electrical current flow on a wide variety of scales (Freeman, 1975; Ingber & Nunez, 1990; Scott, 1995; Nunez, 1995, 2000). Depending on the scientific question and scale of interest, these measurements are taken either from inside or outside the body. For studying changes in electrical activity of the brain, measurement scales range from neuronal studies using micro-fibre depth electrodes to measure either intra- or extra-cellular potentials, to electrocorticography (ECoG) studies measuring directly from the surface of an exposed brain, to scalp measurements using electrode arrays (electroencephalography - EEG). The problem with these different scales lies in resolving the relationship between the potentials they measure. Intracranial recordings provide much smaller scale measures of neocortical dynamics, with scale depending on electrode size. The smaller the scale the lower the expected correlation with scalp data, since at micro-scales a mixture of coherent and incoherent sources generates the recorded potentials, whereas EEG data are due mostly to similarly oriented coherent sources over several centimetres of cortex (Mangun & Hillyard, 1995).

Nunez and Srinivasan (2006) provide a good sociological metaphor for the issue of spatial scale in electrophysiology. Data collected from large metropolitan areas will typically differ from data collected at the city, neighbourhood, family and person levels. The information obtained is both qualitatively and quantitatively different and the same is true for electrical potentials measured at the various scales. So rather than striving for

reductionism, information at all spatial scales is valuable and can complement each scale, depending on the research question. In fact, when looking at higher-level processes, intracranial recordings may be uncorrelated or weakly correlated with cognition and behaviour due to scale-dependent dynamics (Nunez & Srinivasan, 2006). ECoG is also highly invasive and therefore reserved for animal studies or pre-surgical evaluations in humans with various brain pathologies. For research purposes, the non-invasive scalp-recording technique of electroencephalography (EEG) allows safe and relatively quick investigations within the general human population.

2.1.2 Electroencephalography

EEG is the measurement of electrical activity produced by the brain as recorded from electrodes placed on the scalp (Rugg & Coles, 1995; Friedman & Johnson, 2000). Scalp EEG measures the summated activity of post-synaptic currents. An action potential in a pre-synaptic axon causes the release of neurotransmitter into the synapse. The neurotransmitter diffuses across the synaptic cleft and binds to receptors in a post-synaptic membrane. The activity of many types of receptors results in a flow of ions into or out of the post-synaptic neuron. This results in compensatory currents in the extracellular space. It is these extracellular currents which are responsible for the generation of EEG voltages. While it is the post-synaptic potentials that generate the EEG signal, it is not possible to determine intracellular activity within dendrites or neurons using scalp EEG. Surface EEG is the summation of the synchronous activity of thousands of neurons that have similar spatial orientation, radial to the scalp (Otten & Rugg, 2005). Currents that are tangential to the scalp are not picked up by the EEG. The EEG therefore

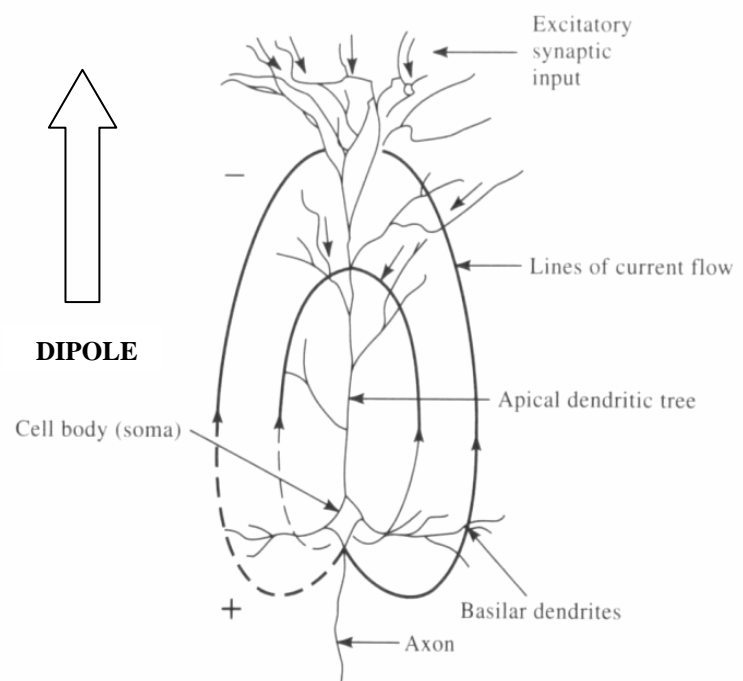
benefits from the parallel, radial arrangement of apical dendrites in the cortex. Because voltage fields fall quickly with distance (Smythe, 1950), activity from deep sources is more difficult to detect than currents near the skull. The majority of the EEG signal therefore comes from the pyramidal layer of cells in the cortex.

One way to analyse this electrical activity is to calculate event-related potentials (ERPs) for the occurrence of specific events. An ERP is calculated by averaging many epochs of EEG signal that are time-locked to the occurrence of an event in the experiment, usually the appearance of a stimulus (Rugg & Allan, 2000; Handy, 2005). The visualisation of the resulting averaged values is known as an ERP waveform and is plotted as voltage, (in microvolts; μV), over time, (in milliseconds; ms). The waveform gives a detailed temporal account of neural activity induced by the presentation of a particular stimulus. ERPs are calculated by averaging over many events so that the random noise of the background EEG (being uncorrelated with the event of interest) will be averaged out, while the aspects of ERP waveforms (called components or peaks) that are common among the individual epochs of EEG signal will become more profound (Handy, 2005). ERP topography is a neuroimaging technique which calculates intermediary values for the spatial points lying between electrodes on the basis on the value of the neighbouring recording sites. This is achieved through mathematical techniques of interpolation and the result is displayed as a coloured isopot map of the head in which areas of positive fluctuations appear in red and negative activity appear in blue, darkening as a function of amplitude. ERP topography allows for easy visual inspection of the scalp data and identification of sites of interest for further comparative analyses.

2.1.3 Principles of EEG

The human head is a volume conductor, albeit a complex one. As such, current travelling through the brain must adhere to the basic physical laws of conduction and electromagnetism; therefore the potentials recorded at the scalp level can be deconvoluted to the dura level and the underlying cortex – provided accurate estimates of the conductive/resistive properties of the media involved are available. The potentials which combine to give the EEG waveforms spread in three dimensions from their source in a multi-polar fashion (Nunez & Srinivasan, 2006). The reduction of this multi-polar expansion and the retention of the dipolar field (i.e. greatest current density along a straight line connecting the positive pole to the negative pole) is a simplification which allows the essence of electric brain potentials to be understood in terms of current sources and sinks – see Figure 2.1. These sources and sinks come from the excitatory post-synaptic potentials (EPSPs) and the inhibitory post-synaptic potentials (IPSPs) measured in EEG. EEG measures meso-scale changes in electric potential from dipole layers, which are areas in the pyramidal layer of the cortex which have large populations of neurons firing in synchrony.

Figure 2.1. *Illustration of current sinks and sources involved in an EPSP. The extracellular field lines flow from the axonal sources to the current sinks at apical dendrite sites causing a (-) dipole. IPSPs would cause a local source at the dendrite membranes and the reverse polarities would be seen (+). Of course dipoles arise from layers of synchronous cortical activity and not just a single neuron.*



Although realistically, the brain is non-linear and anisotropic, meaning current travels in all directions differently, the extracellular potentials measured by EEG travel (mostly) parallel to the radially aligned apical dendrites in the pyramidal layer of the cortex. This provides a degree of linearity and isotropy which reduces the complexity of the equations necessary to understand how electric fields behave in the brain. The human head is also inhomogeneous consisting of different tissues and fluids which will attenuate electric fields in different ways. This problem can also be simplified into distinct homogeneous materials which current must pass through to reach electrode sites e.g. brain, CSF, skull, scalp. Knowledge of the conductivity coefficients of the different homogeneous parts again informs conduction modelling equations. Volume conductor models of EEG rely on Poisson's equation. This equation is used to solve the *forward problem* for volume conductors. The forward problem involves known sources and an unknown (to be calculated) scalp distribution. In EEG, solving the forward problem involves the calculation of the superficial potential distribution (i.e. the scalp distribution) for any possible configuration of the sources. The scalp distribution can be calculated by solving the Maxwell equations within the model. This is called the *forward solution*. The 'model' here relates to the simplified conception of the head as a volume conductor with layers of homogeneous media and their corresponding conductivity coefficients and volumes. Working backwards from recorded scalp distributions to unknown source locations (as we do in EEG) presents a more complicated problem. The localisation of the sources is called the *inverse problem*, in which everything except the source parameters is known. The next section will explain this problem and how it pertains to EEG research.

2.1.4 The Inverse Problem and Limitations

As mentioned, the human head is a volume conductor. Imagine a salt water tank with a current source and sink like that shown in Figure 2.2. Once the conductivity (σ) and the volume (ml) of water are known along with the location and the charge of the sources, the surface pattern of potential (with respect to a reference) could easily be ascertained without direct measurement. Finding the surface distribution is accomplished using the forward solution described in the previous section.

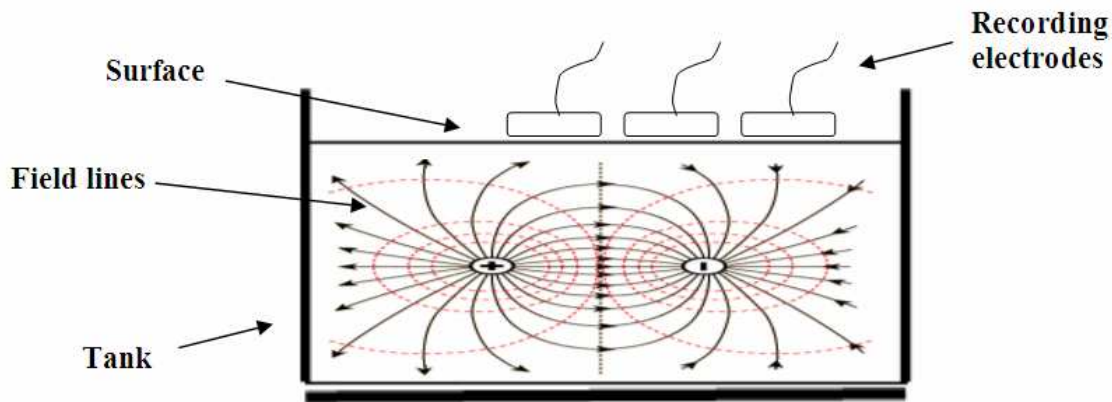


Figure 2.2. The forward problem in a volume conductor can be solved with knowledge of the medium and the sources. The inverse problem arises when you have collected data at the surface and are trying to locate the sources. No unique solution is available and knowledge of the medium's conductivity will only give more informed estimates.

EEG measures the resultant scalp topography after the interaction and supposition of underlying current sources. The inverse problem in EEG is to find the locations and strengths of the current sources on the right-hand side of Poisson's equation from discrete samples of the potential V_j (with respect to some reference) on the surface of the volume conductor. In order to locate these sources it is necessary to distinguish each from the other and untangle their interactions. This is unfortunately impossible. A problem arises straight away because the number of sources is unknown. It is similar to asking which

numbers add up to 100. The answer could be $(95 + 5)$ or $(16 + 20 + 44 + 11 + 9)$ or even $(200 - 100)$. There is *no unique solution to the inverse problem*. This is emphasised by its exploitation in cryptography with the use of inverse operators. For source localization in EEG, accurate solutions to the forward problem allow for the construction of head models which can be compared to recorded data to get estimates of source location. Prior theory or hypotheses can inform these models, and the conductivities of the relevant materials and boundary information give more accurate solutions to the forward problem. By comparing the measured values of the electrical potentials with the values of the forward solution, the dipole sources are iteratively moved into such a position that the measured data fit the forward solution data optimally (Kemppainen & Peters, 1991). Studies using implanted dipoles in mathematical and physical models have found accurate estimates of source localization, (Cohen *et al.*, 1990; Leahy *et al.*, 1998) using, for example, the Brain Electrical Source Analysis (BESA) algorithm with temporal smoothing (Nunez *et al.*, 1994). However no elaborate mathematics can trump fundamental physical limitations (Nunez & Srinivasan, 2006) and these solutions remain, at best, oversimplified estimates of source location.

2.1.5 Advantages and disadvantages for Research

Using ERPs in research offers a number of advantages to the neuropsychologist. These include (1) their high temporal resolution allows the observer to view them at the millisecond level. (2) Their ability to record voltage fluctuations that correlate behavioral conditions with underlying brain activity (without the need for an overt reaction from an experimental participant) is a convenience not provided by behavioral testing. (3) They permit the comparison of patterns of neural activity at different locations on the scalp, giving insight into the possibility of functionally distinct processes at different locations (Rugg, 1995). The first point mentioned is the greatest advantage and is most obvious when comparing the temporal resolution of EEG/ERP (ms) and fMRI or other brain imaging techniques (secs; Lee *et al.* 1995; Robson *et al.* 1998). Brain dynamics can be observed in real-time with EEG. For example, the activation timecourse of the ventral visual stream has been outlined by Doniger *et al.* (2000) with regard to object-recognition and perceptual closure.

The relatively low cost of running an EEG laboratory is another advantage of the technique. Set-up can start from as little as €50,000 whereas magnetoencephalography (MEG) can cost ten times as much. Magnetic Resonance Imaging (MRI) costs approximately €1,000,000 per Tesla. On comparison with the next most affordable technique, high-resolution EEG is just as accurate (Nunez & Srinivasan, 2006), although MEG and EEG are preferentially sensitive to different subsets of sources – tangential and radial respectively. Table 2.1, adapted from Reeve (2003), summarises the two techniques. EEG measures near field potentials and is immune to magnetic induction effects (which only interact at far fields). At the low frequencies of brain dynamics electric and magnetic fields are uncoupled (Nunez & Srinivasan, 2006).

Table 2.1. *Comparison of electroencephalography and magnetoencephalography.*

| Variable | EEG | MEG |
|--|--|--|
| Time Domain | Milliseconds | Milliseconds |
| Physical sources of artifact | Scalp; Bone; CSF; electrode contact | Non-physiological magnetic and electric fields |
| Records directly | Electrical potentials | Magnetic fields |
| Orientation of recorded sources | Radial (and tangential with surface Laplacian) | Tangential |
| Cost | ++ | ++++++ |
| Established clinical standards | Yes | No |

ERP experiments have a few smaller advantages over brain imaging techniques with regard to design and set-up. Participants may experience claustrophobia inside the bore of the magnets involved in MRI. Head movements can have catastrophic consequences in a functional imaging experiment and are much more easily identified and compensated for by filtering and trial rejection techniques in ERP studies. Magnetic susceptibility is also a problem in MRI experiments. When two tissues with different magnetic susceptibilities are juxtaposed, it causes local distortions in the magnetic field. There are natural interfaces between air and tissue in the oral and nasal orifices. This results in artifacts in the MR image, mostly a loss of signal, but also a distortion of the image. This particular problem does not affect EEG signals. Finally, in designing experiments it is easier to incorporate an event-related paradigm into an ERP experiment as jitter needs to be added for *fMRI* studies which have more typically used blocked designs. The ‘event-related’ approach allows for measurements of individual trials, or even sub-components of trials (Donaldson & Buckner, 2000).

The main disadvantages in using EEG have been discussed in the previous section outlining the inverse problem and difficulties with spatial resolution and source localization. However, another disadvantage which cannot be overlooked is the inability of this technique to establish causation. The recording of brain potentials along with behavioural measures merely gives a correlational account of cognition and behaviour. This is a disadvantage inherent in all brain imaging and recording methodologies. To establish causation, comparisons would have to be made between participants with brain lesions (or structural abnormalities) and ‘normal’ participants. Alternatively, transcranial magnetic stimulation (TMS) could be used to administer temporary lesions and help to establish causation.

2.2 Application of EEG, Stimulus Construction and Task

Presentation

2.2.1 ERP Recording & Set-up

For all ERP experiments reported in this thesis, the EEG activity was recorded with tin electrodes (BrainVision©) mounted in an elastic cap fastened with a chest strap (Easy-Cap©). EEG data were collected from 128 scalp sites (Figure 2.3), using the extended version of the International 10-20 system for electrode placement (American Electrophysiological Association, 1999).

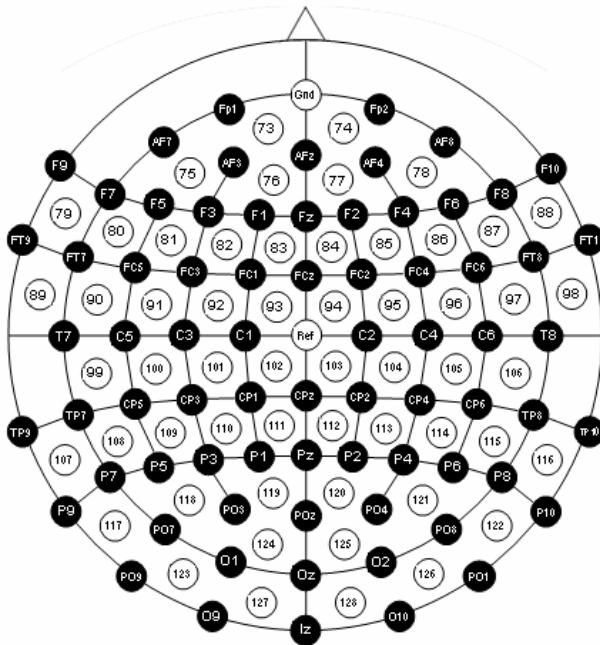


Figure 2.3. *The International 10-20 system for electrode placement. The black electrode positions designate the 10%-system. The white ones are placed on the intersection of the lines of equal distances between those electrodes, which lie opposite to each other in the parallelogram. Reproduced from www.easycap.de*

We used a reference electrode located between the nasion and the tip of the nose. Vertical and horizontal eye movements were recorded using electrooculography (EOG). VEOG was recorded from electrodes located above and below the left eye, and HEOG from electrodes positioned at the outer canthus of each eye (Figure 2.4). Blinks were averaged

off-line and a blink reduction algorithm was applied to the data. This algorithm involved automatic artifact correction employing variations of the Berg and Scherg (1991), and Ille *et al.* (2002) strategies. The correction process consists of four steps:

1. Define the topography for each type of artifact
2. Determine the brain signal topographies underlying the displayed EEG segment
3. Reconstruct the artifact signal at each scalp electrode with a spatial filter taking into account artifact as well as brain signal subspace
4. Subtract the reconstructed artifact signal from the original EEG segment

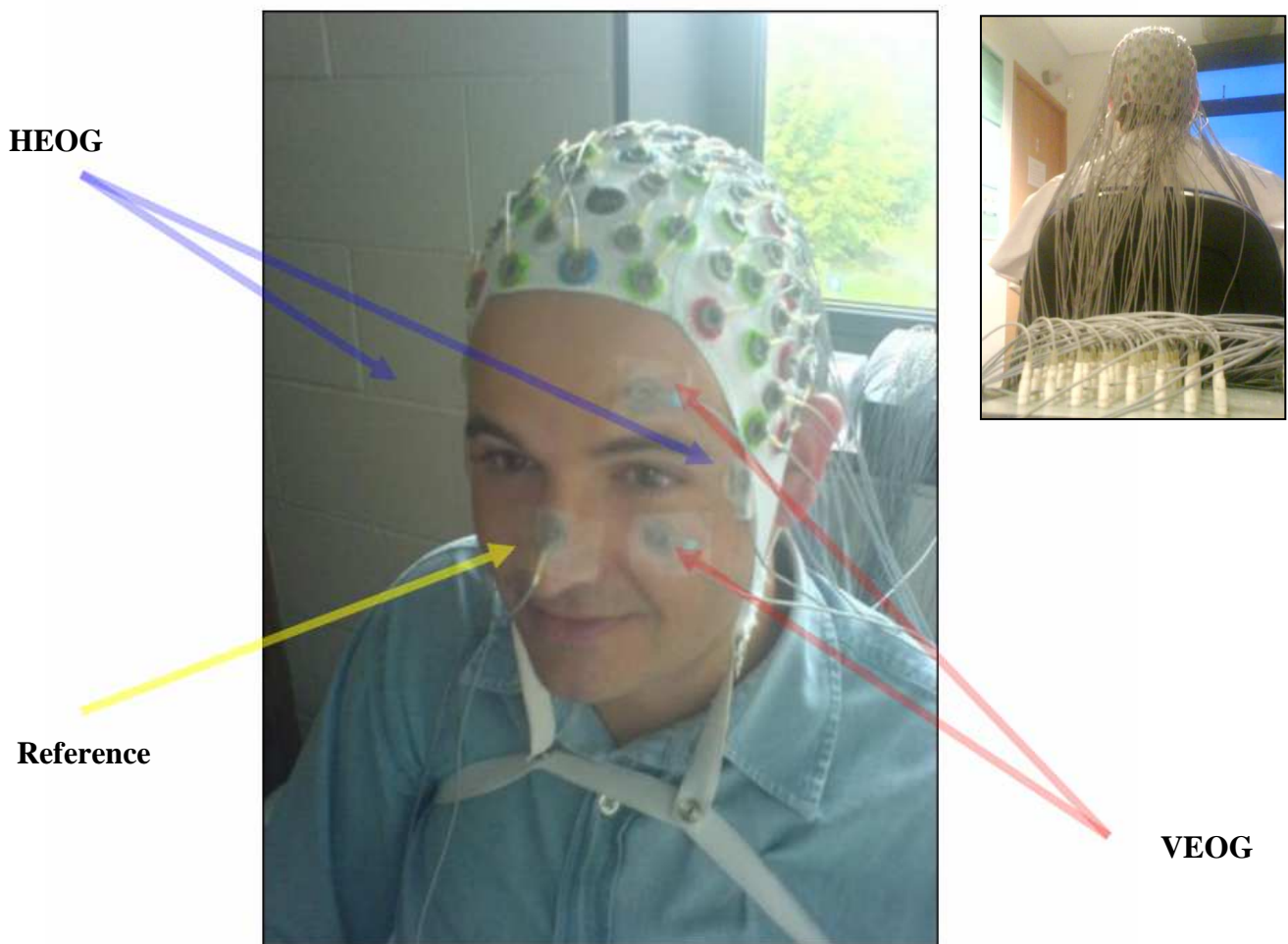


Figure 2.4. A participant with electrode cap illustrating the placement of the reference and ocular electrodes. Inset: Rear-view of electrode set-up showing the plugs connected to the amplifier.

The impedance level was kept to below 10k Ω in all cases. Electro-conductive gel (Abralyte) was used to reduce impedance. The amplifier used was supplied by Brainvision©. EEG activity was amplified using a band-pass of 0.16-100Hz and a gain of 1000. The conversion rate was 2000 Hz per channel and the range was 150mV.

After the electrophysiological preparation participants were seated 50cm from the LCD² computer screen on their own in a darkened, electrically shielded and sound-attenuated testing cubicle (150cm x 180cm) with access to a mouse for responses. For each task, a study block preceded a test block. Instructions were presented on screen prior to these blocks. Recordings were notch filtered off-line at 50Hz. EEG data were digitized at a sampling rate of 500Hz, and were averaged offline using BESA© software. Any epochs where the maximum amplitude exceeded 50 μ V were rejected. Stimulus-locked average ERPs³ were obtained by averaging the EEG using stimulus presentation as the trigger. Stimulus presentations were marked on the EEG recording by transistor-transistor logic (TTL) or voltage triggers. This was done by means of a parallel port connection between the E-Prime computer and the EEG computer. Specific time-locked ERPs calculated for each experiment are described in the relevant experimental chapters. Averages were obtained for each condition and Grand Mean Averages (GMAs) were used for analyses. Most often only ‘correct response’ trials were used in the analyses. For measurements of waveform topography (i.e. maximum peak amplitude, mean peak amplitude area under the curve, peak latency) the nasion electrode was used for reference.

² Liquid Crystal Display (LCD) screens cause little interference to the EEG signal compared to older Cathode Ray Tube (CRT) monitors. Voltages of several kV are used for scan deflection on CRT screens causing significant interference in signals (Barber *et al.*, 1998)

³ The terms “stimulus-locked” is used here to describe averaging binned by stimulus. Averages based on stimulus triggers are referred to as Stimulus Triggered Averages (STA)

2.2.2 *The Spatial Grid Task*

As this thesis is concerned with spatial representation and memory we needed to develop an easy to administer test which had an objective form of scoring and could be used in conjunction with EEG recording. A computerised test was considered the best option but large-scale navigable VR environments were immediately ruled out as we could not re-create the proprioceptive and vestibular inputs present in real-world scenarios. A small-scale table-top task assessing object-location memory was deemed appropriate to allow investigations into mental representation without the need to account for the absence of functional information.

Many previous neuropsychological studies have used procedures in which the participant views three-dimensional arrays of objects or locations from different directions, or has to navigate through complex spatial environments (see: Burgess *et al.*, 2002; Morris & Parslow, 2003). An early example of a computerised array task is the human analogue of the Olton Maze test (Olton, Becker & Handelmann, 1979), developed by Feigenbaum, Polkey and Morris (1996) – Figure 2.5a. In their ‘rotate task’, arrays of locations were presented on a computer screen, with the arrays rotated in between responding to particular locations. The authors showed a specific impairment in location memory for right temporal lobe patients. Abrahams, Pickering, Polkey and Morris (1997) used a similar task using a circular layout of small containers, placed on a central table (Figure 2.5b). Rather than relying on rotation of the spatial array to induce allocentric representation, the participants had to walk around the table in between placement of the objects and memory testing, relying on room cues to remember specific locations. This was enforced to avoid the potential problem that the participant could ‘mentally rotate’ the array and therefore remember the locations using egocentric memory. Nonetheless,

similar temporal lobe damage was again found to impair performance. In two studies by Holdstock, Mayes, Cezayirli, Aggleton and Roberts (1999, 2000), where hippocampally damaged patients had to remember locations on a display board, signified by light emitting diodes (Figure 2.5c), impairments were only found in the allocentric experimental condition. In this condition, the patient had to walk around the display board in between inspection of locations and subsequent recall, making use of room cues to identify the position. The egocentric memory condition involved having to recall the location, but from the same inspection condition. King, Burgess, Hartley, Vargha-Khadem and O'Keefe (2002) explored allocentric memory in patient Jon who had early focal hippocampal damage (see Introduction section 1.3.1). In their 'courtyard task' participants were placed on the outside of an array and had to view objects placed within it (Figure 2.5d). Subsequently they had to view the courtyard and decide which objects had been displaced. Substantial impairments were seen when the patient performed this task from novel viewpoints. These findings contrast those of Holdstock *et al.* (1999, 2000) suggesting that participant movement around an array is not necessary to explore allocentric representations. Additionally and crucially, Jon was not found to be impaired on mental rotation tasks, suggesting that a different process/strategy is employed during shifted-array tests.

While keeping these studies in mind, the Spatial Grid Task was designed based primarily on the spatial array of Johnsrude *et al.* (1999) consisting of an array with landmarks into which objects could be placed at various locations (see also Milner, Johnsrude, & Crane, 1997; Owen, Milner, Petrides, & Evans, 1996). Figure 2.6 shows the Johnsrude array with examples of their task included. Subjects were scanned using

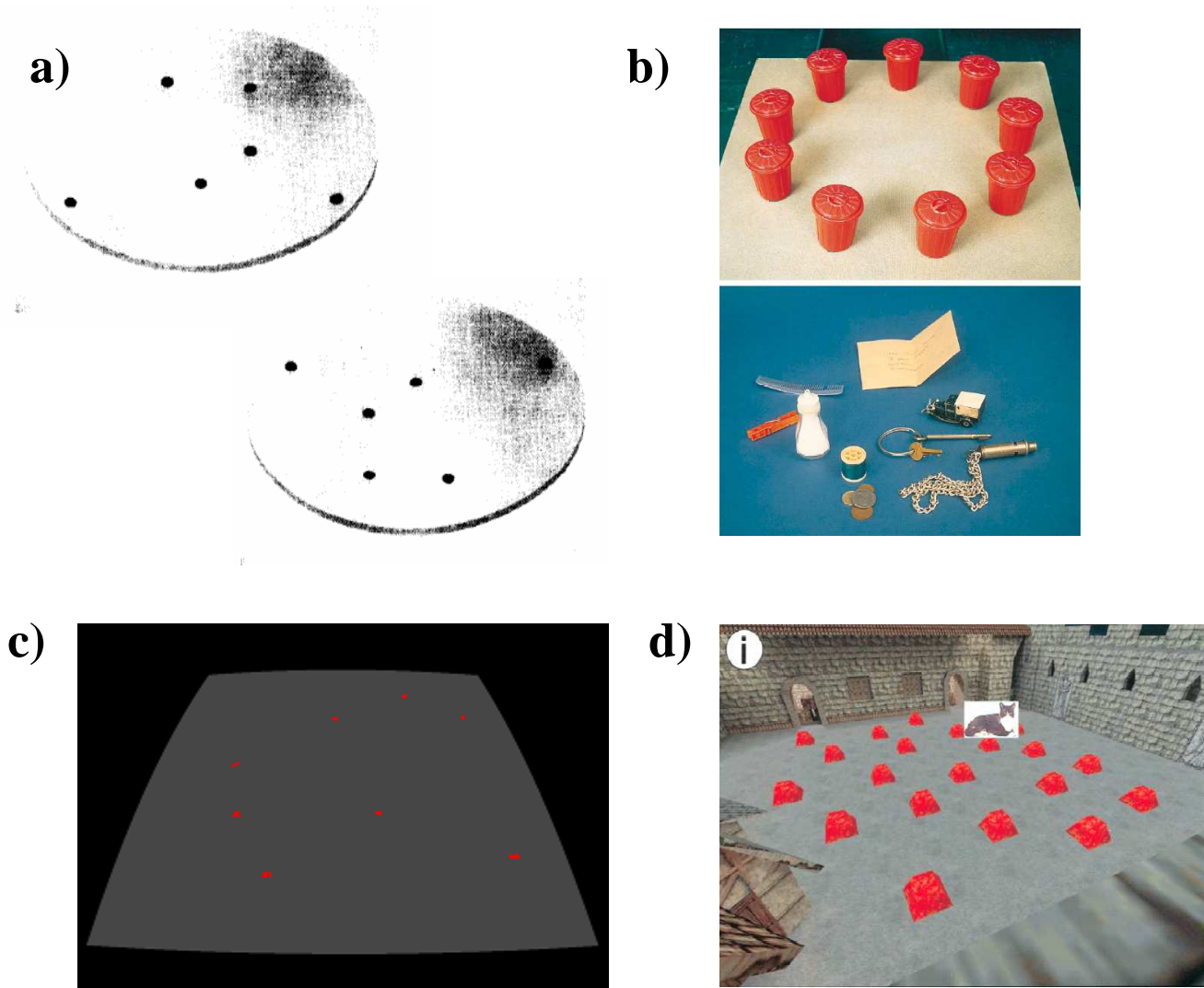


Figure 2.5. Example of previous array tasks **a)** the rotate task - arrays rotated in between responding to particular locations (Feigenbaum, Polkey, & Morris, 1996) **b)** the container task measured object and location memory (Abrahams, Pickering, Polkey & Morris, 1997) **c)** graphical interpretation of the LED board used by Holdstock et al (1999, 2000) based on their descriptions **d)** the courtyard task for ego-/allocentric memory used by King et al. (2002)

positron emission tomography (PET) while performing forced-choice recognition of object location in four conditions, using either the original landmarks (white squares) or two of the other objects as cues. There were two fixed-array conditions where the absolute location of the objects was unchanged from the time of encoding, and two shifted-array conditions, where the location of the objects was shifted but the spatial relationship between objects and landmarks was maintained. Comparing these conditions to a control task (which had the same perceptual and motor demands as the recognition tasks without the mnemonic component), they observed activation in the right, but not

left, inferior temporal gyrus when both shifted-array conditions were compared to their respective cue-matched fixed-array conditions. Activation of the right parahippocampal gyrus was found for conditions with landmarks as cues. In conclusion, Johnsrude and colleagues suggested that right infero-temporal cortex is involved in extracting the invariant relational features of a visual scene.

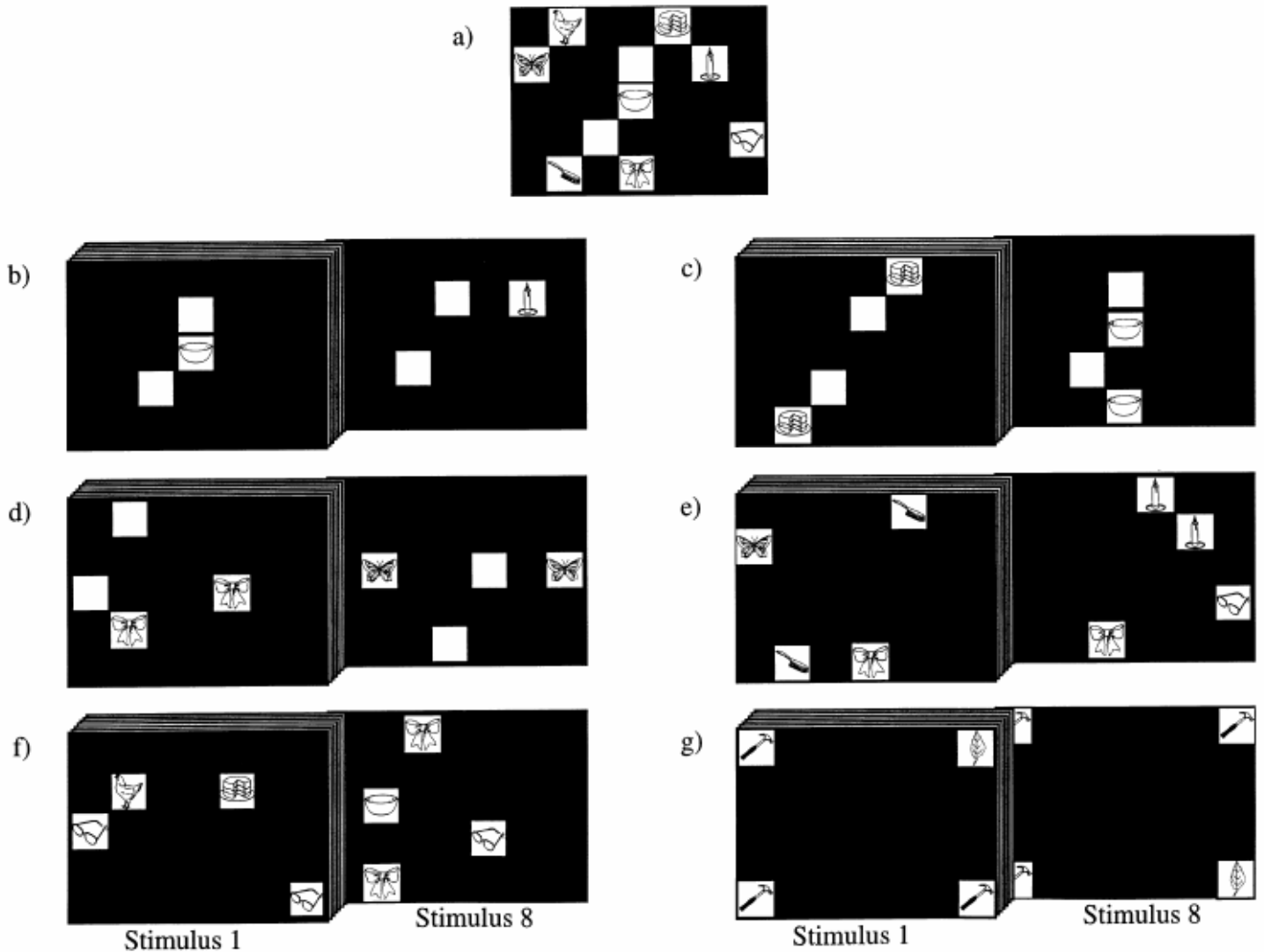


Figure 2.6. *The spatial array of Johnsrude et al. (1999) with representative stimuli seen in each of the conditions. (a) The complete stimulus-landmark array. Note that participants never saw the entire array as presented here; (b) Study block: encoding object-locations; (c) Retrieval of fixed-array locations using landmark cues; (d) Retrieval of shifted-array locations using landmark cues; (e) Retrieval of fixed-array locations using object cues; (f) Retrieval of shifted-array locations using object cues; (g) Visuomotor control.*

The use of fixed- and shifted-array landmarks provided an interesting way for testing spatial representation. However, although this task allows for investigations of object-location and relational memory, the use of translations to test allocentric representation may not be as appropriate as rotational viewpoint change (Rieser, 1989; Presson & Montello, 1994; May *et al.*, 1996). An egocentric strategy can be used for translational shifts as these are easier to reconcile (since ego-oriented bearings remain constant) compared to perspective changes due to rotation (Klatzky, 1998). Tests like this (and table-top tasks in general) have also been criticized for their singular aerial viewpoint and questionable ecological validity (see Maguire *et al.*, 1999).

We aimed to address some of these concerns in the development of the Spatial Grid Task by introducing a number of differences; most importantly, a change from a 2D black and white aerial view (which retains the criticisms levelled at table-top tasks) to a 3D colour oblique view with the less obtuse environmental geometry no longer dictated by the screen edges. For the Spatial Grid Task the objects and environments were constructed using Google SketchUp™, which allowed for three-dimensional rendering in full colour. SketchUp is a powerful, intuitive 3D modelling tool for conceptual design, documentation and presentation (Figure 2.7). Several features allow designers to easily navigate through and around their designs and manipulate them in various ways, unlike

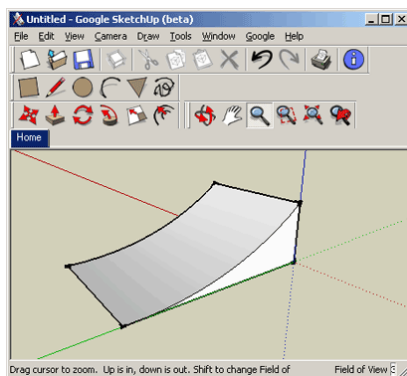
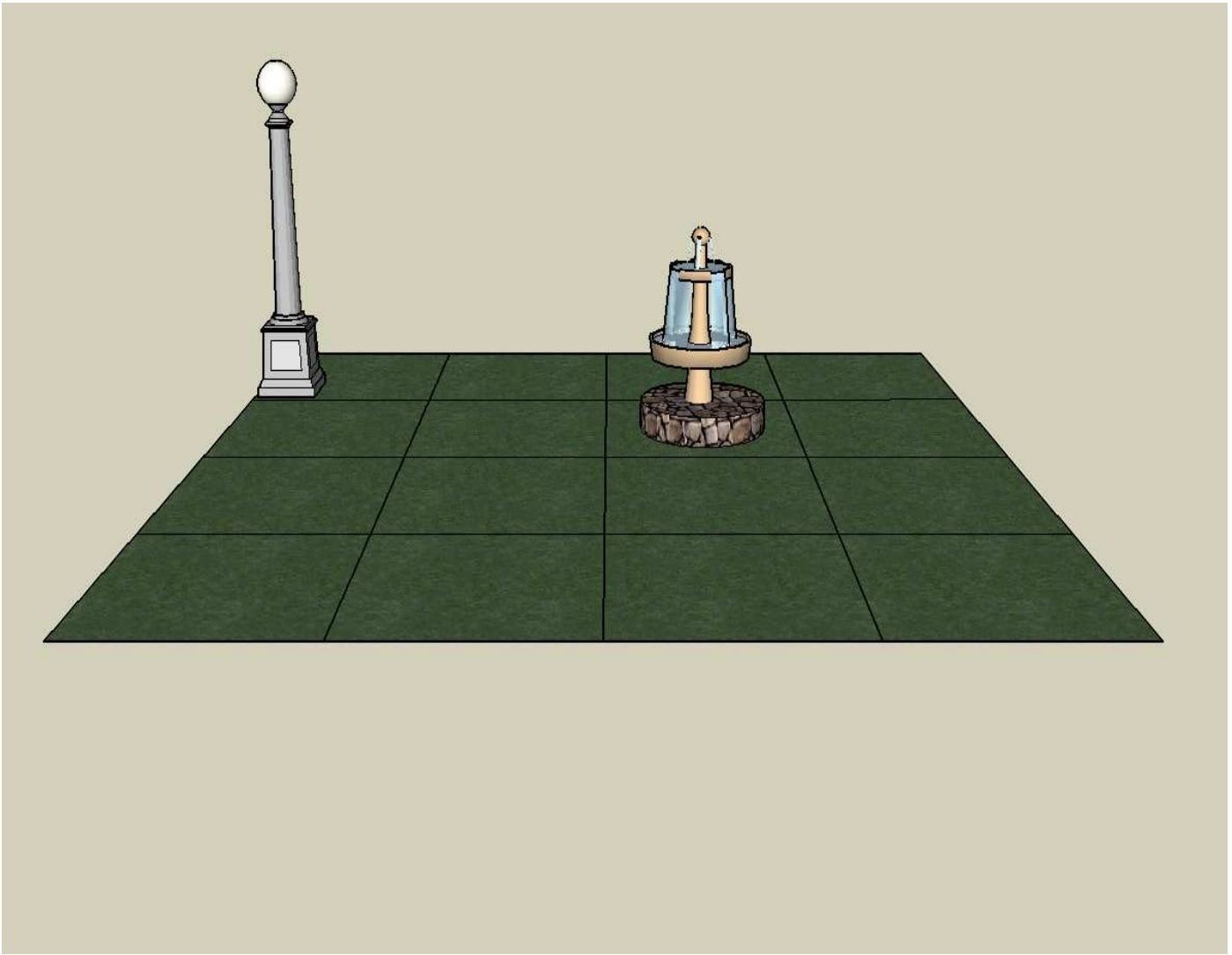


Figure 2.7. Example of the design process in SketchUp with selected toolset and 3D coloured axes for measurement and depth relations.

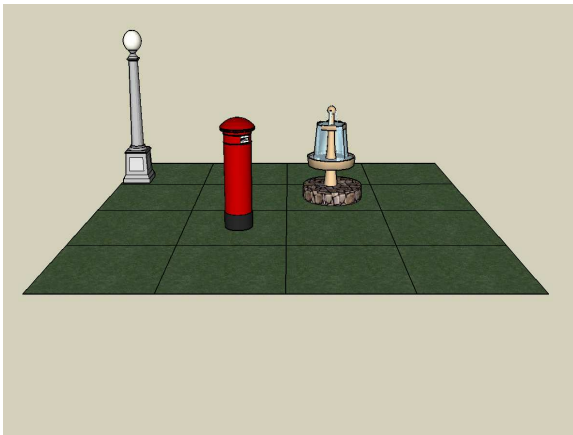
3D CAD programs. It is marketed as an easy-to-use conceptual tool with a simple interface. All stimuli were constructed in SketchUp or downloaded from the 3D Warehouse. A well known feature in the SketchUp user community, the 3D Warehouse is a resource depot for components and models. Stimuli were used to create a virtual object array which could be navigated around, changing viewpoints and object locations. Screen capture was used to get freeze-frame bitmaps (.bmp) which could then be re-scaled and presented to participants for study and evaluation.

After the array was constructed additional changes were introduced; the translations in viewpoint used by Johnsrude *et al.* (1999) were replaced by rotations in viewpoint (0° , 90° , 180° , 270°) for experiments in which viewpoint was manipulated i.e. Chapter 3, Chapter 4, Chapter 5 and Chapter 6 (Experiment 2). Because the environment was rotated in these experiments during a proportion of retrieval trials, the grid was changed from a 5x7 array to a 4x4 grid with equally spaced squares (16 segments) so environmental geometry/dimensions could not be used as retrieval cues after rotation. This square array can be seen in Figure 2.8 alongside an example of object placement in the grid and a shifted-viewpoint trial. The 0° study view permitted egocentric spatial encoding and retrieval, while the rotated views allowed for the assessment of allocentric representation, mental rotation and allocentric/egocentric translations. Participants performed the experiments described in Chapter 6 (Experiment 1) and Chapter 7 entirely from the stationary 0° viewpoint as no viewpoint manipulations were made for these studies, whereas the experiment in Chapter 5 involved viewpoint manipulations in both the study and test phases.

a)



i)



ii)

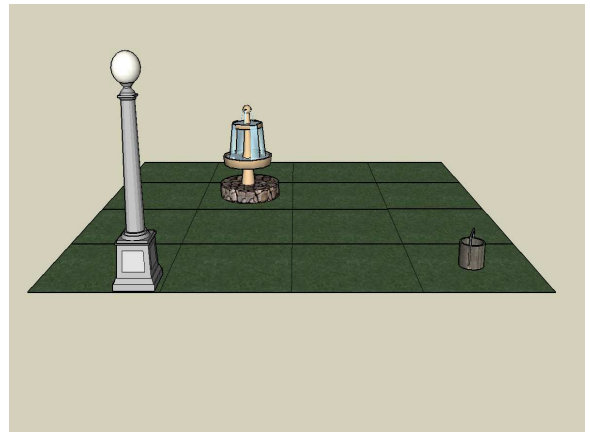


Figure 2.8. *The Spatial Grid Task with an example of object-location (i) and a shifted-viewpoint trial from the left i.e. 90° right rotation.*

Two landmark objects were always present in the environment in all experiments. These were a lamp-post and a fountain. Landmarks were used to allow an allocentric (object-centred) reference frame as well as the egocentric reference (grid; see Johnsrude *et al.*, 1999). All objects were presented in one of the 14 free segments in the grid. All were of comparable size, not exceeding 15° of visual angle and were chosen for having no canonical viewpoint for successful recognition. Stimuli were presented using E-Prime® (Psychology Software Tools Ltd., USA)

2.3 Data collection & analyses

2.3.1 Behavioural Data

Typically, participants would perform the task in a testing cubicle, being presented with a study block of trials before proceeding to a test block. The study block was similar for all experimental chapters – participants were required to view the grid (with the landmarks present) and learn either object-locations, the objects themselves or both. Participants were then required to respond to object presentations during the test block. In all experiments participants were required to respond using a mouse, with left and right button clicks assigned different response values depending on the experiment being conducted. Mean accuracy and reaction times were recorded for participants across conditions and subsequently analysed using the statistics package SPSS. Psychology Software Tools Ltd published the Stimulus Response Device Timing Values for E-Prime at <http://www.pstnet.com>. Table 2.2 shows the average and standard deviation results for the timing test paradigms used by PST to determine device latency on a 3.0 GHz machine running Windows XP. This gives the expected millisecond accuracy of E-Prime for

recording responses (via mouse) and marking presentations on the participants' EEG (Parallel Port). See *Section 2.2.1* (p. 58) for more details on E-Prime→EEG synchronisation.

Table 2.2. Average and standard deviation results (msec) for E-Prime timing

| Experiment Station Machine. Response Device Expected | Data | Total |
|--|---------|-------|
| Keyboard (USB Dell) | Average | 13.98 |
| | StdDev | 0.74 |
| Mouse (USB Microsoft Intellimouse Infrared) | Average | 17.60 |
| | StdDev | 2.52 |
| Parallel Port | Average | 0.16 |
| | StdDev | 0.37 |

2.3.2 ERP analysis

Topographic voltage maps of selected ERP results were generated using the source analysis software BESA©. A referential montage was used with the naison as reference. Component structure was defined in an *a priori* manner with no prior knowledge of the pattern of effects the data may present. BESA© was used to conduct selected waveform analyses after early visual inspection of the data. All ERP measures were subjected to repeated-measures ANOVAs. Since violations of sphericity are inherent in repeated-measures analyses, all effects with 2 or more degrees of freedom in the numerator were corrected for by using Greenhouse-Geisser F-values. Bonferroni-corrected t-tests were employed to examine paired comparisons and elucidate results from the ANOVAs. Only scalp sites selected after a visual analysis of the data were included in the inferential statistics. These sites corresponded to areas of maximal difference between conditions.

2.3.3 Brain Electrical Source Analysis:

BESA© employs a least squares fitting algorithm, over which the user has interactive control. Source localization proceeds by a search within the head model for a location where the sources can explain a maximal amount of variance (Scherg & Picton, 1991). We conducted whole-epoch modeling as well as individual component modeling using a data-driven step-wise approach and sequential fitting strategies where possible. Single or symmetric dipoles were added to each model until the solution presented became implausible. Implausibility was determined by dipole migration out of brain space. Source waveforms were also plotted in BESA© to assess latent component differences across conditions with model fit calculated using residual variance measurements. Transverse MRI slices (e.g. Figure 2.9), also generated in BESA©, are included in chapter results. The modelling process yields XYZ Talairach co-ordinates which were imported into Talairach Daemon software (Talairach & Tournoux, 1988) to determine the nearest cortical structures and Brodmann's Area (BA). However, the modelled dipoles represent an oversimplification of the activity in the areas and should be considered as representative of centres of gravity of the observed activity rather than pinpoint localizations of exact generators (Molholm *et al.*, 2004; Sehatpour *et al.*, 2006)



Figure 2.9. BESA generated transverse MRI slice displaying dipole location and orientation within brain space.

2.3.4 Temporal Spectral Evolution

Temporal Spectral Evolution (TSE) is a type of time-frequency mapping which can be carried out using BESA©. Unlike the spectral analyses based on Fast Fourier Transformations (FFTs), a TSE analysis can show variation across the frequency spectra over time (Vázquez *et al.*, 2001), hence the use of the word ‘evolution’. An early description of the technique is provided by Salmelin and Hari (1994). For its use in source coherence, TSE maps are computed at the source level. Source waveforms are transformed into time-frequency space to calculate the amplitude and phase of each brain activity as a function of frequency and latency (Hoechstetter *et al.*, 2004). The change of power of each source with respect to the baseline is averaged over trials and displayed as a function of frequency and latency in event-related (de-)synchronization plots (ERD/ERS; Pfurtscheller & Lopes da Silva, 1999) to illustrate the increase or decrease of activity in the time-frequency domain for each modelled brain region separately (Figure 2.10).

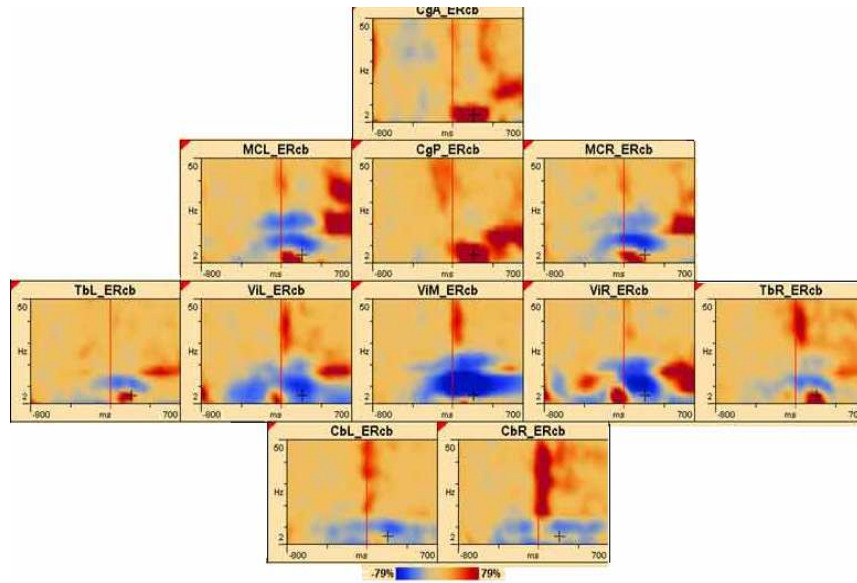


Figure 2.10. BESA generated TSE maps for each source comparing evoked and/or induced activity in the time-frequency domain against baseline levels (Red=increases, Blue=decreases) for 11 dipoles

2.3.5 Summary of Methods

This chapter provides background information on the use of EEG (advantages and limitations) as well as detailing the construction of and the rationale behind the Spatial Grid Task, versions of which are used in all experiments of this thesis. In addition to this, the general methodology employed throughout this thesis is outlined with descriptions of the methods used for data collection, filtering and analysis. I make reference to this chapter in general as well as specific sections of this chapter in the methods sections of the individual experimental chapters. However, some studies will detail additional methods of analysis, used for specific comparisons that have not been outlined here. A simplified timeline is displayed below (Fig. 2.11) to illustrate the stimuli, responses and TTL triggers involved in a typical trial.

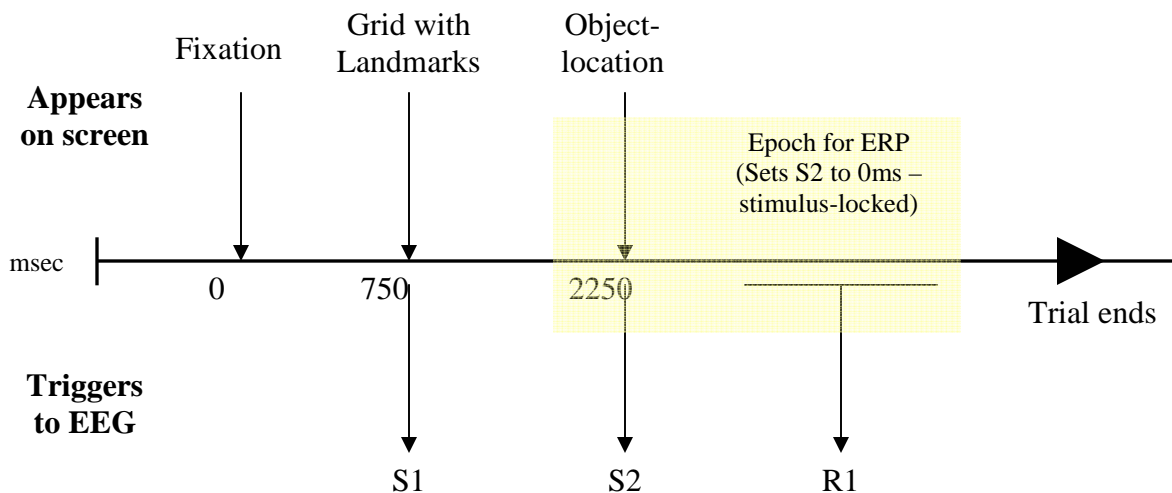


Figure 2.11. Timeline showing the millisecond progression of a trial in terms of stimulus presentations and responses and the triggers related to these events. Triggers time-stamp the EEG at particular points to allow the subsequent generation of stimulus-locked ERPs (In this example ERPs are stimulus-locked to trigger S2).

3

Chapter III

Electrophysiological indices of
egocentric and allocentric
representation

3.1 Abstract

Participants were required to study objects in specific locations within a spatial grid containing 2 fixed landmarks from a fixed viewpoint. Following this, participants were required to respond to object presentations in correct and incorrect locations from rotated viewpoints - i.e. 0° , 90° left, 90° right or 180° , which allowed for manipulation of participants' spatial reference, and comparison of ego- and allocentric representation. Behavioural results indicated that participants were both faster and more accurate in identifying locations from the studied viewpoint. Accuracy was found to be higher for identifying incorrect locations when new viewpoints were presented. Presentations involving new viewpoints resulted in greater parietal positivity before objects were presented for evaluation, compared to presentations of the studied viewpoint. During object presentation, correctly located objects as well as presentations from the studied viewpoint elicited greater parietal positivity, demonstrating an old/new effect. Furthermore, correct locations, irrespective of viewpoint, elicited unique positive deflections in the rise of the P3 component. Source analysis revealed a complex distributed network underlying spatial representation, involving numerous temporo-parietal sources, recruiting regions of the cingulate gyrus and medial temporal lobe. This study reveals the temporal characteristics of spatial memory retrieval, examining the properties of the ERP waveform across representations.

3.2 Introduction

More than a half century ago, the term “cognitive map” was first used to describe our internal mental representations of physical space (Tolman, 1948), although the idea of mental maps predates even Tolman. The ‘cognitive map’ described by Tolman and developed by O’Keefe and Nadel (1978), is used to describe the mental representations of space, whereby one’s location within an environment is updated through the relative associations of distal cues in addition to, yet distinct from, any proximal information available. The cognitive map has been widely accepted as a means for long-term spatial representation and memory. This is mainly due to the coding of location and goal direction in a universal manner, irrespective of a person’s body-centred orientation, therefore yielding a less redundant and more flexible allocentric (survey-based) representation. Although the basic premise of a cognitive map is shared by most researchers, the qualities, capacity, anatomy and nature of such a map are topics of debate, and the interaction of representations within the brain is poorly understood (Roche *et al.*, 2005).

In the last decade there has been a resurgence of interest into how humans encode, update, manipulate, and retrieve spatial information from environments. This interest is manifest in the volume of publications detailing behavioural, electrophysiological and neuroimaging studies. A number of behavioural studies test spatial memory in the real-world. To test the functional contribution from proprioception and vestibular input, real-world travel is necessary and has received some attention (Berthoz *et al.*, 1995; Israel *et al.*, 1997; Loomis *et al.*, 1993; Rieser *et al.*, 1989). Traditionally, tasks involving table-top presentations of object arrays have been more widespread in the testing of egocentric and allocentric contributions to spatial representation (reviewed in Section 1.3.3). These tests

have been criticized for their singular aerial viewpoint and questionable ecological validity and comparability to actual navigation (see Maguire *et al.*, 1999). In order to capture the qualities of real-world navigation, virtual reality (VR) simulations are now the tool of choice (Riva, 1999; Rizzo *et al.*, 1998; Slater & Wilber, 1997; Witmer *et al.*, 1996; see Slater, 2005 for a review). Objects presented in spatial arrays can be interesting to study as opposed to larger, navigable virtual environments. They allow for the study of landmark processing, and object/location processing both at encoding and retrieval. Also, through rotation, VR ‘array’ tasks allow for manipulations of viewpoint, which a number of (viewpoint-dependent) studies have shown is an effective way to test differences in egocentric/allocentric representations (e.g. Christou & Bulthoff, 1999; Johnsrude *et al.*, 1999; King *et al.*, 2002). The Courtyard task (King *et al.*, 2002) in particular advocates the use of spatial array tasks in the study of ego-/allocentric representation. After learning the location of objects from a single viewpoint, an amnesic participant with focal bilateral hippocampal pathology showed a substantial impairment in recognising ‘correct’ location objects for shifted viewpoint trials. Interestingly, simple mental rotation was spared in the amnesic patient.

This paradigm, coupled with neuroimaging methods, has helped highlight the neural basis of spatial representation. Studies have identified the importance of and reliance on environmental features, especially landmarks, and have implicated the parahippocampus (Parahippocampal Place Area - PPA; Epstein & Kanwisher, 1998) and lingual gyrus (Lingual Landmark Area - LLA; Aguirre *et al.*, 1998) in scene and landmark recognition. Although electroencephalography has been used to probe differences in brain activity for object and/or location encoding (Mecklinger, 1996, 1998; Moscovitch *et al.*, 1995; Tresch *et al.*, 1993; Ungerleider & Haxby, 1994) it has seldom

been used as a technique for dissociating egocentric and allocentric reference frames, compared to the many studies reporting *fMRI* and PET findings (e.g. Filimon *et al.*, 2007; Holdstock *et al.*, 2000; King *et al.*, 2002; Maguire *et al.*, 1997; Parslow *et al.*, 2005; Roche *et al.*, 2005; Shelton & Gabrieli, 2002).

With this approach in mind, a ‘Spatial Grid Task’ was designed based on the spatial array of Johnsrude *et al.* (1999) – see Methods section. The 0° study view permitted egocentric spatial encoding and retrieval, while the rotated views allowed for the assessment of allocentric representation, mental rotation and allocentric/egocentric translations. It is predicted that with encoding of egocentric information about spatial locations, an allocentric reference frame would begin to develop secondary to the egocentric representation. We also attempt, using event-related potential (ERP) analysis and source analysis, to identify waveform components and sites that may be associated with egocentric and allocentric representation and processing. Dipole source modelling will be used to identify potential cortical and subcortical generators of the scalp recorded ERP componentry. Specifically we predict that egocentric retrieval should activate parts of the parietal cortex, bilateral HF and parahippocampal and lingual gyri (Aguirre *et al.*, 1998; Devan *et al.*, 1996; Epstein & Kanwisher, 1998; Maguire *et al.*, 1998; Potegal, 1972, 1982; Roche *et al.*, 2005; Stein, 1989; Wiener, 1993). Retrieval from an allocentric representation should activate many of the same regions with increased activation in a subset of superior parietal areas (Roche *et al.*, 2005). Vargha-Khadem *et al.* (1997) concluded that the use of an allocentric process capable of arbitrary manipulations of viewpoint within 3D space appears to be specifically dependent on the HF. Ekstrom *et al.* (2003) found support for the role of the hippocampus in allocentric representation using single unit recording and also discovered human cells somewhat analogous to ‘place’

cells found in rodents (O'Keefe & Dostrovsky, 1971). Cells that responded at specific spatial locations were found primarily in the hippocampus while cells that responded to views of landmarks were found in the parahippocampal region (Ekstrom *et al.*, 2003). A PET study by Owen *et al.* (1996) found that the parahippocampal gyrus is activated when the recall of object location in a spatial array is required, akin to traditional table-top tasks. Consistent with most studies in the area of spatial memory, it is predicted that waveforms will be lateralized predominantly in the right hemisphere and that the right anterior parahippocampal gyrus will be involved during retrieval in all conditions. Cortically, we predict the elicitation of parietal componentry with latencies between 300-800ms. Finally we predict an increased parieto-occipital P300 for correct location presentations, consistent with the old/new findings of Mecklinger (1998), as well as latency and amplitude differences between rotations, with the studied egocentric view eliciting most positivity.

3.3 Methods

3.3.1 *Participants*

Twenty volunteers participated in this experiment aged between 21 and 30 (mean 24.5 years). After data screening, two participant's data were removed from ERP analysis due to excessive EEG/EOG artifacts or head movements. Of the remaining 18 participants, six were female and fifteen were right-handed. Subjects were recruited *ad hoc*, from the student population of the National University of Ireland (NUI Maynooth). All participants were in good health and had normal or corrected-to-normal vision. The experiment was conducted in accordance with the Code of Ethics of the World Medical Association and the ethical standards of the APA and approved by the NUI Maynooth University Ethics Board.

3.3.2 *Stimuli*

The Spatial Grid Task was used for this experiment – see General Methods section 2.2.2. All stimuli were presented using E-Prime on an Intel Pentium 4 Processor (3.00GHz CPU) and displayed on an LCD monitor. They consisted of 8 different objects. The particular set of objects presented included a bin, a bucket, a post-box, a road-cone, a fire hydrant, a tree, a tyre and a keg.

3.3.3 Procedure

Participants were seated in a copper-plated electrically shielded cubicle (150cm x 180cm) half a metre from the computer monitor and had access to a mouse for responses. A study block preceded a test block. Instructions were presented on screen.

STUDY BLOCK

During the study block participants were required to memorise the locations of each object within the environmental grid. The study block consisted of 64 trials (each of the 8 objects presented 8 times). The temporal sequence of a trial is displayed below in Figure 3.1a. The presentations were pseudo random (objects were presented randomly in a run of 8 and this was repeated 8 times) so that numerous presentations of the same object did not coincide. More instructions followed the study block, explaining how to respond in the test block.

TEST BLOCK

Participants were instructed to respond to objects in their *correct* location by clicking the left mouse button with their index finger and by clicking the right mouse button with their middle finger when objects were presented out of location. For the Test block, the sequence of a single trial followed the same pattern as Figure 3.1 (i.e. Fixation→Landmarks→Stimulus). For the Test Block, the stimulus presentation was also the response interval. The test block began with 24 trials presented from the same viewpoint as in the study block (Figure 3.1a). This allowed participants to adapt to the response criteria before the rotated trials were presented. Each object was presented once in its correct location and twice in an incorrect location.

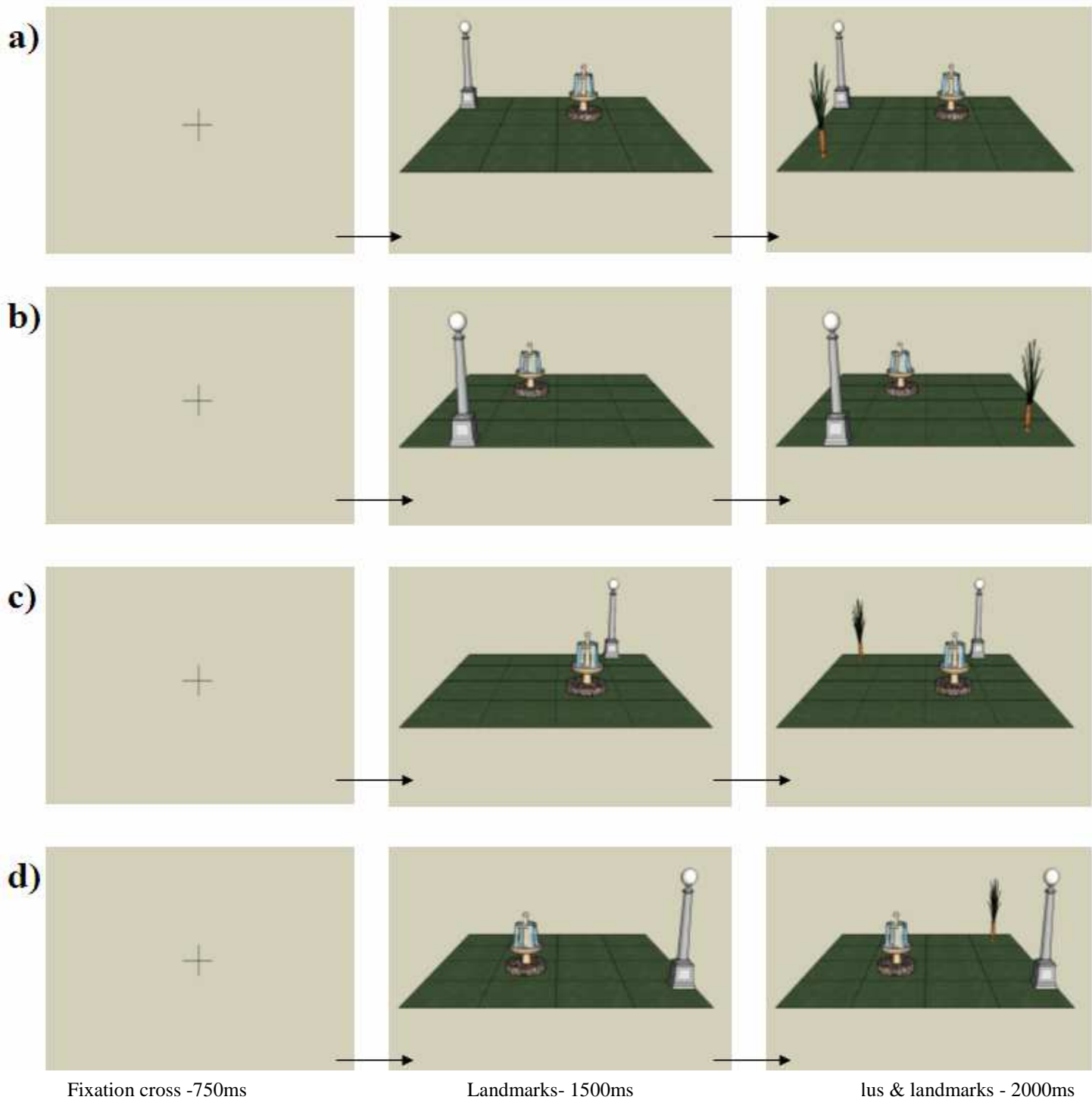


Figure 3.1 Temporal sequence (columns) of a single trial in the experiment. Example of (a) study trial / 0° test block trial (b) 90° right rotation test trial, (c) 90° left rotation test trial, and (d) 180° rotation test trial.

There were four possible incorrect locations pseudo-randomly chosen from the 13 remaining squares (16 squares minus 2 landmarks minus the correct location). Presentations were randomised in the construction of the task and this random order was the same for all participants. The participants were instructed to respond as speedily as possible within a 2 second time limit while also attempting to respond accurately. After the initial 24 trials, participants were again required to recognise the location of a particular stimulus that they had previously seen in the study block. However they were instructed that the environment would be rotated on a proportion of trials. Following these instructions the test continued through 488 trials (approx. 35mins.) with 3 self-timed rest breaks (one every 122 trials). The environment (including the landmarks) was rotated by 0° , 90° left, 90° right, or 180° (see Figure 3.1a-d) on each trial. Therefore, including the initial twenty-four 0° trials participants were presented with 128 trials at each rotation (512 trials in total).

3.4 Results

3.4.1 Behavioural Data

Mean accuracy scores and response times for each rotation (0° , 90° left, 90° right, 180°) when objects were in correct and incorrect locations are illustrated in Figure 3.2a and 3.2b respectively (Accuracy/RT tradeoffs are shown in Figure 3.3). Location had a significant effect on accuracy [$F(1,19) = 9.381$, $P < 0.01$] but not response time [$F(1,19) = 2.659$, $P > 0.05$]. Participants were more accurate when responding to objects in incorrect locations than when the objects were in their studied correct location, but only when the viewpoint had been rotated from the studied perspective. The effect of viewpoint was visible in both accuracy scores [$F(3, 57) = 12.662$, $P < 0.001$] and response times [$F(3, 57) = 17.932$, $P < 0.001$]. Interactions between viewpoint and location were obtained for accuracy scores [$F(3, 57) = 4.074$, $P < 0.02$] but not response times [$F(3, 57) = 1.265$, $P > 0.05$]. Paired-samples t-tests were performed comparing mean accuracy scores for correct and incorrect locations on each viewpoint (see Figure 3.2a). Higher accuracy scores were seen, regardless of object location, for the 0° orientation (studied viewpoint) trials. The fastest response times were also found for the 0° orientation.

Finally, a separate set of ANOVAs were carried out to assess the effect of viewpoint changes between the novel, rotated test conditions. For correct locations, no effect of viewpoint on accuracy across was found [$F(2, 38) = 0.715$, $p > 0.05$] but a significant effect was seen for incorrect locations [$F(2, 38) = 3.565$, $p < 0.05$]. No significant effects were found for response times, either for correct locations [$F(2, 38) = 1.832$, $p > 0.05$] or incorrect locations [$F(2, 38) = 0.356$, $p > 0.05$].

Mean Total Accuracy for object location across rotations

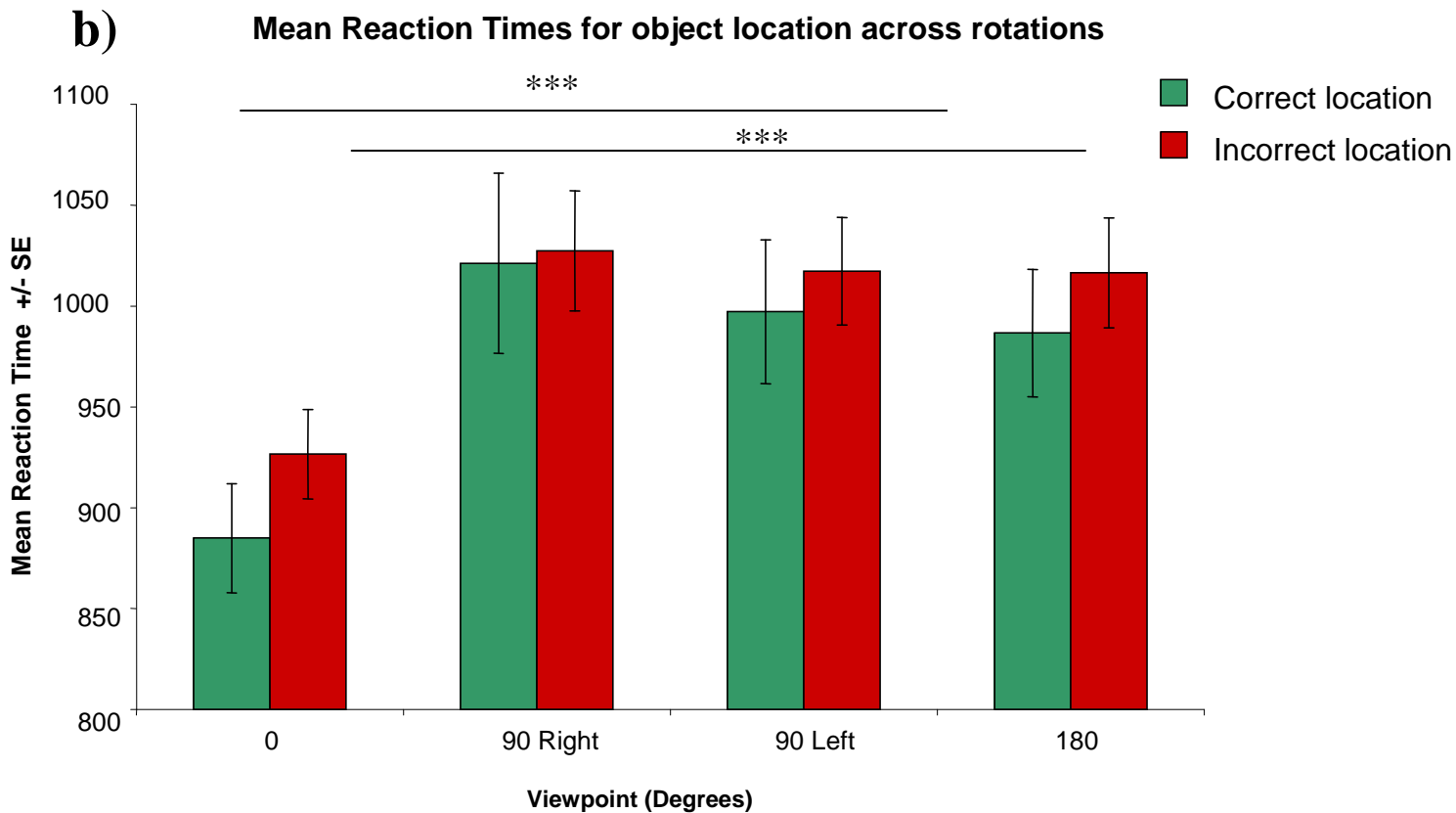
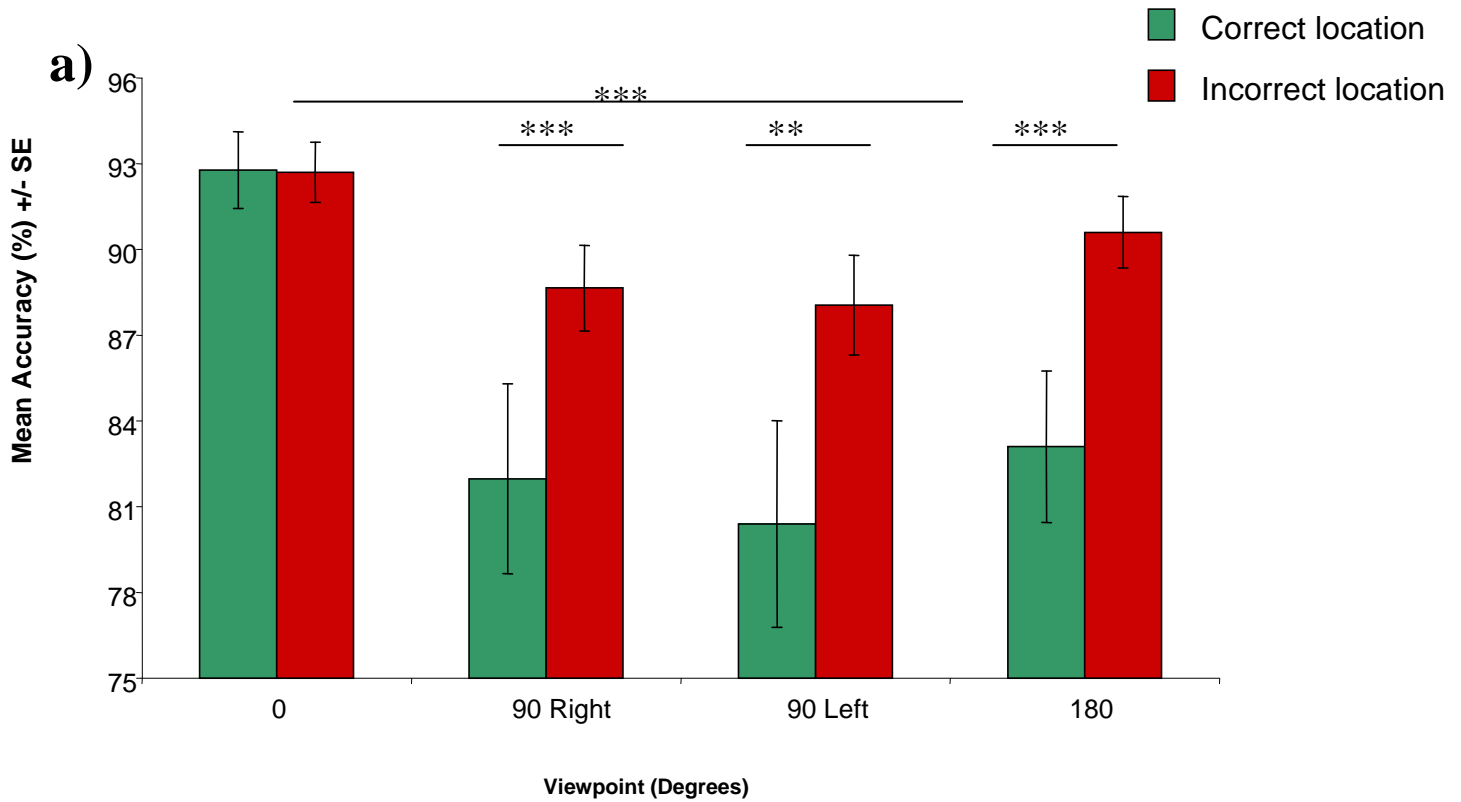
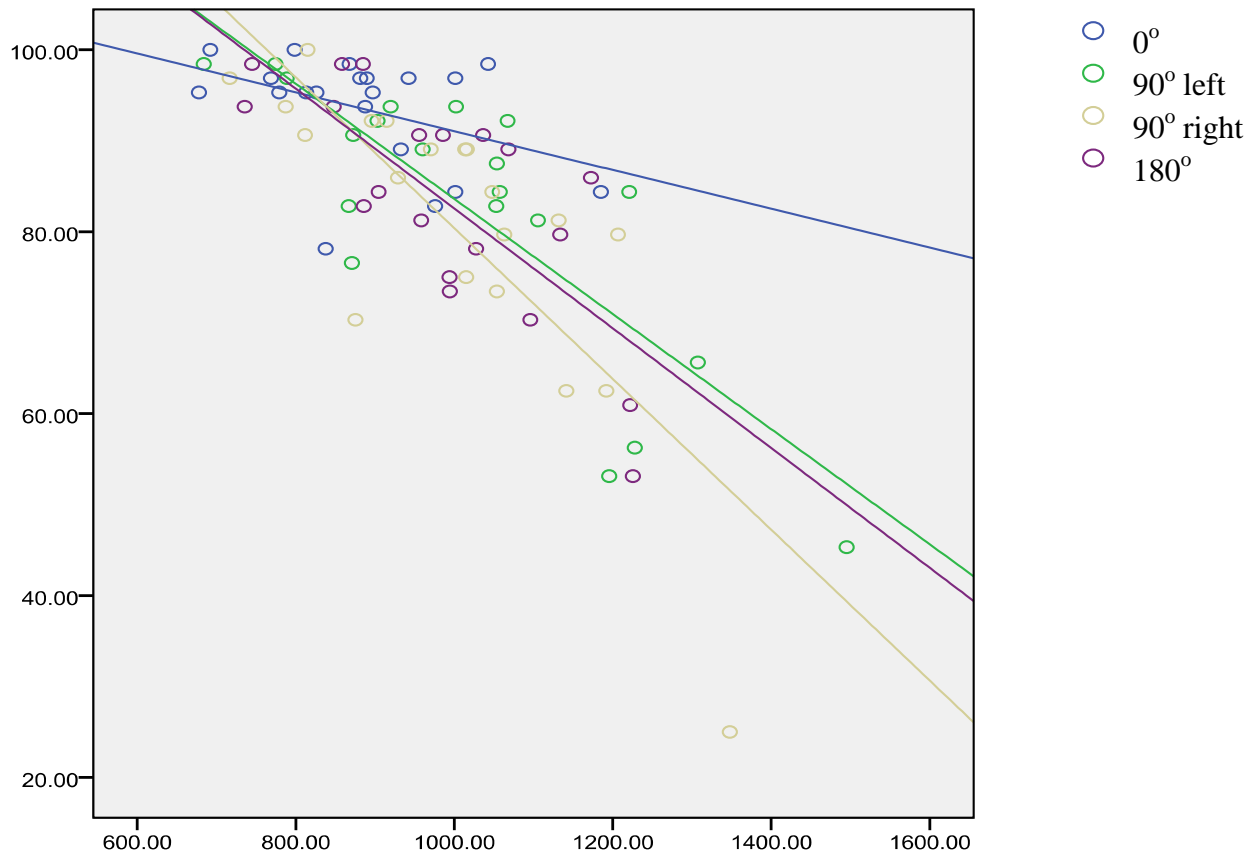


Figure 3.2 Histograms of performance results (a) Accuracy scores and (b) Response times for object presentations in correct and incorrect locations for the four rotations. Error bars illustrate +/- Standard Error of the mean. (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$)

a)



b)

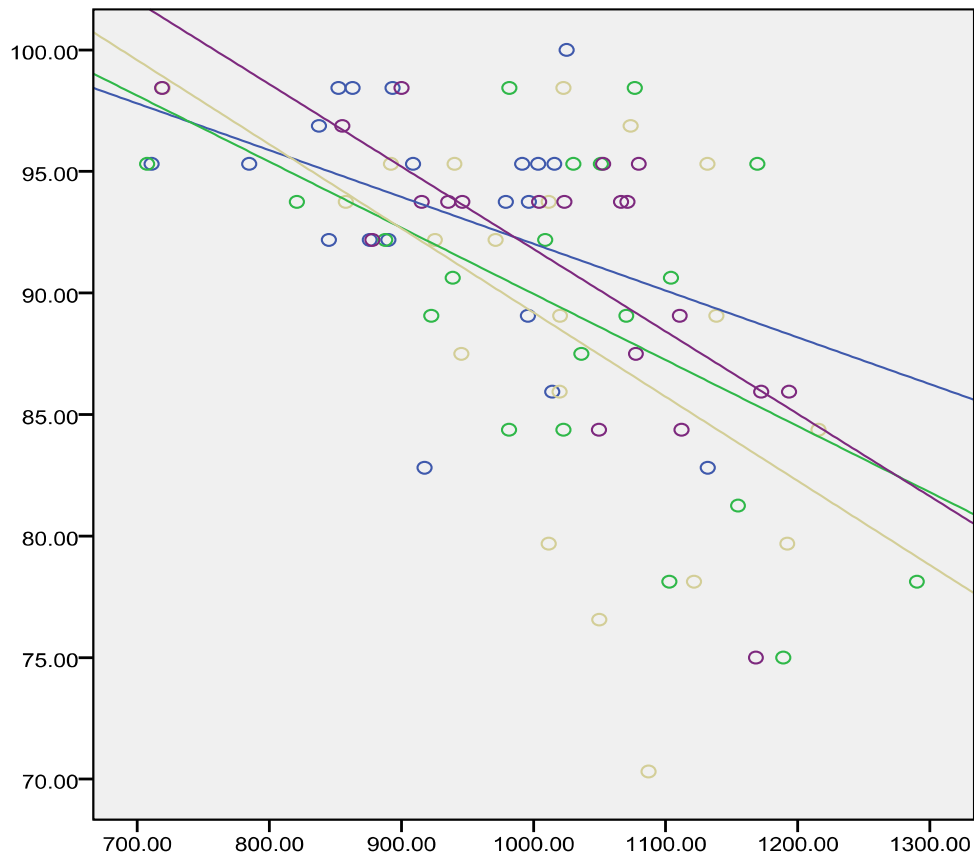


Figure 3.3 Scatterplots plotting individual performances i.e. accuracy/RT correlations for **a)** Correct location targets and **b)** incorrect location targets) for all viewpoints.

3.4.2 Electrophysiological data

ERP analyses were conducted during different phases of the test presentations. These were 1) landmark presentations at each viewpoint and 2) object presentation (correct and incorrect locations) again at each viewpoint tested around the array. Midline electrodes are displayed for anterior→posterior comparisons alongside selected electrode sites which illustrate the differences assessed in each phase.

ERPs during Landmark phase: Generally, the landmarks evoked early parieto-occipital visual P170 components (red dashed boxes, Fig. 3.4) and even more pronounced parietal maximal P300 components (blue dashed boxes, Fig. 3.4). Differences between landmark presentations at the four viewpoints emerged in parietal latency shifts after the P300 peak (between 400-500ms) – e.g. CPz blue box. The waveforms evoked by 0° landmarks were attenuated during this time interval at parietal recording sites as can be seen by the earlier drop in positivity at electrodes P3, CPz, and P4 in Figure 3.4. The difference waveform between 0° and rotated conditions (Figure 3.4) reveals an extra parietal positivity, maximal at 400ms, specific to the rotated conditions. This is represented and localised in the topographic map in Figure 3.5. This difference also took the form of a frontal right lateralized more negative slow wave for the rotated landmarks and was evident in prefrontal waveforms to a lesser extent (not illustrated).

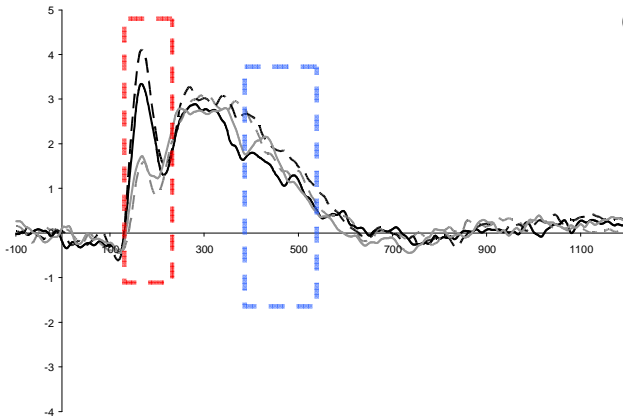
These observations were confirmed with statistical analyses. A repeated-measures ANOVA to test for differences in the P300 component across each viewpoint was performed for mean maximum amplitudes in the time interval 360ms-500ms. Maximum amplitudes were calculated from two parietal electrode sites, CPz and E112. These sites

VIEWPOINTS

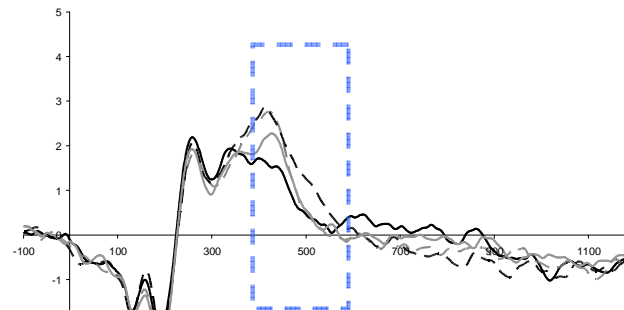
LANDMARK PRESENTATIONS

- landmark 0 degrees
- - landmark 90 degrees right
- - landmark 90 degrees left
- landmark 180 degrees

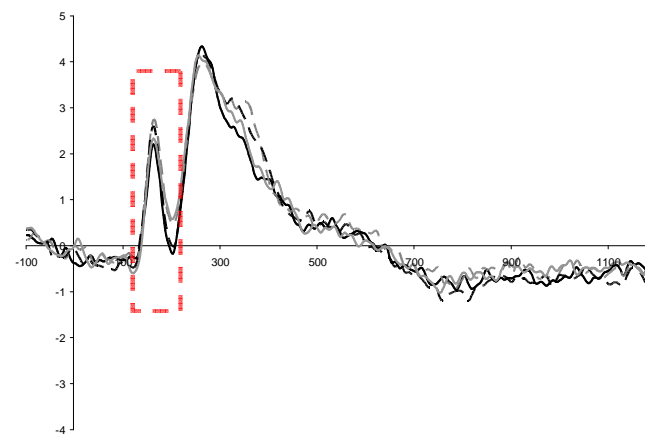
P3



CPz



POz



P4

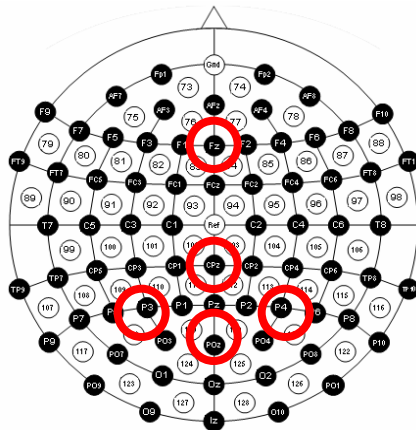
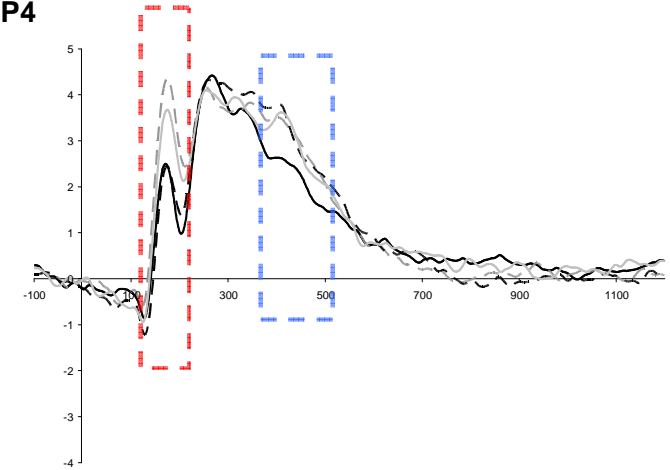


Figure 3.4 ERP waveforms averaged across participants elicited by the landmark presentations at the four rotations: 0° , 90° rotated right, 90° rotated left and 180° . The x-axis represents stimulus onset and the epoch displayed begins at -100ms and ends at 1200ms. Electrodes are displayed based on visual analyses and for anterior-posterior comparison of the cortical gradients. The legend is displayed in the upper left corner and the location of electrode sites on the scalp is displayed in the lower left. Dashed boxes are referred to in the text and highlight specific areas of difference and components targeted for analysis.

were chosen as they showed the greatest differences between viewpoints (based on the topographic map of Figure 3.5). A significant main effect of viewpoint was found [$F(3, 105) = 7.874, p < 0.0005$]. Paired-samples t -tests (Bonferroni corrected) showed significant decreases between max amplitudes for 0° (Mean=2.4750, SE=0.364 – Fig. 3.3 black solid line) and 90° right (Mean=3.2894, SE=0.506 – Fig. 3.3 grey dashed line), $t(35) = 3.094, p < 0.05$, for 0° and 90° left (Mean=3.3275, SE=0.457 – Fig. 3.4 black dashed line), $t(35) = 4.833, p < 0.05$, and between 180° and 90° left and $t(35) = 3.116, p < 0.05$ (solid grey and black dashed line). None of the other comparisons yielded significant differences in maximum peak amplitude for the P400 component.

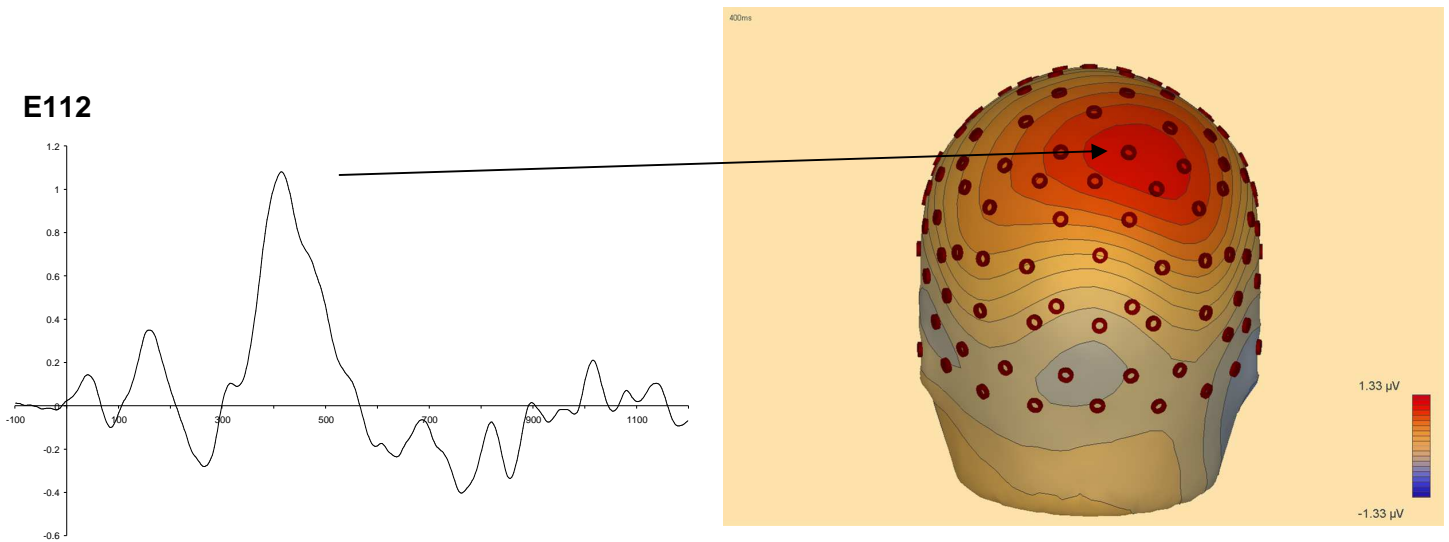


Figure 3.5 Topographic map of the difference between ERP responses to the rotated landmarks and the 0° landmark cue at 400ms after cue onset. The dark red parietal area indicates a positive difference between the two conditions graphed by the difference waveform.

Hemispheric parietal differences were also identified in the early P170 components of the waveforms at P3 (illustrated in Figure 3.4), P5, E118 (in the left parietal cortex) and their contra-lateral P4 (illustrated in Figure 3.4), P6, E121 recording sites. At P3 the largest P170 component was elicited by landmarks rotated to the left i.e. a

viewpoint from the right of the studied orientation (black dashed line). The opposite was seen at P4 where the largest P170 was elicited by rotations to the right i.e. observation from the left of the grid (grey dashed line). The lowest P170 amplitudes at these sites highlighted a concurrent attenuation of the opposite rotation, as the highest peak at P3 is the lowest at P4 and vice versa. The lateralization of the early ERPs component evoked by the landmarks is further illustrated in Figure 3.6 with the topographical distribution maps at 170ms.

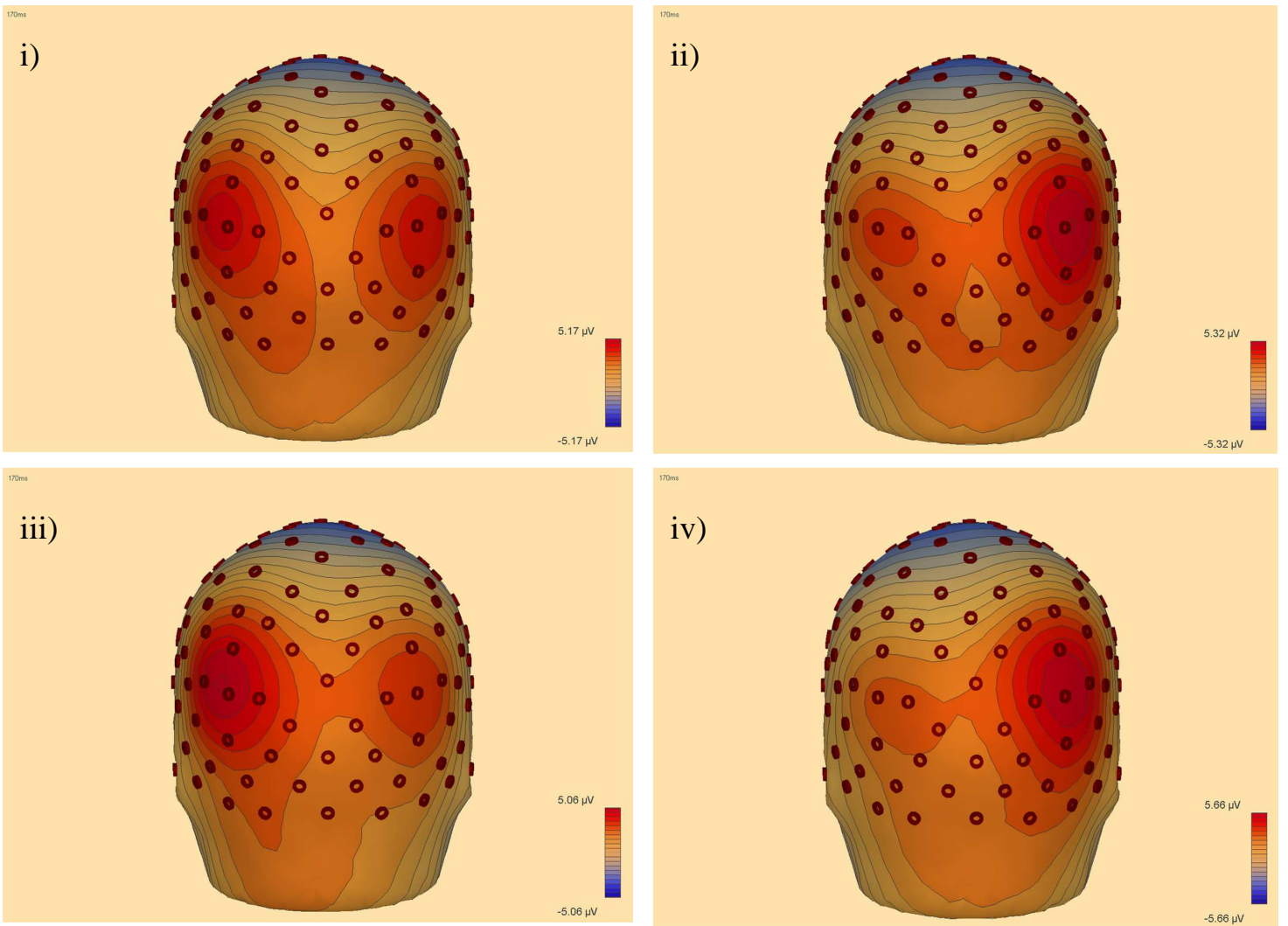


Figure 3.6 Topographic maps of ERP responses to the landmark cue at each of the four rotations 170ms after cue onset, illustrating the hemispheric dissociation found in the parietal cortex for left and right 90° rotations: (i) 0° – bilateral parietal positivity (ii) 180° – right lateralised positivity (iii) 90° left – left lateralised positivity (iv) 90° right – right lateralised positivity. The topographic maps in (iii) and (iv) were based on difference waveforms and show activations additional to the opposite 90° rotation.

A repeated-measures ANOVA was conducted to compare the mean maximum amplitudes between a group of left parietal and right parietal electrodes during the P170 component (120ms-220ms). The left hemisphere group consisted of the P3, P5 and E118 identified above and their contra-lateral sites P4, P6 and E121 represented right parietal activation. A significant interaction effect of hemispheric activation*landmark rotation was found, Wilks' Lambda = 0.647, $F(1, 17) = 9.281$, $p < 0.01$, with a large effect size, eta squared = 0.353. There was no main effect of rotation or hemisphere found suggesting the inter-hemispheric effect was only elicited on specific viewpoints. As the landmark cue terminated at 1500ms, the remainder of the epoch was not analysed for components elicited by landmarks (based on visual inspection of the scalp topography).

ERPs during Test phase – objects in correct location: A comparison of the ERP waveforms for each of the rotated conditions against the 0° studied viewpoint can be seen for midline and selected electrodes in Figure 3.7. Large parietal positivity can be seen peaking at ~560ms with P1, P2 and P3 components all contained in the rise (200-500ms) – see Fig. 3.7, CPz blue dashed box. Between P3 and the maximum positive parietal peak we found a divergence between the ERP waveform for 0 degrees and the waveforms for the rotated conditions (red dashed box, Fig. 3.7). The 0° trials elicited greater parietal positivity from 500-800ms. This difference was manifest around temporo-parietal areas also, but in the negative domain with a slightly later divergence occurring from 600-800ms (green dashed box, Fig. 3.7). The 0° trials elicited the greatest negativity at temporal sites and the difference was most prominent at TP10 indicating a slight right lateralization. No differences between the rotated conditions were evident from visual inspection of the ERP waveforms.

VIEWPOINTS

CORRECT STIMULI PRESENTATIONS

- 0 Degrees
- - 90 Degrees Right
- - 90 Degrees Left
- 180 Degrees

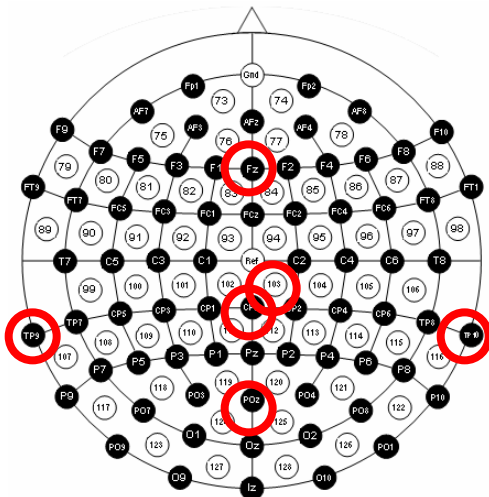
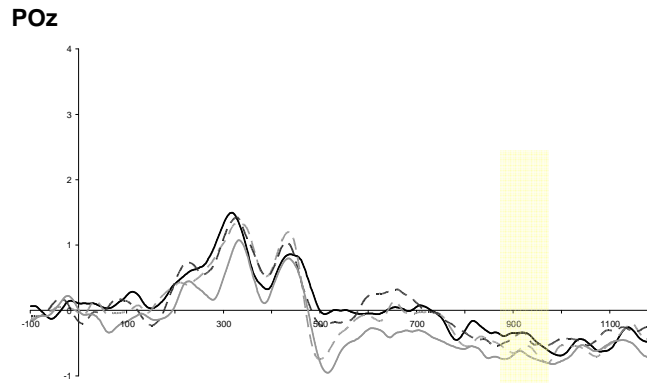
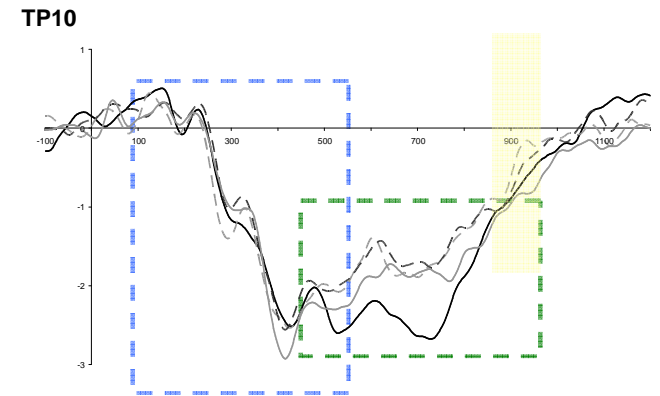
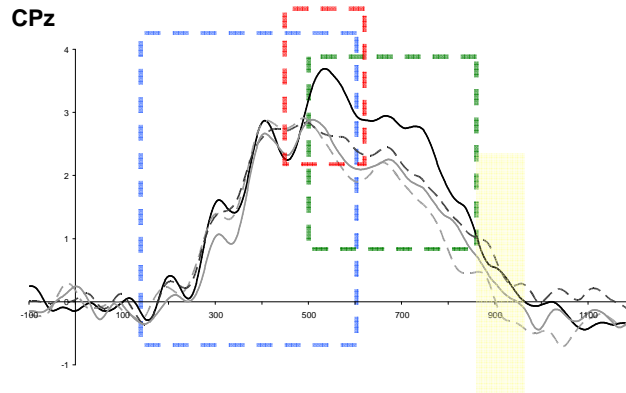
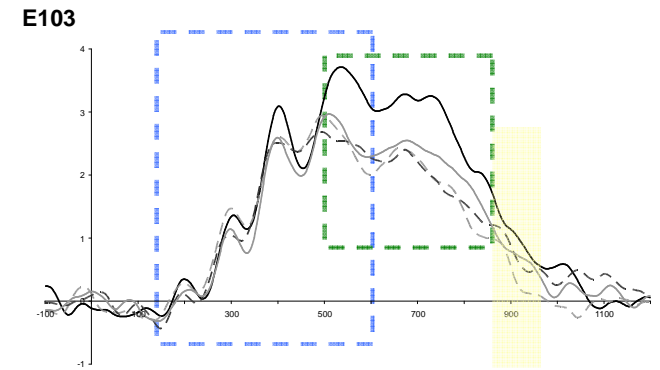
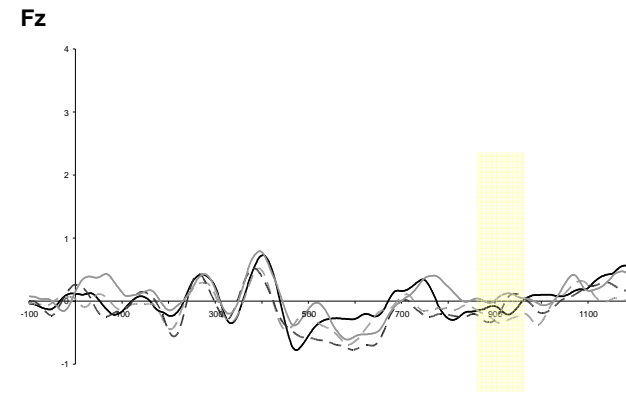
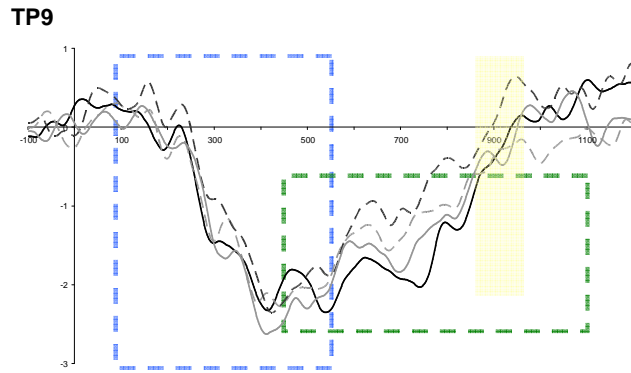


Figure 3.7 ERP waveforms averaged across participants elicited by the stimulus presentations at the four rotations: 0°, 90° rotated right, 90° rotated left and 180°. The x-axis represents stimulus onset and the epoch displayed begins at -100ms and ends at 1200ms. Electrodes are displayed based on visual analyses and for anterior-posterior comparison of the cortical gradients. The legend is displayed in the upper left corner and the location of electrode sites on the scalp is displayed in the lower left. Dashed boxes are referred to in the text and highlight specific areas of difference and components targeted for analysis. Shaded areas highlight approx. RTs with the left edge indicating 0° RTs and the right edge RTs for novel views.

A series of repeated-measures ANOVAs revealed significant differences in maximum peak amplitude (500-800ms) between the rotations at selected electrode sites (based on visual analysis): CPz [$F(3, 51) = 5.718, p < 0.005$]; E102 [$F(3, 51) = 3.950, p < 0.05$]; E103 [$F(3, 51) = 5.022, p < 0.005$]; and TP10 [$F(3, 51) = 4.682, p < 0.01$]. T-tests revealed that the differences in the ERP waveforms at these sites existed between the 0° waveform and the rotated conditions (Table 3.1). Comparing mean peak amplitudes at 0° with the combined means from all rotated viewpoints, we found significant differences at each site analysed in the cluster - CPz: $t(17) = 3.653, p < 0.05$; E102: $t(17) = 3.051, p < 0.05$; E103: $t(17) = 3.259, p < 0.05$; and TP10: $t(17) = 3.194, p < 0.05$.

Table 3.1 *P-values from t-tests comparing maximum amplitudes for viewpoints in waveforms related to correct location objects with Bonferroni corrections in parentheses.*

| <i>df=17</i> | CPz | E102 | E103 | TP10 |
|--------------------|----------------------------|---------------------------|---------------------------|---------------------------|
| 0 vs. 90L | 0.003** (0.018) | 0.008** (0.048) | 0.011* (0.066) | 0.008** (0.048) |
| 0 vs. 90R | 0.001*** (0.006) | 0.028* (0.168) | 0.003** (0.018) | 0.005** (0.03) |
| 0 vs. 180 | 0.031* (0.186) | 0.026* (0.156) | 0.042* (0.252) | 0.043* (0.258) |
| 90L vs. 90R | 0.761 | 0.526 | 0.785 | 0.631 |
| 90L vs. 180 | 0.691 | 0.534 | 0.312 | 0.680 |
| 90R vs. 180 | 0.384 | 0.929 | 0.191 | 0.253 |

*Significance levels *= $p < 0.05$, **= $p < 0.01$, ***= $p < 0.001$ without Bonferroni correction*

ERPs during Test phase – objects in incorrect location: A comparison of the ERP waveforms elicited by incorrect location trials can be seen for midline and selected electrodes in Figure 3.8. A large P500 component is visible across all rotations (see Fig. 3.8, CPz/E103 for example). Differences between the 0° trials and the rotated conditions

appeared at parietal sites ~600ms where positivity elicited by the rotated conditions began to decline more rapidly than the 0° waveform (blue dashed boxes, Fig. 3.8). The topographic map and corresponding difference waveform in Figure 3.9 show that the 0° trials elicited more positivity in parietal cortex. The maximum difference reached almost 1.2µV at 800ms. The isopot map shows a slight right lateralisation. Statistical analyses were conducted at parietal and temporo-parietal sites testing for differences in maximum peak amplitudes from 600-1000ms. A series of repeated-measures ANOVA's found significant differences at the chosen sites, except for CPz where $p > 0.05$ – E102 [$F(3, 51) = 3.016, p < 0.05$]; E103 [$F(3, 51) = 4.838, p < 0.01$]; and TP9 [$F(3, 51) = 8.014, p < 0.05$]. A series of paired-samples t-tests were carried out to assess the differences between the viewpoints (Table 3.2). The t-test results for the maximum peaks from 0° trials versus combined rotated trials at the four selected electrode sites again showed the difference existed between these viewpoints: E102: $t(17) = 3.018, p < 0.05$; E103: $t(17) = 4.071, p < 0.005$; and TP9: $t(17) = 5.279, p < 0.005$; CPz: $p > 0.05$ (Bonferroni corrected).

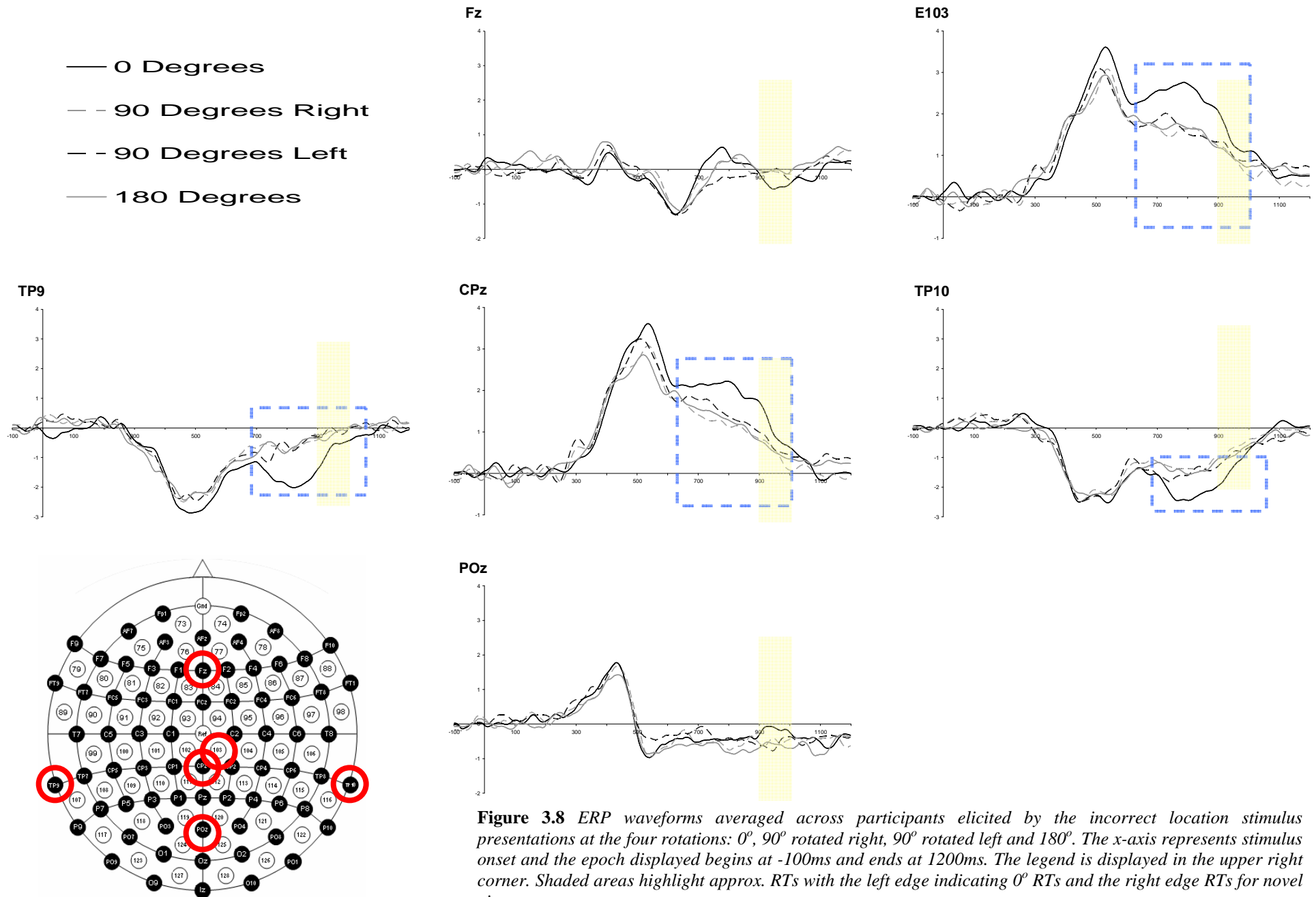
Table 3.2 *P-values from t-tests comparing maximum amplitudes for viewpoints in waveforms related to incorrect location objects with Bonferroni corrections in parentheses.*

| <i>df=17</i> | CPz | E102 | E103 | TP9 |
|--------------------|--------------------------|---------------------------|----------------------------|----------------------------|
| 0 vs. 90L | 0.013* (0.078) | 0.013* (0.078) | 0.001*** (0.006) | 0.001*** (0.006) |
| 0 vs. 90R | 0.221 | 0.116 | 0.019* (0.114) | 0.003** (0.018) |
| 0 vs. 180 | 0.033* (0.198) | 0.007** (0.042) | 0.005** (0.030) | 0.000*** (0.001) |
| 90L vs. 90R | 0.507 | 0.483 | 0.605 | 0.441 |
| 90L vs. 180 | 0.991 | 0.971 | 0.594 | 0.892 |
| 90R vs. 180 | 0.441 | 0.452 | 0.998 | 0.437 |

*Significance levels *= $p < 0.05$, **= $p < 0.01$, ***= $p < 0.001$ without Bonferroni correction*

VIEWPOINTS

INCORRECT STIMULI PRESENTATIONS



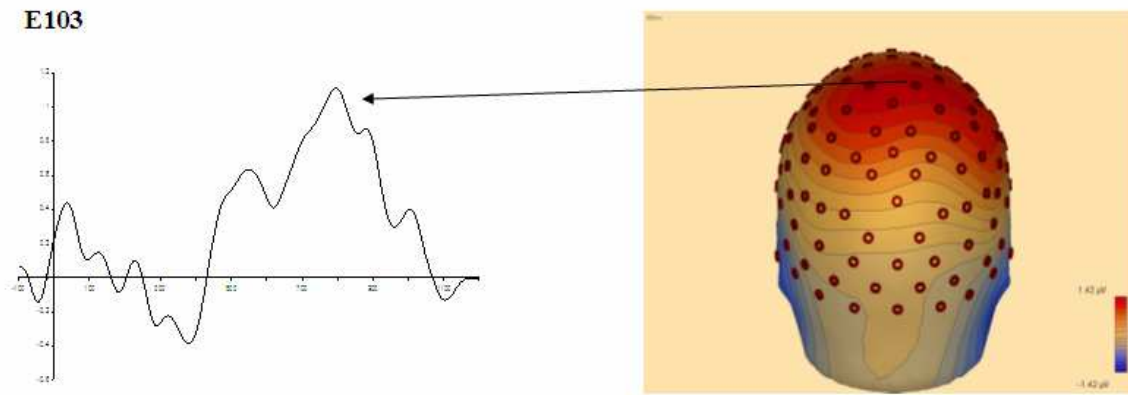


Figure 3.9 Topographic map of the difference between ERP responses to 0° incorrect presentations and the incorrect rotated conditions at 800ms after stimulus onset. This is graphed by the difference waveform at electrode site E103.

Test Stimuli - Correct vs. Incorrect location. We then decided to compare the ERP waveforms for the correct location presentations versus the trials with incorrect stimulus location. CPz was chosen as this site was used in the analyses of both conditions and appeared to reflect differences on inspection of a subtraction waveform (not illustrated). The waveforms for each location (and viewpoint) are presented in Figure 3.10. A topographical difference is evident early on in the rise of each waveform, where the correct locations elicit an oscillatory pattern absent in the waveforms elicited by incorrect locations. Both conditions elicit a maximum positive peak between 500-600ms. At each of the rotations, differences in amplitude emerge ~600ms contributing to a latency shift after 800ms. After 800ms the fall in positivity is steeper for stimuli in correct location presentations. A series of repeated-measures ANOVAs revealed significant differences for Area Under the Curve (AUC)⁴ across all but the earliest of the time intervals. No significant difference was found for the first time interval 170-230ms ($p > 0.05$), but significance was reached for 230-330ms [$F(1,17)=5.995$, $p < 0.05$]; 330-440ms [$F(1,17)=11.111$, $p < 0.005$]; and 580-780ms [$F(1,17)=18.458$, $p < 0.001$]. Where significant

⁴ AUC was chosen for this comparison as measures of maximum amplitude are subject to artefacts for epochs which contain oscillatory multi-peaking waveforms.

p-values were found a number of t-tests were conducted to assess differences across the rotations. The most apparent differences were found for the 0 degree trials with AUC at each time interval reaching significance 230-330 : $t(17) = 2.327$, $p < 0.05$; 330-440 : $t(17) = 3.356$, $p < 0.005$; and 580-780: $t(17) = 2.781$, $p < 0.05$.

CPz

— Correct location Stimuli
 - - - Incorrect location Stimuli

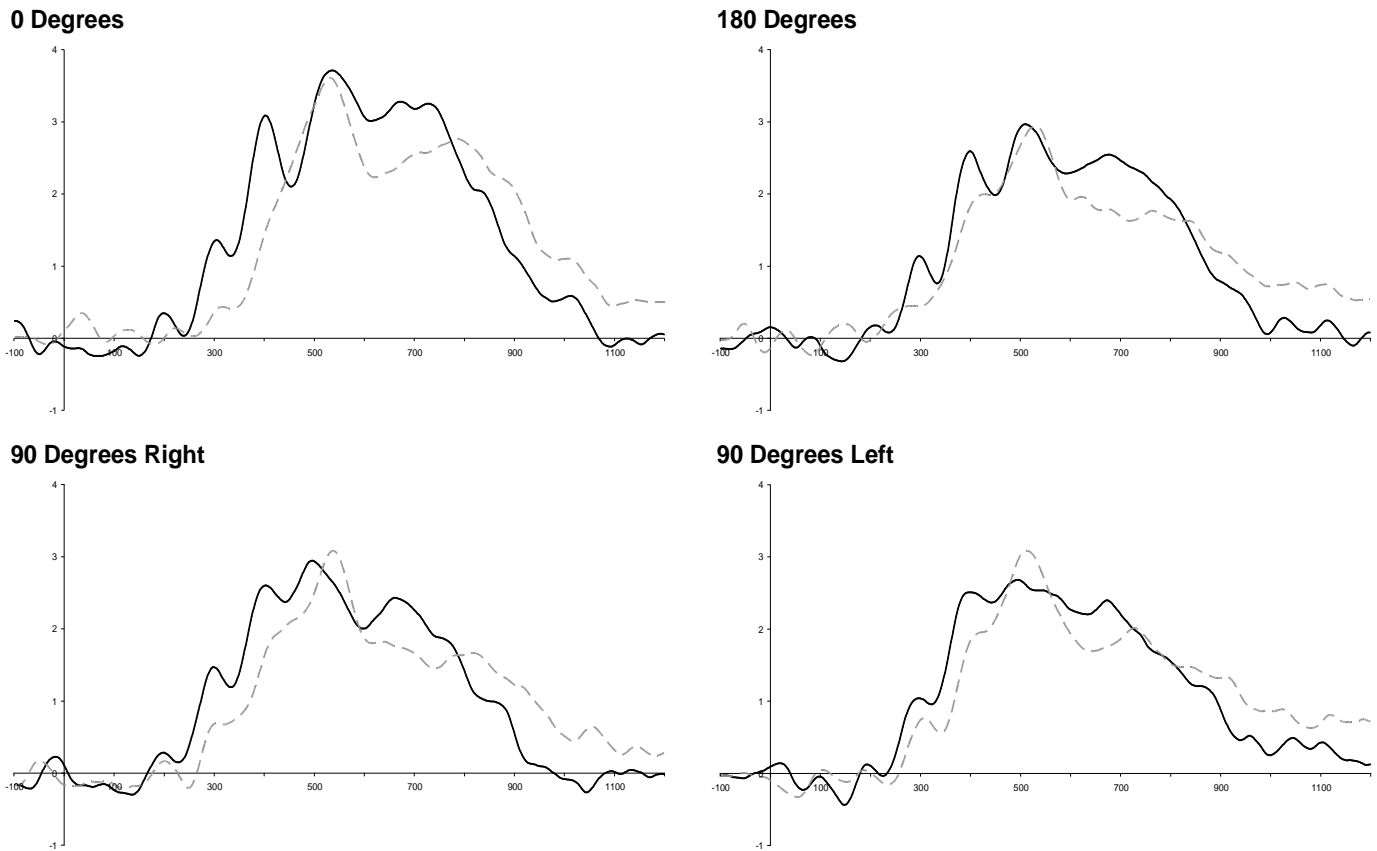


Figure 3.10 ERP waveforms from CPz averaged across participants elicited by the correct and incorrect location stimulus presentations at the four viewpoints: 0°, 90° rotated right, 90° rotated left and 180°. The x-axis represents stimulus onset and the epoch displayed begins at -100ms and ends at 1200ms. The legend is displayed in the upper right corner.

Effects of task difficulty: Since it is maintained that the Spatial Grid Task allows investigation of two distinct types of mental representation by means of viewpoint change (Old vs. New), the differences observed in the ERPs may simply be due to differences in task difficulty. As is apparent from behavioural data, participants took about 100ms

longer to respond and made more errors when performing the task from an altered viewpoint. From this it follows that rather than reflecting dissociations in the retrieval of spatial locations from different representations, the topographical distributions of the old/new effects could also be related to task difficulty. Therefore we decided to conduct a median split of the 18 subjects, similar to Mecklinger (1998), based on the performance difference between 0° trials and rotated trials. Firstly, we conducted a median split based on participants' reaction time differences on 0° and rotated viewpoints (i.e. either side of the median difference of 81.69ms. We then split the participants by accuracy differences. For this analysis corrected recognition scores (CR) i.e. the hit rates minus the false alarm rates (Snodgrass & Corwin, 1988) were used as a measure of accuracy. Here, hit rates were defined as correct responses to correctly located stimuli and false alarms were taken as the errors made in responding to incorrectly located objects. Two groups were again formed either side of the median (i.e. 7.95%). Finally, we produced two groups of participants, based on both median splits i.e. a group with large differences in both RT and CR (Poor Recognition Group) and a group with small differences in these measures across viewpoints (Good Recognition Group). Participants were excluded if they did not fall into the same group on both performance measures, giving an n=7 for both groups.

The ERPs for each group were then analysed separately. If the topography of the waveforms for both of these groups is similar to that of the Grand Mean Averages analysed in the study then there is a strong argument that it is a task-modulated recruitment of differing brain regions based on the differing ego-allocentric requirements of the task. Conversely, if the topographic effects arose from differences in task difficulty they should be absent for the subjects with small differences in task performance (Mecklinger, 1998). For the Good Recognition Group the corrected

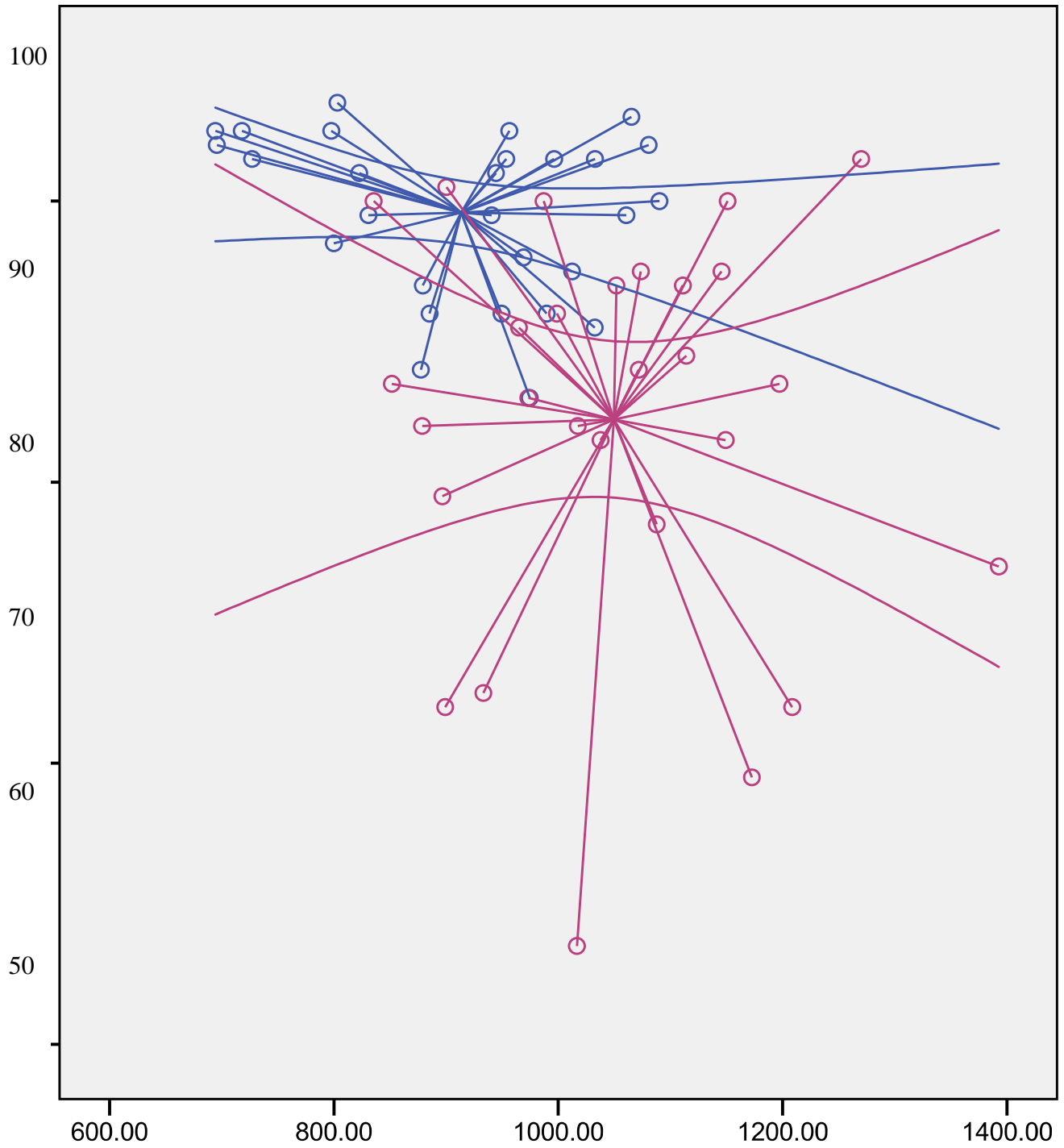
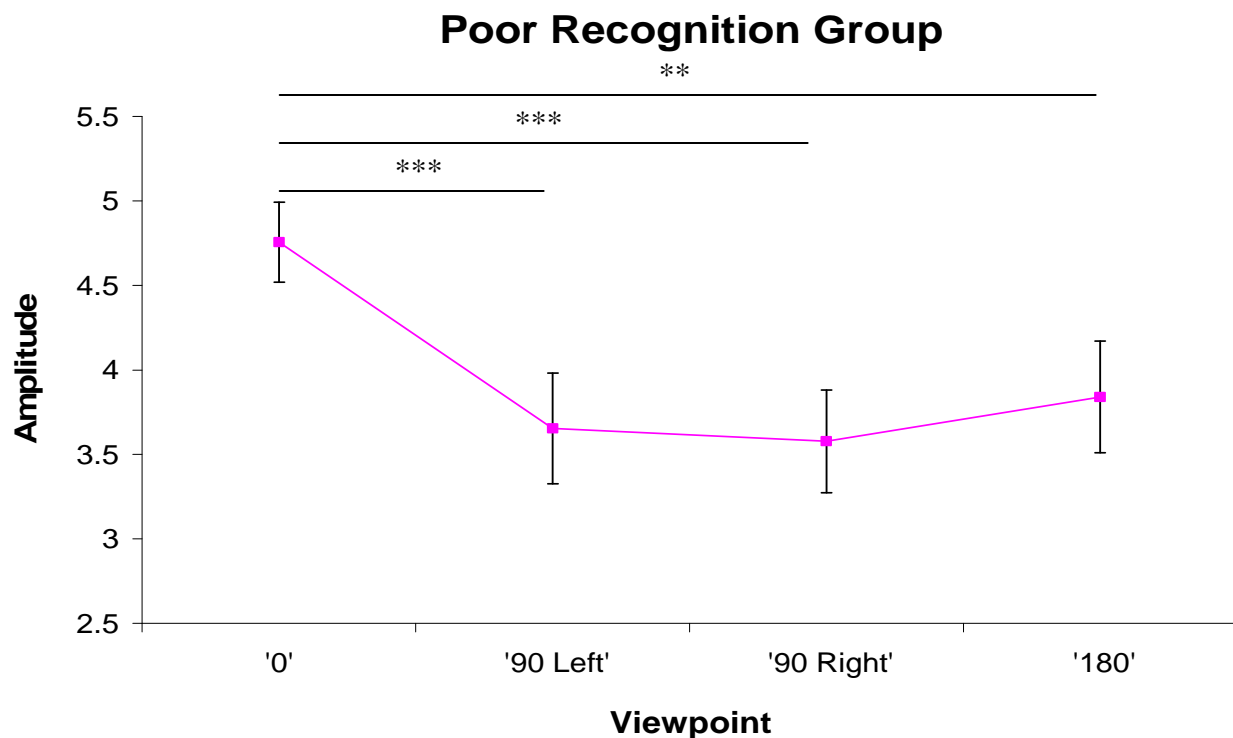


Figure 3.11 A graphical representation of the Good and Poor Groups with performance scores i.e. accuracy/RT correlations distributed around centroid points.

recognition scores were 87.9% and 85.9% for the 0° and rotated conditions respectively. The corresponding values for the Poor Recognition Group were 83.6% and 59.9% demonstrating their difficulty performing on the rotated views. As revealed by paired-samples t-tests, the difference was significant for the Poor ($p < 0.01$) but not for the Good Recognition Group ($p > 0.05$).

Differences in the ERPs for the two groups were also found after statistical analyses using the same epochs as before. For the Poor Recognition Group (Figure 3.12a), an ANOVA revealed a main effect for viewpoint [$F(3, 93) = 15.239$, $p < 0.001$]. A significant main effect for viewpoint was also found for the Good Recognition Group [$F(3, 93) = 4.093$, $p < 0.01$] demonstrating that although this group showed no significant effects of viewpoint-change in their behavioural data, the shifted-viewpoints still resulted in significantly lower amplitudes in their P300 waveforms (Figure 3.12b). A mixed-factorial between-within ANOVA was conducted to assess the effect of 'group' and its interaction with the viewpoint-change effects. Results showed that although there was a highly significant effect of viewpoint across both groups [$F(1, 62) = 38.842$, $p < 0.001$], there was also an interaction effect for viewpoint*group [$F(1, 62) = 4.739$, $p < 0.05$]. A main effect for group (i.e. difficulty) was also found [$F(1, 62) = 6.623$, $p < 0.05$]. Difficulty seemed to result in an overall increase in P300 amplitudes for the group that performed at the lower level across the rotations i.e. the Poor Recognition Group. This can be seen in Figure 3.13. Significant p-values from paired-samples t-tests are shown in Figures 3.12 & 3.13. These show that differences in P300 amplitudes existed between the 0° viewpoint and rotated viewpoints. Independent-samples t-tests found significantly higher amplitudes for the Poor Recognition Group (compared to the Good Recognition Group) for the 0° viewpoint [$t(62) = 3.324$, $p < 0.001$].

a)



b)

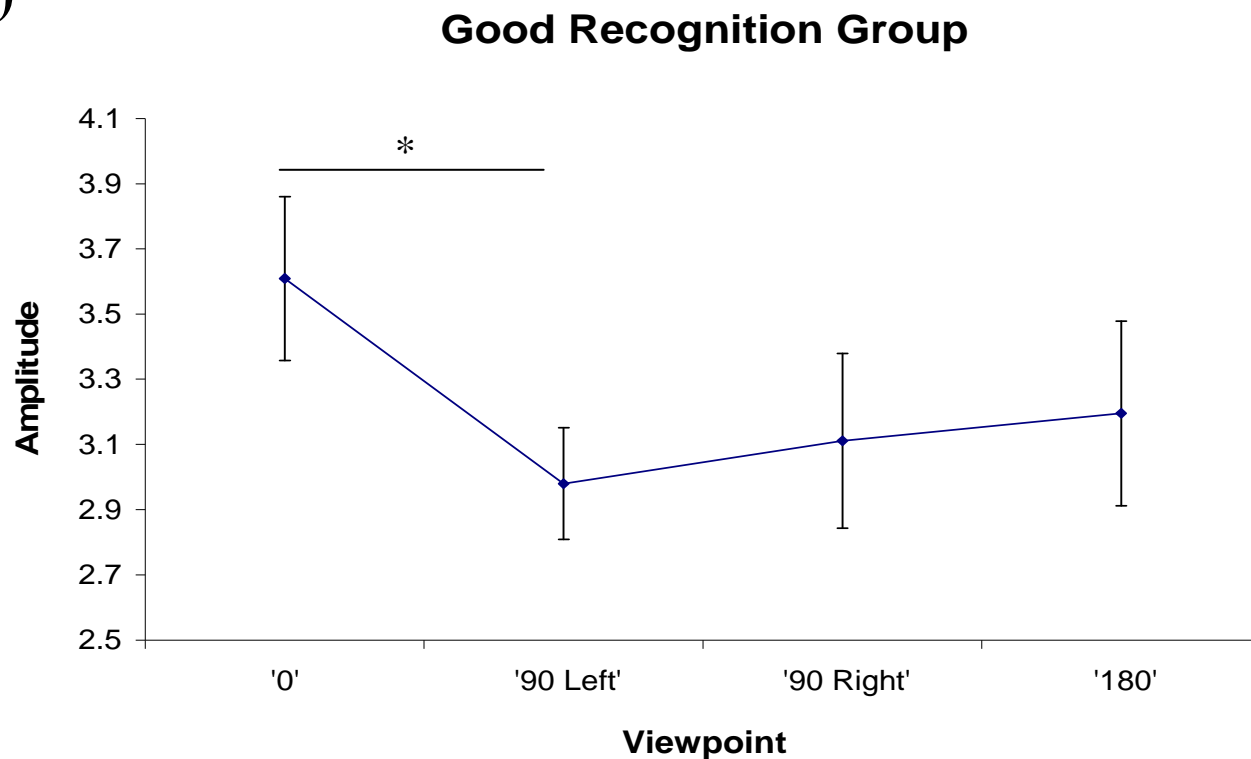


Figure 3.12 a) The effect of viewpoint-change on P300 amplitudes for participants that showed significant behavioural differences across viewpoints (POOR RECOGNITION GROUP) b) The effect of viewpoint-change on P300 amplitudes for participants that showed no significant behavioural differences across viewpoints (GOOD RECOGNITION GROUP) The effect was significant for both groups.

Effect of Difficulty on ERP amplitudes

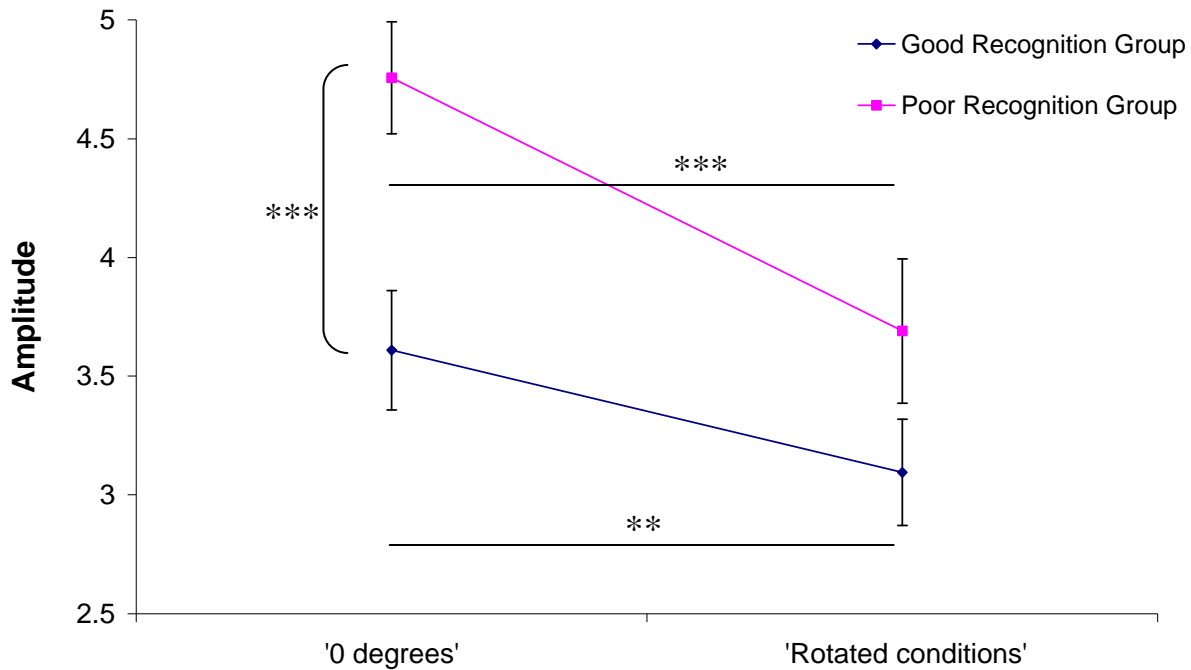


Figure 3.13 Mean differences in P300 amplitudes related to viewpoint for both the good and poor recognition groups showing the possible effect of task difficulty manifesting in increased overall mean amplitudes

3.4.3 Dipole source analysis

Following the analysis of the scalp data, we then decided to examine cortical sources of the ERPs using dipole modelling (see Methods section 2.3.3). This was done to identify possible generators that may underlie some of the differences found between viewpoints. Initial source coordinates were generated for each condition previously analysed as well as some subtraction waveforms (see Table 3.3). Figure 3.14 (a, b & c) shows a selection of these solutions superimposed over transverse MRI slices for anatomical reference. The Residual Variance (RV) was < 10% in most cases. Where this level of fit was not reached the models still retained a goodness-of-fit >80%.

Table 3.3 *Talairach coordinates of dipoles in source models and corresponding Brodmann's Areas*

| | Condition | Dip. | Talairach | (BA) | Nearest Gray Matter |
|----------------------------|---|------|-------------|------|--|
| Landmarks | 0° Landmark | 1 | -48 -59 16 | BA19 | Left Occipital Lobe, Middle Temporal Gyrus |
| | | 2 | 49 -58 8 | BA39 | Right Temporal Lobe, Middle Temporal Gyrus |
| | | 3 | 2 34 41 | BA8 | Right Frontal Lobe, Medial Frontal Gyrus |
| | | 4 | 5 -32 25 | BA23 | Right Posterior Cingulate |
| | | 5 | 28 -78 16 | BA19 | Right Occipital Lobe, Middle Occipital Gyrus |
| | Rotated Landmarks | 1 | -46 -63 23 | BA39 | Left Temporal Lobe, Middle Temporal Gyrus |
| | | 2 | 44 -63 21 | BA39 | Right Temporal Lobe, Middle Temporal Gyrus |
| | | 3 | -10 8 46 | BA24 | Left Cingulate Gyrus |
| | | 4 | 9 -57 13 | BA23 | Right Posterior Cingulate |
| | | 5 | 17 -38 21 | - | Right Caudate |
| | Subtraction: Rotated Landmarks minus 0° Landmarks | 6 | 10 53 6 | BA10 | Right Frontal Lobe, Medial Frontal Gyrus |
| | | 1 | -22 -7 -2 | BA32 | Left Anterior Cingulate |
| | | 2 | 10 -65 39 | BA7 | Right Parietal Lobe, Precuneus |
| | | 3 | -33 -45 17 | BA40 | Left Parietal Lobe, Supramarginal Gyrus |
| | | 4 | 18 -56 33 | BA31 | Right Parietal Lobe, Precuneus |
| | Subtraction: Left rotated Landmarks minus Right rotated Landmarks | 5 | 18 -38 -2 | BA30 | Right Parahippocampal Gyrus |
| | | 6 | -18 -38 -2 | BA30 | Left Parahippocampal Gyrus |
| | Subtraction: Right rotated Landmarks minus Left rotated Landmarks | 1 | -44 -46 20 | BA13 | Left Temporal Lobe, Superior Temporal Gyrus |
| | | 2 | 30 -62 27 | BA39 | Right Temporal Lobe, Middle Temporal Gyrus |
| | Subtraction: Right rotated Landmarks minus Left rotated Landmarks | 1 | 44 -46 20 | BA13 | Right Temporal Lobe, Sup. Temporal Gyrus |
| | | 2 | -30 -62 27 | BA39 | Left Temporal Lobe, Middle Temporal Gyrus |
| Correct Location Stimuli | 0° Presentations | 1 | 50 -58 12 | BA39 | Right Temporal Lobe, Middle Temporal Gyrus |
| | | 2 | -36 -59 26 | BA39 | Left Temporal Lobe, Middle Temporal Gyrus |
| | | 3 | 20 -45 36 | BA31 | Right Cingulate Gyrus |
| | | 4 | -48 -28 49 | BA40 | Left Parietal Lobe, Inferior Parietal Lobule |
| | Rotated Presentations | 1 | 49 41 28 | BA40 | Right Frontal Lobe, Middle Frontal Gyrus |
| | | 2 | -24 -66 33 | BA7 | Left Parietal Lobe, Precuneus |
| | | 3 | 9 -57 20 | BA23 | Right Posterior Cingulate |
| | | 4 | 25 -16 55 | BA6 | Right Frontal Lobe, Precentral Gyrus |
| | Subtraction: 0° minus Rotated Presentations (500-800ms) | 5 | -46 -30 46 | BA40 | Left Parietal Lobe, Inferior Parietal Lobule |
| | | 1 | 4 -34 36 | BA31 | Right Cingulate Gyrus, |
| | | 2 | 0 -36 18 | BA23 | Left Posterior Cingulate |
| Incorrect Location Stimuli | 0° Presentations | 2 | 39 -47 20 | BA17 | Right Temporal Lobe, Sup. Temporal Gyrus |
| | | 2 | -17 -77 37 | BA7 | Left Parietal Lobe, Precuneus |
| | | 3 | 23 -39 37 | BA31 | Right Cingulate Gyrus |
| | | 4 | 1 -38 21 | BA23 | Right Posterior Cingulate |
| | | 5 | 48 -17 36 | BA4 | Right Frontal Lobe, Precentral Gyrus |
| | Rotated Presentations | 1 | 43 -57 9 | BA39 | Right Temporal Lobe, Middle Temporal Gyrus |
| | | 2 | -9 -26 37 | BA31 | Left Cingulate Gyrus |
| | | 3 | 4 -88 33 | BA19 | Right Occipital Lobe, Cuneus |
| | | 4 | 52 -22 30 | BA2 | Right Parietal Lobe, Postcentral Gyrus |
| | | 5 | -52 -22 30 | BA2 | Left Parietal Lobe, Postcentral Gyrus |
| | Subtraction: 0° minus Rotated Presentations (400-900ms) | 1 | 34 -79 27 | BA19 | Right Occipital Lobe, Sup. Occipital Gyrus |
| | | 2 | -14 -60 53 | BA7 | Left Parietal Lobe, Precuneus |
| | | 3 | 17 5 24 | - | Right Caudate |
| | | 4 | -63 -31 -15 | BA20 | Left Temporal Lobe, Inferior Temporal Gyrus |
| | | 5 | 56 -33 16 | BA42 | Right Temporal Lobe, Sup. Temporal Gyrus |

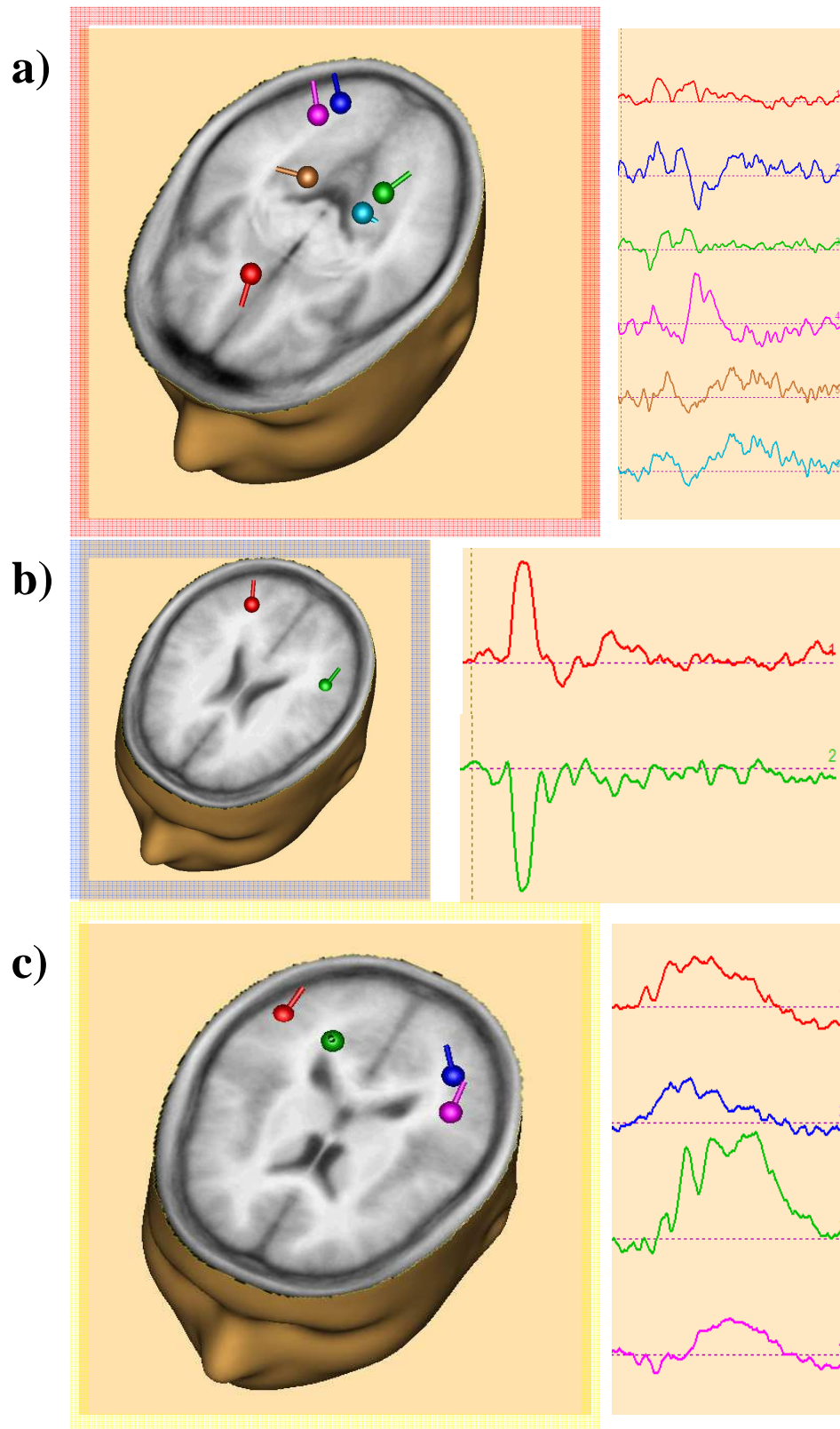


Figure 3.14. Transverse views of source models embedded in composite MRI slices created using BESA©: **a)** The dipolar solution obtained for step-wise modelling of the major deflections in the ERP response to the Rotated-0 degree landmarks. The corresponding source waveforms illustrate the time course of these dipoles and show the involvement of parietal and medial temporal sources. **b)** The dipole solution for source localization of the landmark P1 - (elicited by landmarks rotated right) **c)** The dipole solution obtained for 0 degree correct location stimulus presentations.

3.4.4 Temporal Spectral Evolution (TSE)

In the scalp data we observed distinct oscillatory patterns in the waveforms elicited by correct location stimuli (Figure 3.10). To further investigate this phenomenon and ascertain whether a spectral difference actually exists between processing of correct and incorrect locations, we employed spectral density analysis. The deflections seen in the rise of the P300 for the electrophysiological responses to correct location presentations were modelled most clearly by the right cingulate source in the model displayed in Figure 3.14c – green source waveform (described in Table 3.3). In order to test whether the observed deflections in the source waveform were due to a spectral power increase over a certain frequency range, the entire data set (i.e. the full EEG from all participants) was subjected to a spectral analysis focusing on the ERPs elicited by correct location presentations. Using the source model (Figure 3.15a), a montage was created in BESA to transform the surface data into brain space for analysis at the source level (see the Methods Section for more details). A TSE map was computed showing the time-frequency characteristics of the event related data (Figure 3.15b). These plots show increases in slow wave activity (relative to baseline) in both right and left middle temporal gyri and more pronounced activity in the right cingulate source.

To assess the significance of these time-frequency activations, the case re-sampling of 1000+ samples (i.e. bootstrapping) was undertaken. Results showed reliable theta activity exclusively in the cingulate source – significant at the $p < 0.05$ level (Figure 3.15c). The bootstrapping technique provides robust evidence for the involvement of a cingulate generated theta rhythm in the elicitation of the P300 related to correct locations.

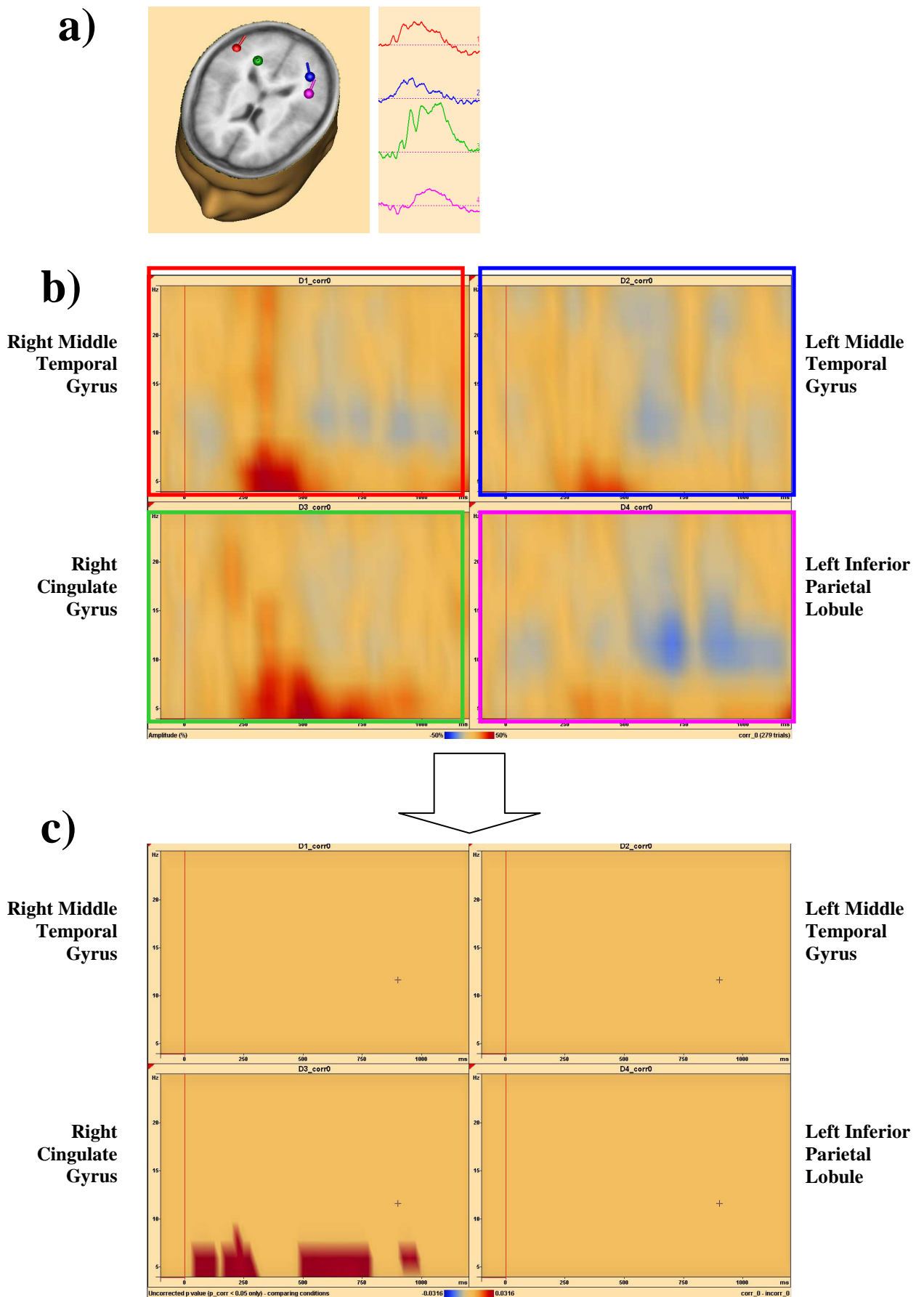


Figure 3.15. *a) The dipole model and source waveforms used to construct a source montage for spectral analysis of the data set b) The temporal spectral evolution of source activity related to correct location presentations c) Plots generated after bootstrapping showing areas of significant power increases in the time-frequency domain.*

3.4.5 Summary of electrophysiological results

A number of significant differences were seen in the ERP waveforms related to the 0° viewpoint compared to the rotated viewpoints. The earliest differences emerged in a P170 related to the landmark presentation. This component was found to be sensitive to viewpoint with a hemispheric lateralisation found for 90° rotations (Figures 3.4 and 3.6). In addition to this component, modulations in a P300 component resulted in significant differences in amplitude between conditions. This difference was present in the P300 related to landmarks (Figure 3.4) and objects (Figures 3.7 and 3.8). For the landmarks, the rotated viewpoints elicited greater amplitudes, with maximal differences found ~400ms at right lateralised centro-parietal sites (Figure 3.5). Conversely, the P300 related to object presentations showed larger late-going amplitudes for the 0° viewpoint compared to the rotated viewpoints. These amplitude differences in the P300 were not found to relate to differences in difficulty between viewpoints (Figures 3.12 and 3.13). Source models were generated to assess possible differences in the structures underlying these scalp components. Finally, electrophysiological differences based on object location were also found where correct locations elicited theta oscillations in the P300 with a modelled cingulate generator (Figures 3.10 and 3.15).

3.5 Discussion

Performance measures

This study examined the processing components and corresponding sources of spatial memory for egocentric and allocentric representations. The behavioural data indicate that participants responded faster and more accurately to objects presented at 0° (egocentric orientation), and of the less accurate responses after rotation, the incorrectly located objects were more readily recognised. The second finding here may be an artifact due to probabilistic aspects of the task; an object could be incorrectly located in 13 out of 14 free squares, whereas only in one square out of the 14 free squares could it be classified as correct. The lack of a significant difference in accuracy on the 0° trials between correctly and incorrectly located objects suggests that participants were not responding with a bias, favouring a response type (correct; incorrect). The longer response time during the rotated conditions may be due to stimulus evaluation processes and transformation of allocentric views to egocentric representation or vice versa. The result that participants' performance on rotated conditions was similar no matter the degree of rotation suggests that there was more involved than just mental rotation, and perhaps suggests an egocentric / allocentric distinction.

Mental rotation studies have linked degree of rotation to accuracy and response time. Diwadkar and McNamara (1997) found that when subjects were shown a scene of scattered objects from one viewpoint and given a recognition memory test using scenes from a second viewpoint, their response latencies varied linearly with the angular difference between the views (see also Jordan *et al.*, 2001). This linear relationship was not evident in the present study, thereby arguing against the probability that mental rotation alone is sufficient to execute this task. When dealing with an environment like

the one presented in this experiment, which had no walls or surrounding ‘distal’ room cues, the left and right rotations seem to prove more difficult than previously reported in experiments, for example the courtyard experiment (King *et al.*, 2002). Since differences between the rotated viewpoints did not reach significance, the data warrant further comparative studies using enclosed and open environments. It may be the case that geometric room cues play a confounding role in enclosed environments, enabling participants to use mental rotation more readily.

Overall, behavioural results agreed with the current consensus on viewpoint-dependence and orientation specificity in spatial representation. Recognising views from orientations that are not trained requires extra processing time and is subject to errors (Christou & Bühlhoff, 1999; Chua & Chun, 2003; Diwadkar & McNamara, 1997; Nakatani, Pollatsek, & Johnson, 2002; Shelton & McNamara, 1997, 2001; Sholl & Nolin, 1997). Recently Waller (2006) highlighted the importance of viewpoint specificity and the confounding effect of viewpoint on studies that manipulate orientation. It seems both orientation and viewpoint translations may occur after rotation of an array, each effecting cognitive load and response time.

Event-related potentials and sources

In addition to the behavioural differences, we found significant differences in the waveforms related to 0° and rotated viewpoints. These differences were seen in both the Landmark and the Object presentation phases of the test. It is worth noting, that although anatomical distinctions have previously been made between spatial representations using other imaging techniques, the current study provides, we believe, the first

electrophysiological support for this egocentric-allocentric dissociation along with valuable temporal information that is not readily available with other imaging techniques.

Landmarks

The differences observed in the ERPs for 0° and rotated viewpoints during landmark presentation suggests that even during this initial presentation that allocentric/egocentric translations may be taking place. There is a growing consensus that dependence on allocentric representations increases with the amount of change between presentation and retrieval (Burgess, 2006). The extra positivity in the P300 elicited by rotated conditions could be associated with extra excitatory responses in parietal areas that may be due to the translations required for allocentric processing. The fact that all three rotations elicited higher positive amplitudes suggests that similar cognitive processes were occurring; perhaps drawing on an allocentric representation. Burgess (2006) states that input to and output from allocentric systems are mediated by transient egocentric representations due to the egocentric nature of perception and imagery. Therefore the additional positivity found at parietal sites may represent three cognitive processes, allocentric and egocentric, and the translations between them.

Differential sources underlying the propagation of the P300 may untangle these processes. For example, the posterior cingulate gyrus (PCG) was modelled as a source for both 0° and the rotated landmarks. Although Dean and Platt (2006) implicated the PCG in the allocentric representation of visual space (recording from depth electrodes in the macaque), earlier evidence suggests a more mediating role for this structure i.e. translational processing. Sutherland *et al.* (1988), for example, implied that posterior cingulate areas play an essential role in the use of topographical information, by

transmitting and elaborating information passing between the hippocampal system and neocortical association areas. Similarly, Vogt *et al.* (1992) posited that the PCG participates in the transformation of egocentrically referenced visuospatial representations in parietal cortex into allocentrically referenced spatial representations in the hippocampus and surrounding cortex. This suggested role of the PCG in egocentric/allocentric translations is supported neurophysiologically, as the cingulate receives direct afferents from the subiculum (Finch *et al.*, 1984; Cavada and Goldman-Rakic, 1989).

The sources from the allocentric vs. egocentric difference waveform for the landmarks highlight the right precuneus, the cingulate gyrus and the parahippocampal gyrus, suggesting a possible role for these regions in allocentric processing. Previous support for the involvement of the precuneus in allocentric spatial location encoding and recognition comes from mental rotation studies. Frings *et al.*, (2006), for example, found that regions in the precuneus were bilaterally associated with allocentric encoding and retrieval of spatial locations in virtual 3D. Suchan *et al.* (2002) also identified the importance of the precuneus in spatial memory using PET during a mental rotation task, while Harris & Miniussi (2003) demonstrated using repetitive transcranial magnetic stimulation (rTMS), the importance of this area in general, for mental rotation. Disrupting neural activity in the right parietal lobe interfered with task performance, but only when rTMS was delivered 400 to 600 msec after stimulus onset. Interestingly, as was observed in the subtraction waveform for the landmarks in the current study (Figure 3.5), the greatest difference between allo- and egocentric conditions was found during this time interval. This would perhaps suggest that spatial manipulations within a mental representation occur with the peaking of a P300 component.

The source in the parahippocampus may reflect the role of the medial temporal lobes (MTL) in spatial memory and may provide additional evidence that egocentric/allocentric translations occur during the landmark phase. Although the involvement of the MTL in allocentric representation is well documented (Duvernoy, 2005; Maguire *et al.*, 2000; Nadel, 1991; O'Keefe, 1991; Rolls *et al.*, 2005), the source waveforms give a temporal aspect to their involvement (Figure 3.12a) showing a possible intermediary involvement of the parahippocampus between precuneus and parietal activations, further suggesting translations.

Prior to the P300, the P170 (henceforth referred to as P1) also seems to suggest that reorienting oneself to the rotated environment occurred during the landmark phase. As illustrated, before the object appears onscreen, a P1 related to degree of rotation is elicited by the landmarks. This P1 had a hemispheric dissociation, and was followed by a P300 where, as mentioned, the rotated conditions evoked significantly greater maximum amplitudes over parietal sites. It seems that the recognition of orientation in an environment may occur at a perceptual level, implicit and somewhat separate from later cognitive processing. However, depending on the 90° viewpoint, visual input was lateralised to the left or right hemifield (Figure 3.1b & c). Electrophysiologically, basic hemispheric differentiation in sensory input (visual spatial selective attention) is usually observed over occipital cortex (Mangun *et al.*, 1998), so although the dissociation was observed over parietal sites (Figure 3.6), the P1 effect could have been driven purely by higher-level processing of the differences in retinal input.

Object Presentations

When the Test objects were presented, the 0° trials elicited the greatest positivity, and this was again most pronounced over parietal sites. Translations may still occur after the object is presented, but the additional positivity during this period may also be due to stimulus evaluation processes and visual scene recognition. Due to the large number of trials in the study block, the egocentric 0° orientation may have elicited a larger parietal positivity as it was being recognised as a scene (this possibility will be examined later in Chapter 5). Indeed, Shelton (1999) suggests that spatial representations may consist of little more than the views experienced during training; therefore performance after rotation requires internal manipulations of a scene back to the original view. Waller (2006) found evidence that moving viewpoint without changing orientation leads to a decrease in performance on scene recognition/object location tasks, suggesting that to evaluate location, internal manipulations of viewpoint take place. The additional positivity may be merely an electrophysiological marker of recognition of a familiar scene (the studied view). When spatial knowledge is acquired and tested through scene recognition, what is stored may be little more than a 2-D image of the scene that was viewed during training (Waller, 2006). If, as suggested above, allocentric/egocentric translations occurred predominantly during the landmark phase then once the object was presented, the task may be as basic as matching-to-sample (where 0° and ‘correct location’ trials elicit larger P300’s than rotated or ‘incorrect location’ trials respectively). This topographical difference between the waveforms demonstrated an old/new effect for viewpoint as well as spatial location (Mecklinger, 1998). Whatever the reason, source analysis found that when objects were in their correct location, irrespective of orientation, a putative source in the inferior parietal lobule (BA40) was activated. Interestingly, in a

PET study comparing visual long-term memory for spatial location and object identity, Moscovitch *et al.* (1995) also identified this region's involvement in the retrieval of spatial location.

The cingulate gyrus (BA31) was also identified in the source analyses and accounted most for the positive deflections seen in the ERP waveforms. It is possible that the theta activity exhibited by BA31 (Figure 3.15) may have entrained more neurons across parietal areas giving rise to the larger P300 amplitudes seen for correct vs. incorrect locations (Figure 3.10). This would fit with a study by Klimesch *et al.* (2001) who reported that increases in theta seem to be related to general memory retrieval processes. Although significant differences between retrieval (hits) and correct rejections were not found in the theta band for their study, the authors suggest a role for theta in the old/new effect (Figure 3.16). Thereby, an increase in theta power is observed following presentation of studied vs. novel stimuli; which was the case in our study.

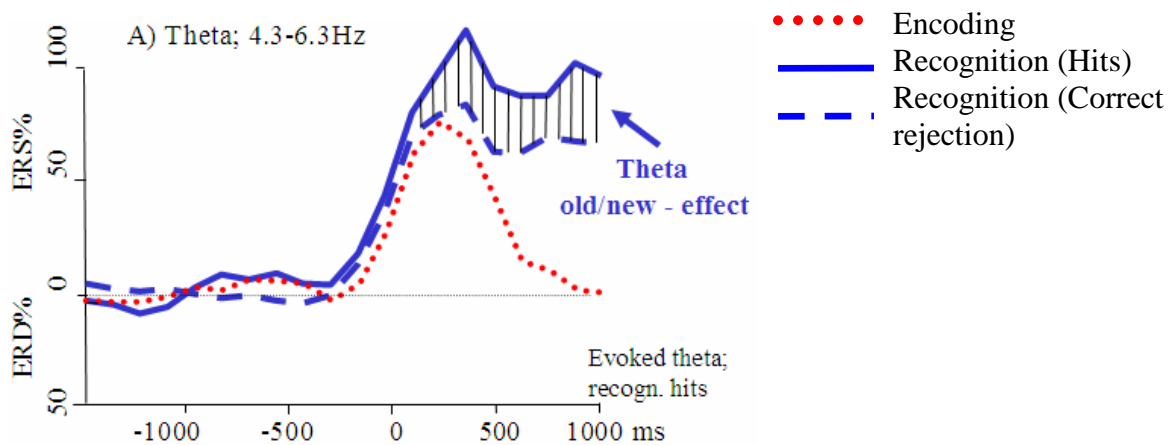


Figure 3.16. Cumulative ERD/ERS data from Klimesch *et al.* showing relative increases in theta power between encoding and retrieval. This data is reproduced from Klimesch (2008) *Workshop for Consciousness, Brain Rhythms and the Action-Perception cycle*.

In an attempt to avoid the criticism that the differences observed in our data, particularly between 0° and rotated viewpoints, was merely due to differences in task difficulty we re-analysed the data by splitting the participants based on performance and comparing the grand mean ERPs for both groups. The re-analysis of the data after splitting by recognition group (Good and Poor) suggests that an attempt to simply explain the electrophysiological differences between the studied and novel viewpoints by task difficulty would be paradoxical. The mean amplitudes of the P300 were seen to increase based on task difficulty (i.e. in the Poor Recognition Group – Figure 3.13), whereas mean amplitudes significantly decreased for both groups when performing on the novel viewpoints. This advocates an alternative explanation, involving an internal process which modulated the observed differences which we propose to be a spatial process involving ego- and allocentric mental representations.

Finally, the prediction on stimulus evaluation (correct minus incorrect location) was supported with an increased parieto-occipital P300 for correct location presentations, agreeing with Mecklinger's (1998) findings. In terms of our other predictions, source analyses did not provide many deep subcortical dipoles in medial temporal areas such as HF. Egocentric retrieval was predicted to activate parietal cortex which was confirmed and activations were predominantly right lateralized. However the medial temporal sources were less medial than predicted with dipoles instead in the middle and superior temporal gyri. Parahippocampal activation was only found in one dipole model, modelling the additional positivity seen for the rotated landmarks, but the identification of parahippocampal sources from data recorded from the scalp is a remarkable finding and avows to current opinion about the importance of the medial temporal lobes in spatial representation. It is noted as a caveat however, that source localization from ERPs is not

an infallible technique with the disadvantage of low spatial resolution (See Methods section 2.1.4).

In summary, our findings suggest that reorientation was demonstrated to occur with the aid of intra-environmental landmarks, with left/right rotations being differentiated rapidly, and accompanied by distinct electrophysiological componentry. To our knowledge, this is the first study to report electrophysiological differences between spatial representations. A parietal P1, displaying a hemispherical dissociation was followed by a P300, also sensitive to rotations from the studied viewpoint. Dissociations in cortical activation during the presentation of the landmarks manifested ~400ms suggesting that ego-/allocentric conscription occurred before object-location evaluations were made. Correct location objects elicited greater parietal positivity; with the related P300 exhibiting unique theta power compared to incorrect location waveforms. Parahippocampal sources along with a number of sources in the cingulate and parietal cortices were found to model a distributed network underlying spatial representation, where allocentric and egocentric processes interact in a reciprocal manner.

Although we have ruled out task difficulty as a possible confound in the present chapter, other issues concerning scene recognition, mental rotation, ecological validity and the possibility of intrinsic axes that aid performance all remain likely criticisms. The following chapters aim to address these concerns.

4

Chapter IV

Extrinsic cues and their effect on
allocentric task performance after
viewpoint-change

I would like to thank Della Rath and Andrea Hughes for their help in collecting the data for this chapter

4.1 Abstract

This Chapter reports an experiment undertaken to test the validity of the method of viewpoint presentation in the Spatial Grid Task. Here we investigated the possibility that the lower levels of performance observed on novel, compared to studied viewpoints in the original experiments were due to the detrimental effect of instantaneous transition. For this experiment, two groups of participants received either verbal or visual cues during the Spatial Grid Task recognition test, prior to rotations of viewpoint around an object array. These cues informed the participants of the angular displacement in viewpoint to expect before they then responded to object-locations within the array. A third, control group received no cue information. Results revealed that the method of presenting shifted viewpoints without a participant's observation of the transitions between the viewpoints was ecologically valid as no significant effect of cue type was found.

4.2 Introduction

One issue that arose while conducting our Spatial Grid Task in Chapter 3 was the use of instantaneous transitions to novel viewpoints i.e. the presentation of test viewpoints without the participant witnessing the transitional change. This led us to examine the question of whether this type of ecologically invalid presentation could be detrimental to performance on the rotated trials. The importance of preparatory cues on recognition of objects from shifted viewpoints was first suggested in experiments by Shepard and Cooper (1982). In 2D mental rotation exercises they presented subjects with shapes and then gave them a prior indication of the direction in which the shape might be rotated. Participants were asked to first imagine what the object would look like from the cued orientation prior to the presentation of the test stimulus. The time taken to perform this imagined rotation was suggestive of an analogue process, as suggested in their previous experiments (Shepard & Metzler, 1971). However, the authors found that the time taken to respond to the self-initiated stimulus presentation was not view-dependent suggesting that the time-consuming variable in responses is the time taken to work out the appropriate transformation. If the orientation difference between the learned view and the current view is known this could allow for preparatory processing that facilitates view-independent recognition (Christou *et al.*, 2003).

The importance of extrinsic cues in the perception and recognition of spatial layout has also been documented by Simons & Wang (1998) who found that participants who perform their own movements around a collection of objects are less prone to making mistakes in identification of their spatial layout than when the objects are rotated by the same amount while the participant stands still (see also Wang & Simons, 1999). The authors attributed this to an ability to spatially update one's mental representation

according to the knowledge of their own movement (i.e. an extrinsic cue). However, a replication of this result using purely visual virtual reality (Christou & Bulthoff, 1999) suggested that rather than movement cues, merely witnessing the viewpoint transition could, in itself, cue object recognition from the new viewpoint. To further test the possibility that knowledge of the extent or direction of the transformations in viewpoint can aid subsequent object recognition, Christou *et al.* (2003) conducted four experiments to assess the effect of view information (e.g. extrinsic visual cues) on object recognition from novel viewpoints. Christou and colleagues also conjectured that much of the difficulty found in recognising novel objects in previous studies may relate to their presentation in isolation, without contextual or background information; their first experiment therefore assessed whether the environmental background influences recognition performance. The second addressed more specifically the benefits of the environment as a fixed frame of reference for specifying the changes in viewpoint. The third experiment tested the utility of an abstract but explicit indication of the observer's original viewpoint presented simultaneously with the test objects, and the final experiment assessed the effect of an explicit viewpoint indicator available only prior to the presentation of the object. Results showed a significant reduction in error rates when the environment was present as a fixed frame of reference. In addition to context, cue information about the new viewpoint relative to the original significantly facilitated object recognition. Facilitation occurred for accuracy rather than reaction time (Shepard & Cooper, 1982) suggesting a qualitative difference in task demands for 2D and 3D object recognition.

Cued presentations have been used extensively in the selective attention literature. For example, Posner (1980) distinguished between central and peripheral cues in

selective attention. Central cues typically appear at fixation and indicate symbolically where the target is likely to appear (e.g. the cue might be an arrow; see Posner, 1980). Peripheral cues appear away from fixation, usually at the location of the target (e.g. Eriksen & Hoffman, 1972; 1973). As central cues are separated from the target presentation, they must be interpreted before the observer knows how to re-orient. Posner (1980) believed that orienting could be measured in the absence of observable behaviour, i.e. eye or head movements, through the use of cued presentations (see also Posner & Petersen, 1990; Posner, Snyder & Davidson, 1980). Indeed, the final test by Christou *et al.* (2003) utilised a central cue (an explicit viewpoint indicator) as opposed to a peripheral orienting cue. Interestingly, William James (1950/1890) suggested object motion as a class of peripheral cue that could produce reflexive orienting.

The present study aims to use both central (endogenous) and peripheral (exogenous) cues to examine spatial memory performance. More specifically, we aim to assess the effect of extrinsic cues on performance in the Spatial Grid Task (see section 2.2.2) by presenting verbal (central cues) or visual (peripheral cues) information to participants notifying them of the immediate viewpoint transitions and the angular displacements involved. As the objects used in the spatial grid have no canonical view, the viewpoint-dependence of object recognition should not influence performance and the tests should instead isolate the effects of cued viewpoint-change on object-location memory. Participants will be compared to a control group who will receive no cue information, similar to the original experiment described in Chapter 3. This experiment will therefore also test the ecological validity of the original presentation method (i.e. viewpoint changes occurred without the intervening transitions being observed).

If mental rotation is solely responsible for performance differences across viewpoints, then the cued conditions should reduce the time taken to work out the appropriate transformation and consequently, a decrease in reaction time will be observed for the rotated viewpoints. If, on the other hand, differential access times to the appropriate representation are the cause of performance differences across viewpoints, then the cues will reduce reaction times for all viewpoints. It is predicted that the latter case will be supported: i.e. that the introduction of cues will not selectively affect performance on the rotated viewpoints. Nevertheless, for the original task to be ecologically valid, the cues themselves ought not produce significant overall differences in performance when compared to the uncued control group. In addition to this, rotational effects must remain present for the cued groups in order for the argument against pure mental rotation to be upheld.

4.3 Methods

4.3.1 Participants

The participants of this study consisted of an *ad-hoc* sample of 36 undergraduate volunteers. The ages of the subjects ranged from 19-25 years (mean age = 21.8 years). Of these participants, two were removed for misinterpreting the method of responding and one was an outlier (i.e. >3 SDs). All participants gave informed, written consent before participation. The experiment was conducted in accordance with the Code of Ethics of the World Medical Association and the ethical standards of the APA as well as abiding by the NUI Maynooth University Ethics Code.

4.3.2 Stimuli

The Spatial Grid Task was used for this experiment – see General Methods section 2.2.2. All stimuli were again presented using E-Prime on an Intel Pentium 4 Processor (3.00GHz CPU) and displayed on an LCD monitor. They consisted of 8 different objects including a bin, a bucket, a post-box, a road-cone, a fire hydrant, a tree, a tyre and a keg and distractors included a parasol, a microphone stand, a cactus plant, a blender, a fire extinguisher, a stool, a lamp and a cinder block.

4.3.3 Procedure

During a Study phase, participants learned the locations of 8 objects (presented one at a time) within the environment. Each object was presented 8 times in a pseudo-random order for a total of 64 trials. A trial consisted of a fixation cross (750ms), landmark

presentation (1500ms), and then the object presentation (2000ms). Trials continued as described for the Test phase; subjects had to recall the objects' locations from various viewpoints (0° study viewpoint, 90° left, 90° right and 180°) and responses were made during the 2000ms object presentation. Subjects were assigned to one of three test conditions: 1) No Cue as to the viewpoint rotation 2), a Verbal Cue (e.g. 180°), or 3) a Visual Cue (the environment was seen to rotate to the next viewpoint). An example of a trial from each of these conditions can be seen in Figure 4.1. The landmark presentations prior to the objects being displayed also allowed for evaluation of the viewpoint changes. The Test phase consisted of 128 randomised trials (8 objects x 4 location (2 x correct/2 x incorrect) x 4 viewpoints).

Accuracy and reaction times were both recorded during the test phase of the experiment. A correct response occurred if the participant pressed the left mouse button when a correctly located object appeared and the right mouse button when an object appeared in an incorrect location. Pressing the opposite button than that required or failure to respond within 2000ms was logged as an incorrect response. Reaction times were measured as the interval between presentation of the stimulus and the response, and were recorded automatically for both correct and incorrect trials.

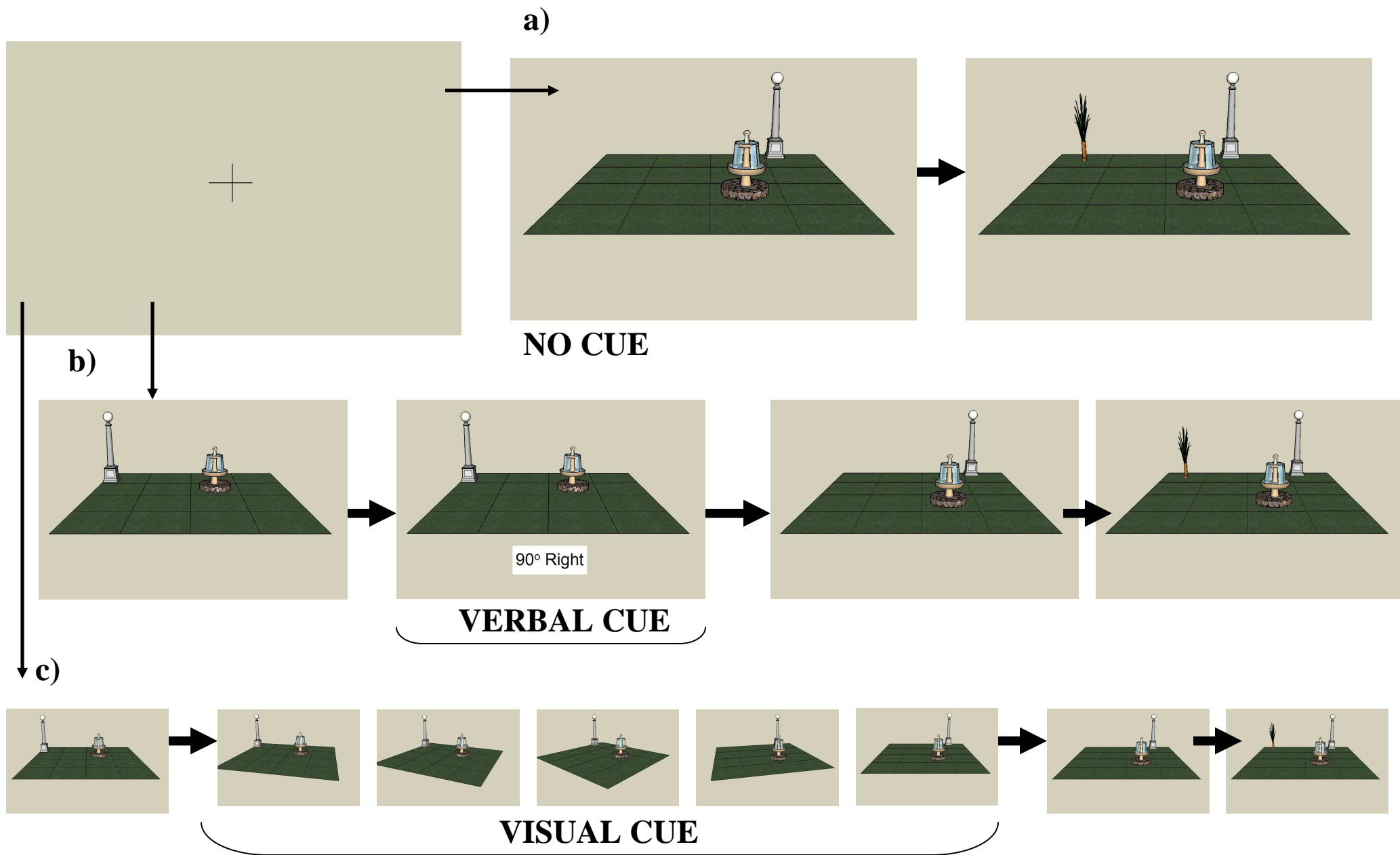


Figure 4.1 Example of the cue types given to participants prior to a stimulus presentation from the right-hand side of the array (clockwise rotation). **a)** Fixation cross (750ms), test viewpoint landmarks (1500ms), object presentation (2000ms) **b)** Fixation cross (750ms), reference viewpoint landmarks (1000ms), verbal cue (2000ms), test viewpoint landmarks (1500ms), object presentation (2000ms) **c)** Fixation cross (750ms), reference viewpoint landmarks (500ms), visual cue (500ms), test viewpoint landmarks (1500ms), object presentation (2000ms)

4.4 Results

Accuracy: A mixed-factorial ANOVA of the accuracy scores with Cue Group (no cue, verbal cue, visual cue) as a between-subjects variable and Rotation (0 degrees, 90 degrees, 180 degrees) and Location (correct, incorrect) as within-subjects variables revealed a significant effect for Rotation/Viewpoint [$F(2, 60)=11.170, p<0.001$]. No main effects of Location [$F(1, 30)=0.013, p>0.05$] or Cue Group [$F(2, 30)=1.630, p>0.05$] were seen and no interaction effects were found (Rotation*Cue Group [$F(4, 60)=1.116, p>0.05$]; Location*Cue Group [$F(2, 30)=1.216, p>0.05$]; Rotation*Location*Cue Group [$F(4, 60)=1.255, p>0.05$]). Although average scores were higher for the groups that received cues (see Figure 4.2), *post-hoc* Bonferroni tests revealed no significant differences for cue type. A series of Bonferroni-corrected paired-samples t-tests revealed significant differences between the average accuracy scores on the 0° viewpoint (86.4%) compared to both the 90° viewpoint (77.8%) [$t(32)=3.691, p<0.005$] and the 180° viewpoint (78.1%) [$t(32)=4.927, p<0.000$]. However, the difference between scores on the rotated viewpoints (90° vs. 180°) was not significant [$t(32)=-0.132, p>0.05$].

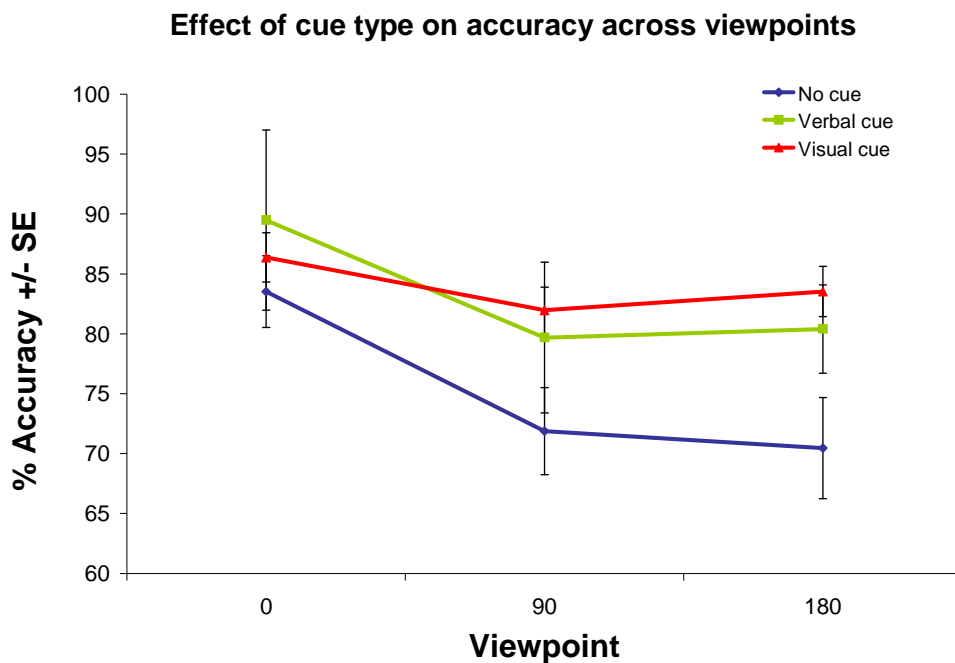


Figure 4.2 The effect of cue type on accuracy across viewpoints +/- standard error.

Reaction time: A second ANOVA examining reaction time (using the same variables as above) again revealed a significant effect for Rotation/Viewpoint [$F(2, 60)=38.892$, $p<0.000$]. A main effect of Location was found [$F(1, 30)=79.191$, $p<0.001$] but Cue Group did not produce significant differences [$F(2, 30)=1.255$, $p>0.05$]. No interaction effects were found (Rotation*Cue Group [$F(4, 60)=0.697$, $p>0.05$]; Location*Cue Group [$F(2, 30)=1.534$, $p>0.05$]; Rotation*Location*Cue Group [$F(4, 60)=1.130$, $p>0.05$]). As can be seen in Figure 4.3, average reaction times were reduced across all viewpoints for the groups receiving the cues but again, *post-hoc* Bonferroni tests revealed the differences did not reach significance. Bonferroni-corrected paired-samples t-tests revealed significant differences between the average reaction times on the 0° viewpoint (943.56ms) compared to both the 90° viewpoint (1044.35ms; $t(32)=-7.810$, $p<0.001$ and the 180° viewpoint (1060.47ms; $t(32)=-6.953$, $p<0.001$). However, the difference between reaction times on the rotated viewpoints (90° vs. 180°) was not significant [$t(32)=-1.281$, $p>0.05$].

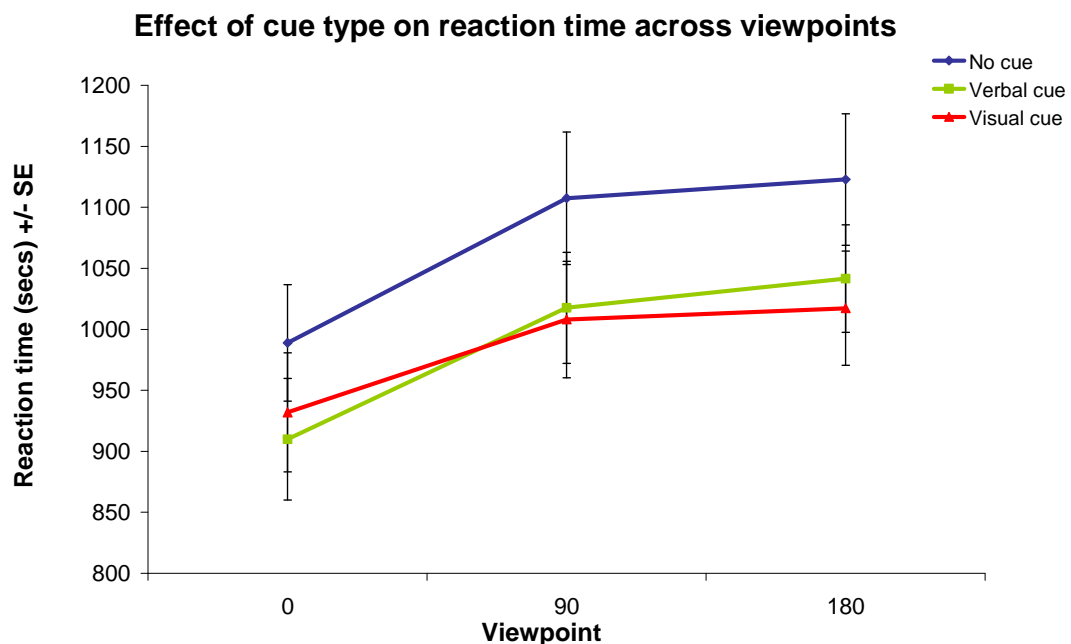


Figure 4.3 The effect of cue type on reaction time across viewpoints +/- standard error.

An examination of the effects of the presentation of any cue versus no cue on performance at each of the test viewpoints was then undertaken. A series of independent t-tests comparing accuracy and reaction times between the uncued control group and the average scores of the cue groups (verbal and visual) revealed only one significant difference in accuracy for the 180° viewpoint (Figure 4.4). Here the presentation of a cue significantly increased accuracy [$t(21)=-2.606$, $p<0.05$]. No significant effects were found for reaction time. A final analysis compared the differences in performance across viewpoints to assess whether the differences significantly increased as the angle of rotation of viewpoint increased. A series of paired-samples t-tests revealed no significant change in the difference between scores across viewpoints.

Cue versus No Cue

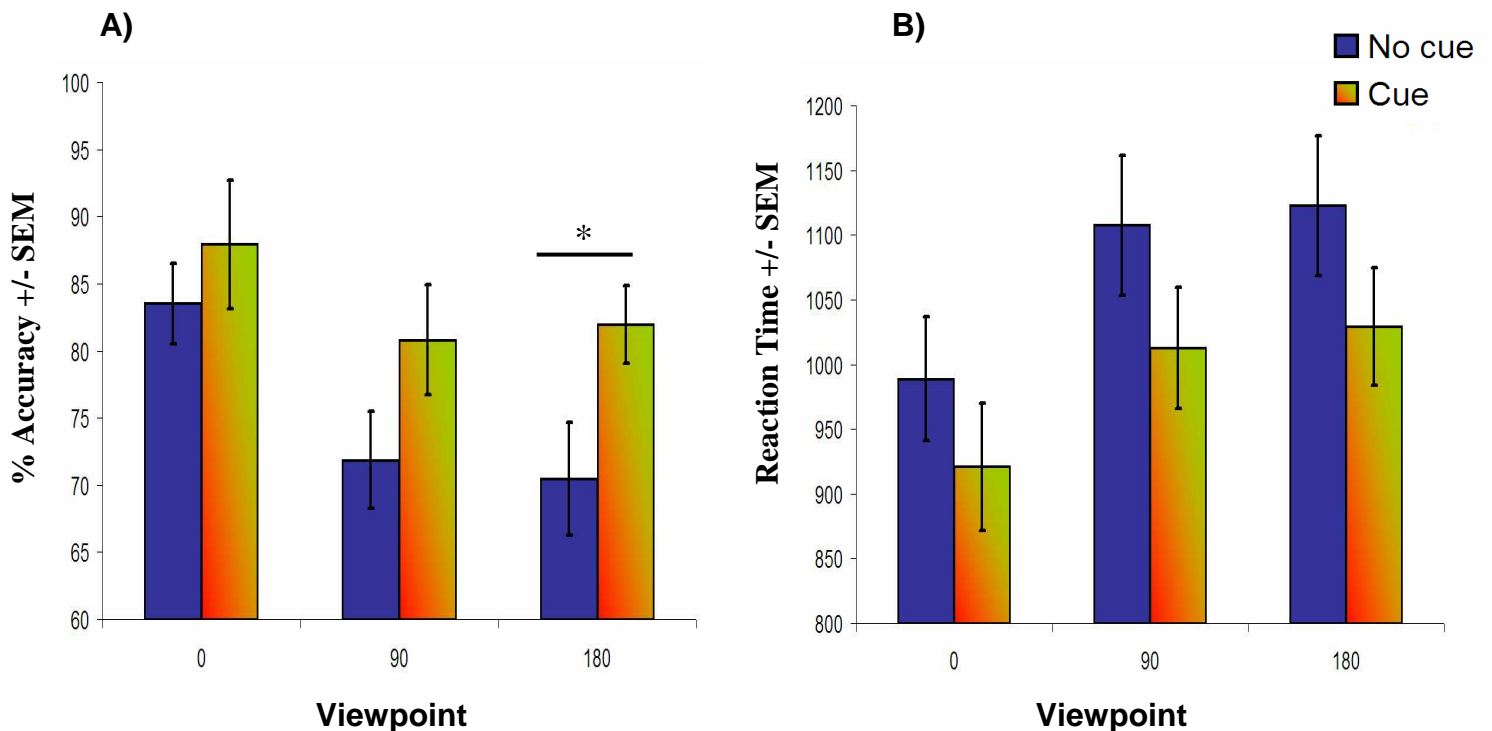


Figure 4.4 a) A comparison of accuracy scores across viewpoints between participants receiving no cues and those who received a cue. **b)** A comparison of reaction times across viewpoints between participants receiving no cues and those who received a cue.

* = $p<0.05$

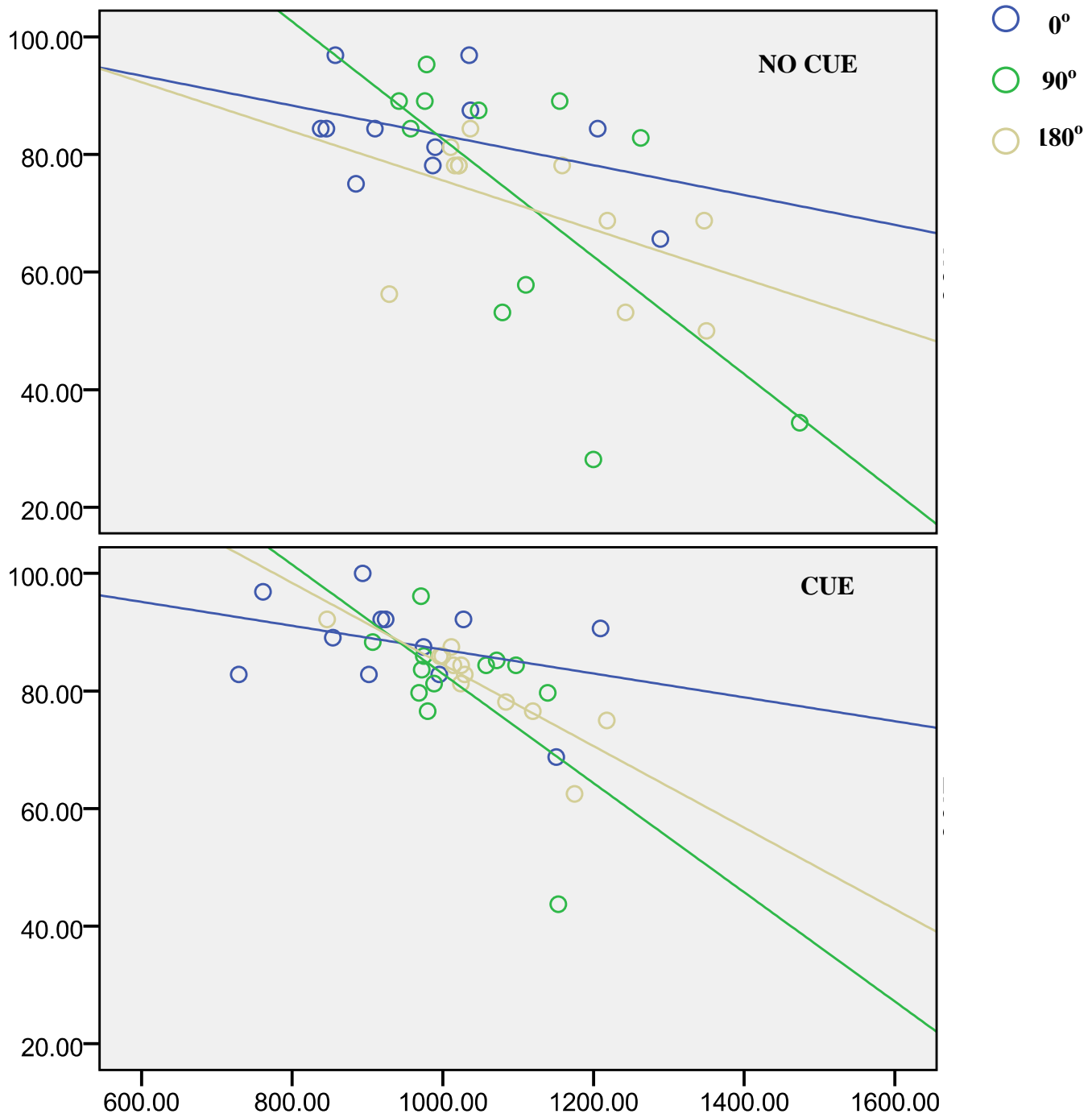


Figure 4.5 Scatterplots plotting individual performances i.e. accuracy/RT correlations for **a)** Uncued viewpoint change and **b)** cued (verbal or visual) viewpoint change.

4.5 Discussion

Christou *et al.* (2003) suggest that without cued viewpoint transformations, participants have to first account for the unknown angular displacement, which may increase uncertainty and introduce a greater potential for making mistakes when recognising objects from novel viewpoints. Rather than a specific effect for novel, rotated viewpoints, there was a trend in the data to suggest that cued viewpoint-change increased accuracy and decreased reaction time across all viewpoints (see Figures 4.2-4.4). However, we found no main effect of cue type and only one significant effect of cued viewpoint-change was found, namely an increase in accuracy related to cued presentation on the 180° trials. This effect was only found after the verbal and visual groups were collapsed into a new ‘all cues’ group i.e. the participants who received any cued presentations. The final analysis showed that the difference in performance between the ‘cue’ vs. ‘no cue’ groups (which overall was found not to be a significant difference) was also found not to significantly increase with angle of rotation from 0°.

There is a fundamental difference between recognising an object from a shifted viewpoint and recognising an object-location. The variation in visual information from novel views of stimulus features may indeed require mental rotation to reconcile different object percepts and allow object recognition from unfamiliar views. However, this experiment demonstrates that locational information may be representational-dependent rather than view-dependent. This conclusion supports the findings of Chapter 3 which purported that differences in electrophysiological responses and behavioural performance on studied, as compared to novel viewpoints, were underpinned by differential recruitment of egocentric and allocentric representations of space.

Having found that the Spatial Grid Task neither contains confounding intrinsic axes (see Appendix 3) or requires extrinsic cues (e.g. visible transitions between viewpoints) to be ecologically valid we returned to the use of the original spatial grid for the remaining experiments. We next decided to run participants on the Spatial Grid Task using different training regimes. Chapter 5 describes this further exploration into the adoption of both ego- and allocentric reference frames within the Spatial Grid Task.

5

Chapter V

Scene recognition, Training effects and
Mental Rotation: Investigating
confounds in the Spatial Grid Task

5.1 Abstract

This Chapter explores spatial representation using two groups of participants, each of which receive differential exposure to the viewpoints of the Spatial Grid Task during the study phase. The group trained from an egocentric stationary viewpoint shows a detrimental effect of viewpoint change during testing on performance. Conversely, no effect of viewpoint is seen for participants who were presented with multiple viewpoints during the study block, demonstrating the construction of a viewpoint-independent representation. The effect of training is discussed in relation to previous chapter findings. Certain confounds, most notably the choice of a survey-like viewpoint for the study trials are also discussed and some limits of the Spatial Grid Task in studying representational differences begin to emerge. Exposure effects, scene recognition and ecological validity are all discussed in terms of their effects on progression.

5.2 Introduction

While the previous chapters validated the Spatial Grid Task and its methodology by assessing task difficulty effects on the ERPs (Chapter 3) and dismissing the need for extrinsic cues (Chapter 4), there remains a number of more complex aspects that have not been addressed. One such aspect is the issue of scene recognition. It is possible to suggest that our findings in Chapters 3 and 4 that demonstrated a more impaired performance on rotated viewpoints compared to 0° was simply due to scene recognition i.e. participant's easily recognised viewpoints in the test block that had previously been presented during the study phase. A second issue is that participants have essentially been 'trained' in an egocentric environment (see Figure 3.1a) so it may be suggested that it would be easier for them to respond to this viewpoint in the test block.

In this chapter, we attempt to address these issues. However, this is by no means trivial. How do we separate out what we would consider an egocentric representation (0°) from scene recognition, or indeed is it possible? Traditionally, in an attempt to show qualitative differences exists between ego- and allocentric representations and their recruitment in a task, it has been common practice to compare the performance of patient groups with selective parietal and medial temporal damage to that of controls (e.g., Andersen, Snyder, Bradley, & Xing, 1997; Burgess *et al.*, 1999; Colby & Goldberg, 1999; Robertson & Marshall, 1993; for review, see Burgess, Jeffery, & O'Keefe, 1999). Alternatively, it is possible to assess the nature of mental representation by manipulating information presented at training and assess the consequential effects on performance. This is commonly done for example, in spatial navigation experiments investigating route and survey knowledge both behaviourally (e.g. Siegel and White, 1975; Perrig and Kintsch, 1985; Streeter *et al.*, 1985; Thorndyke and Hayes-Roth, 1982; Tversky, 1991)

and neurologically (e.g. Mellet *et al.*, 2000; Shelton & Gabrielli, 2002, 2004) – see Introduction section 1.2.1. As clinical populations with pure spatial deficits are difficult to find, in an attempt to behaviourally separate the ego- and allocentric representations that may be involved in the Spatial Grid Task it was decided to manipulate the scene presented during the study phase. To achieve this goal, ideally we need to present a scene during the study phase that is not repeated during the test phase while simultaneously attempting to provide the opportunity to train participants to form either an egocentric or an allocentric representation.

With this goal in mind, we modified our original spatial grid environment where participants were shown the grid at a slight angle and from a single perspective (Figure 5.1a) to a more elevated perspective where they viewed the grid from an aerial viewpoint during the study phase (Figure 5.1b). The arrow on the grid designated the imagined viewpoint for participants.

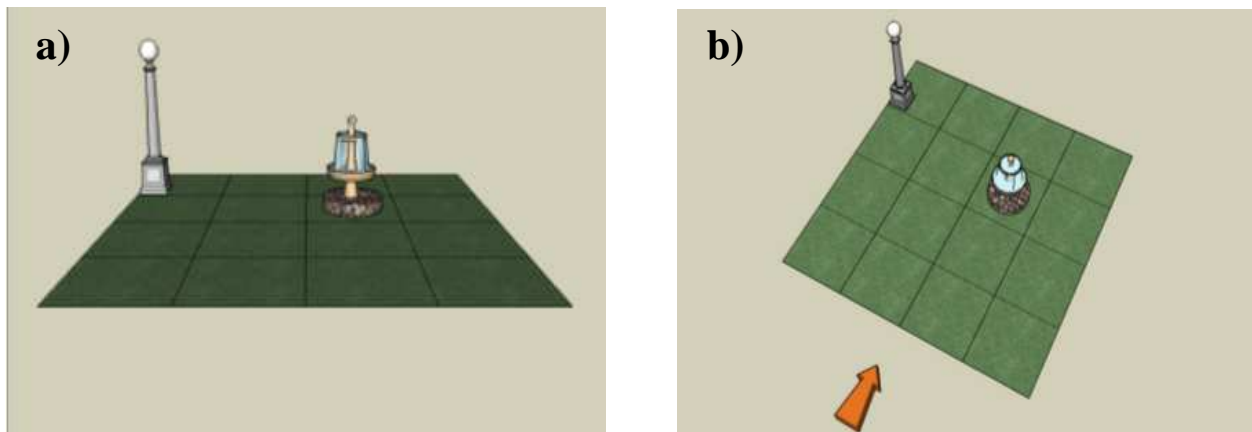


Figure 5.1 a) The original surface viewpoint used in the study block of Chapter 3 b) The elevated perspective used for the study viewpoint in the current experiment with an arrow indicating the to-be-imagined surface perspective

Now participants are trained from one perspective (aerially) and have to respond to another (surface), thereby dealing with the scene recognition issue. However, this alteration does not address the issue of participants being trained egocentrically, therefore making it easier to respond to the 0° viewpoint during the test block. Although the task difficulty analysis in Chapter 3 suggested that this was not the case, a manipulation of the training regime would further prove that behavioural (and electrophysiological) differences arose due to representational differences and not as a training effect. To explore this issue we trained participants either egocentrically or allocentrically. This was achieved by maintaining a single perspective (e.g. Figure 5.1b) during the study phase for the egocentric group while providing exposure to all rotations around the array for the allocentric group (Figure 5.2). Note that we physically rotated the environment rather than simply changing the arrow position around the grid to ensure that the same mental transformations (i.e. from aerial perspective to imagined surface perspective) were required for both allo- and egocentric groups.

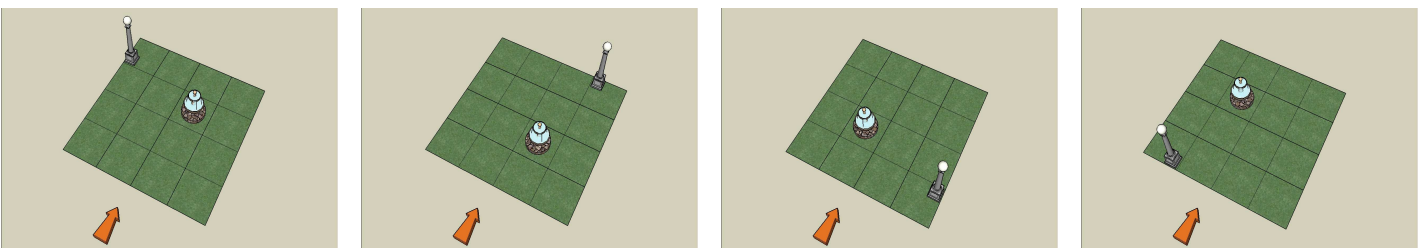


Figure 5.2 *The four aerial viewpoints used in the study block for the allocentric group providing participants with exposure to the array from all test rotations (with an arrow indicating the to-be-imagined surface perspective).*

The current experiment aims to make a clearer distinction between ego- and allocentric encoding in the study phase by providing a variety of viewpoints for study in the allocentric condition compared to a stationary egocentric encoding viewpoint.

Therefore although both groups will be prompted to learn the object locations in relation to fixed landmarks (an allocentric strategy), they will receive exposure to either one (egocentric) or many (allocentric) viewpoints.

If the stationary viewpoint presented to the egocentric group in the study phase results in a disadvantage when testing from alternative viewpoints (as found in Chapter 3 and 4), then an explanation other than scene recognition must account for the performance differences across viewpoints. We would posit that the construction of an egocentric (person-centred) representation, due to the adoption of a preferred (or default) viewpoint based on exposure during the study phase would be responsible for differences across viewpoints. Conversely, the allocentric group (receiving multiple perspectives during the study phase) would presumably have no default viewpoint and therefore should show similar levels of performance on all viewpoints of the Spatial Grid Task. In terms of mental rotation, a comparison of both groups' performance could help determine if additional mental transformations (back to a default viewpoint) were occurring for the egocentric group as these would presumably lead to longer reaction times, compared to the allocentric group. We predict that the performance topography for the egocentric group will show a preference for recognising locations from the studied viewpoint and an even distribution of accuracy and reaction times across novel viewpoints (as seen in Chapter 3 and 4). On the other hand, the allocentric participants will have flat performance topographies. It is predicted that performance will be maximal for the studied viewpoint in the egocentric condition compared to all other viewpoints.

5.3 Methods

5.3.1 *Participants*

An *ad hoc* sample of thirty participants was tested from the student population of the National University of Ireland (NUI Maynooth). This sample was split into two groups of fifteen. Participants in the ‘Ego Group’ were aged between 18 and 32 (mean 21.2 years). Eight were female and all were right-handed. Participants in the ‘Allo Group’ were aged between 19 and 41 (mean 23.8 years). Nine were female and all but one were right-handed. All were in good health and had normal or corrected-to-normal vision. The experiment was conducted in accordance with the Code of Ethics of the World Medical Association and the ethical standards of the APA and approved by the NUI Maynooth University Ethics Board.

5.3.2 *Stimuli*

The Spatial Grid Task was used for this experiment – see General Methods section 2.2.2. All stimuli were presented using E-Prime on an Intel Pentium 4 Processor (3.00GHz CPU) and displayed on an LCD monitor. They consisted of 8 different objects (a bin, a bucket, a post-box, a road-cone, a fire hydrant, a tree, a tyre and a keg).

5.3.3 *Procedure*

Participants were seated in a cubicle (150cm x 180cm) half a metre from the computer monitor and had access to a mouse for responses. A study block preceded a test block. Instructions were presented on screen. These have been described in greater detail in the

General Methods section 2.3. Experimental manipulations in this study involved the presentation of different study blocks across the different participant groups, specifically these were manipulations of study viewpoint.

STUDY BLOCK

Similar to previous experiments, participants were required to memorize the locations of objects in the spatial grid during the study block. All study blocks consisted of 32 trials (4 presentations of each object in their specific locations). The presentations were pseudo random, also similar to the earlier experiments (objects were presented randomly in a run of 8 and this was repeated 4 times). However, unlike the other experiments, the plane of elevation was shifted for the study trials to give a more aerial view. Participants witnessed this transition from the ground-level view to the aerial view so that they had a reference for their to-be-imagined perspective i.e. they were asked to imagine they were looking at the array from the ground-level viewpoint (depicted by an arrow). An example of this ground-to-aerial level transition can be seen in Figure 5.3.

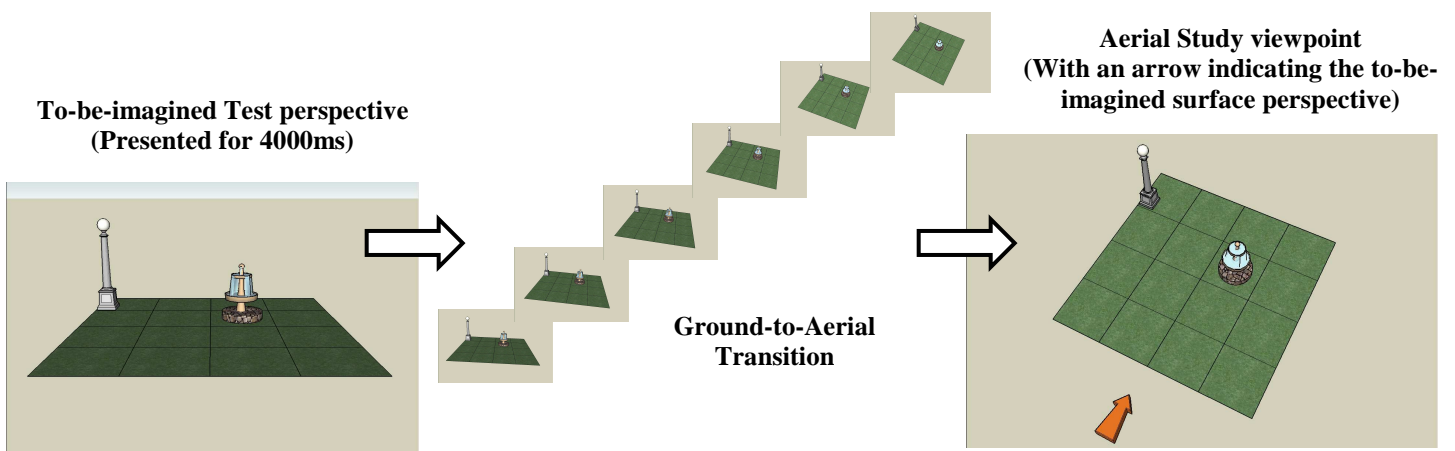
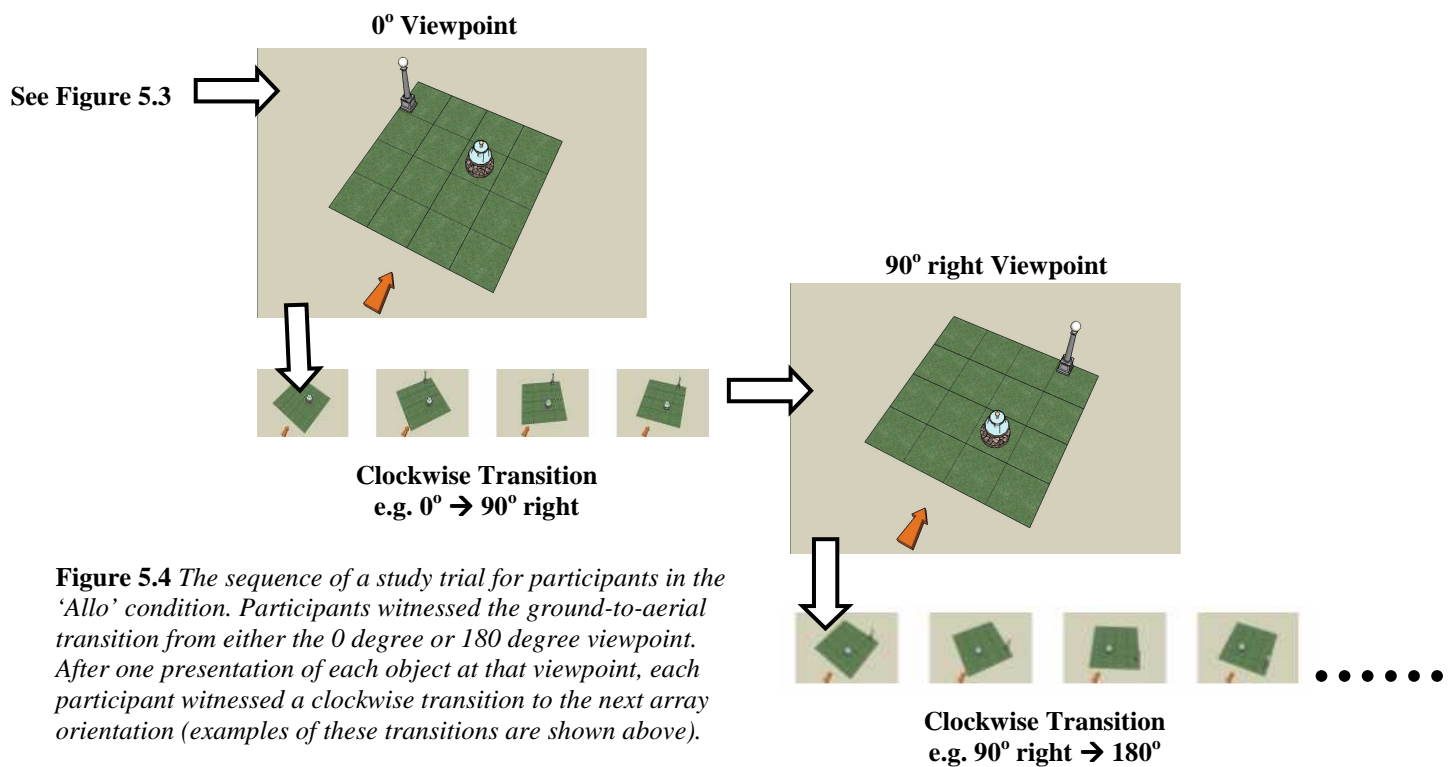


Figure 5.3 The ground-to-aerial level transition witnessed by participants at the start of the study block. All study trials were then presented from the aerial viewpoint with an arrow depicting the imagined viewpoint appropriate for that trial.

The ground-to-aerial transition occurred once for both groups at the start of the study block. All stimuli were then presented from the aerial perspective. For participants in the Ego group, the stimuli were presented from the same stationary viewpoint used in Chapter 3 (i.e. 0°) transformed to the aerial perspective. All stimuli were randomly presented four times for a total of 32 trials (8 objects x 1 viewpoint x 4 presentations). For participants in the Allo group, the study trials were presented from all sides of the array. This began with the ground-to-aerial transition, occurring from either 0° or 180° (labels are imposed here based on the egocentric condition). Then at the aerial perspective, each object was presented once at random. After all objects were presented at this angle there was a clockwise transition and the objects were presented again from another angle (e.g. 90° right or 90° left). Presentation from the other two sides followed with the same manner of clockwise transitions (see Figure 5.4) until each object was presented once from all sides of the array giving a total of 32 trials (8 objects x 4 viewpoints).



All of the transitions used in the study blocks appeared fluid as the still frames were presented in rapid succession. For all participants, instructions followed the study block, explaining how to respond in the test block.

TEST BLOCK

The test trials for both groups consisted of viewpoints from the ground-level perspective (see Figure 5.1a) Participants were instructed to respond to objects in their *correct* location by clicking the left mouse button with their index finger and by clicking the right mouse button with their middle finger when objects were presented in *incorrect* locations. The test block was the same for all participants and followed the same procedure as described in Chapter 3. Objects appeared in their correct location and in an incorrect location for each viewpoint around the array giving a total of 64 trials (8 objects x 2 locations x 4 viewpoints). Trials were presented in the same random order to all participants.

5.4 Results

Accuracy scores

Figure 5.5 shows mean overall accuracy for each test viewpoint along with a split of the data according to (training) Group. An initial mixed-factorial ANOVA comparing Group and Viewpoint revealed no significant main effect in accuracy scores for Group [$F(1, 58)=0.185$, $p>0.05$] but Viewpoint was significant [$F(3, 174)=3.867$, $p<0.05$]. Bonferroni corrected t-tests revealed a significant difference between accuracies on views 90° Right and 180° ($t(59)=3.103$, $p<0.05$) where responses to objects from 90° Right were more accurate. An analysis of Viewpoint within each group using separate ANOVAs found no significant overall differences for the Ego Group [$F(3, 87)=2.056$, $p<0.05$] or the Allo Group [$F(3, 87)=2.257$, $p<0.05$]. However, *post-hoc* tests showed that participants in the Ego Group performed significantly better on 0° compared to 180° viewpoints ($t(29)=2.473$, $p<0.05$) while participants in the Allo Group were more accurate on 90° right compared to 180° viewpoints ($t(29)=2.398$, $p<0.05$).

When each group was examined with Location (correct and incorrect) as an additional factor in the ANOVA, results revealed an interaction effect of View*Location for the Egocentric Group [$F(3, 42)=4.551$, $p<0.01$]. T-tests showed participants in this group were more accurate at 0° compared to 180° when responding to correct locations ($t(14)=2.219$, $p<0.05$) while responses to incorrectly located objects were significantly more accurate at the 90° right viewpoint compared to both 0° ($t(14)=4.183$, $p<0.01$) and 180° ($t(14)=4.559$, $p<0.005$). Although Location was found to significantly effect accuracy for the Allocentric Group [$F(1, 14)=10.279$, $p<0.01$], no effect of View was found [$F(3, 42)=2.755$, $p>0.05$]. Overall, accuracy was significantly greater for incorrect location stimuli (79.4% SE \pm 2.7%) compared to correct locations (70.7% SE \pm 2.5% –

see Figure 5.5b & c). Specific differences related to location emerged at 90° right for the Ego Group ($t(14)=2.750$, $p<0.05$) and 90° left for the Allo Group ($t(14)=2.992$, $p<0.05$) where participants were significantly more accurate when responding to incorrect locations.

MEAN ACCURACY (%)

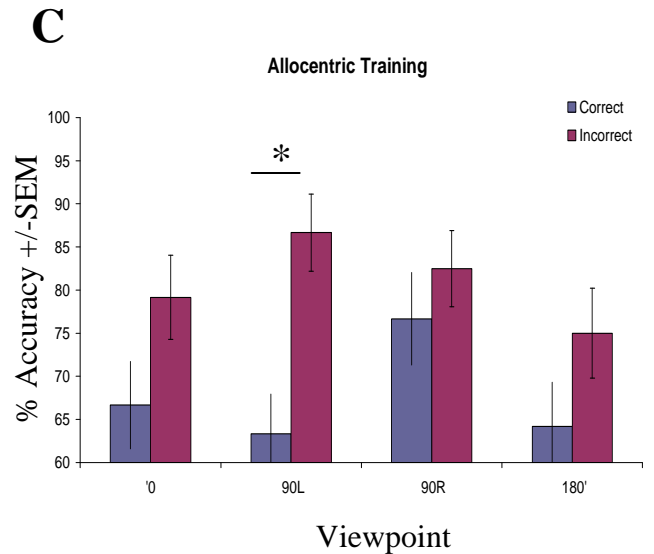
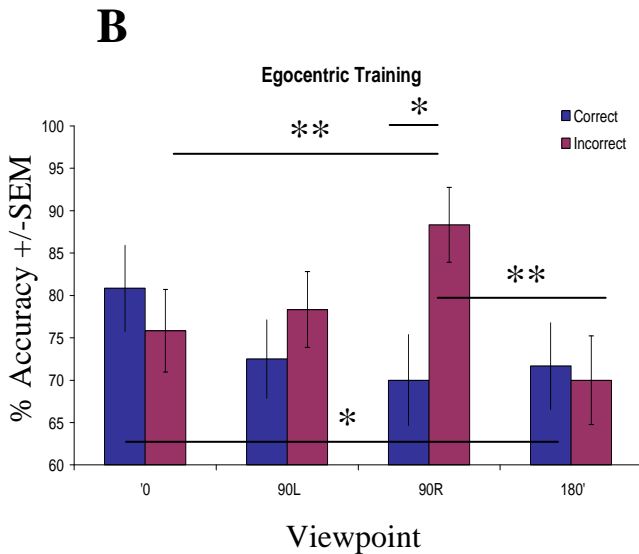
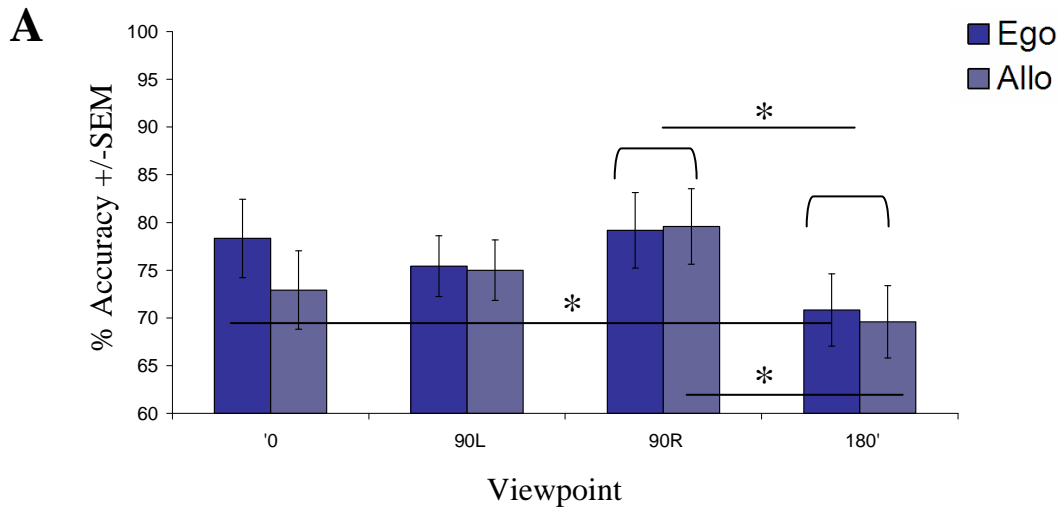


Figure 5.5 a) Overall mean accuracy (+/- Standard Errors) across viewpoints for both the Egocentric and the Allocentric Groups **b)** Accuracy scores for the Egocentric Group on correct and incorrect location stimuli **c)** Accuracy scores for the Allocentric Group on correct and incorrect location stimuli.

* = $p < 0.05$, ** = $p < 0.01$

Response times

We then examined the response times for each group (Figure 5.6). Following a mixed-factorial ANOVA, no significant main effect in accuracy scores for Group were found [$F(1, 58)=2.568$, $p>0.05$] but Viewpoint was significant [$F(3, 174)=5.486$, $p<0.005$]. *Post-hoc* Bonferroni-corrected pairwise comparisons revealed significantly faster response times for 90° left and right viewpoints compared to 180° ($t(59)=3.518$, $p<0.01$; $t(59)=3.280$, $p<0.05$ respectively). After conducting separate repeated-measures ANOVAs an effect of Viewpoint was found for the Egocentric Group [$F(3, 87)=4.938$, $p<0.01$] (Figure 5.6b) with faster response times for 0° compared to 180° ($t(29)=2.793$, $p<0.05$). Viewpoint did not significantly affect response times for the Allocentric Group [$F(3, 87)=2.514$, $p<0.05$] (Figure 5.6c).

Similar to the accuracy scores, each group was then examined with Location as an additional factor in the ANOVA. A significant effect of Viewpoint was still found for the Egocentric Group [$F(3, 42)=3.676$, $p<0.05$] with no effect for Location [$F(1, 14)=2.126$, $p>0.05$]. No significant differences were found for correct locations across viewpoints using paired-samples t-tests. However, it was found that participants responded significantly faster on 90° left views compared to 180° for incorrect locations ($t(14)=3.130$, $p<0.05$). The Bonferroni corrections resulted in the loss of significant differences between 0° and 180° ($p=0.021$) and between 90° right and 180° ($p=0.016$) for incorrect locations. For the Allocentric Group, no significant effects of Viewpoint [$F(3, 42)=2.083$, $p>0.05$] or Location [$F(1, 14)=1.473$, $p>0.05$] were found.

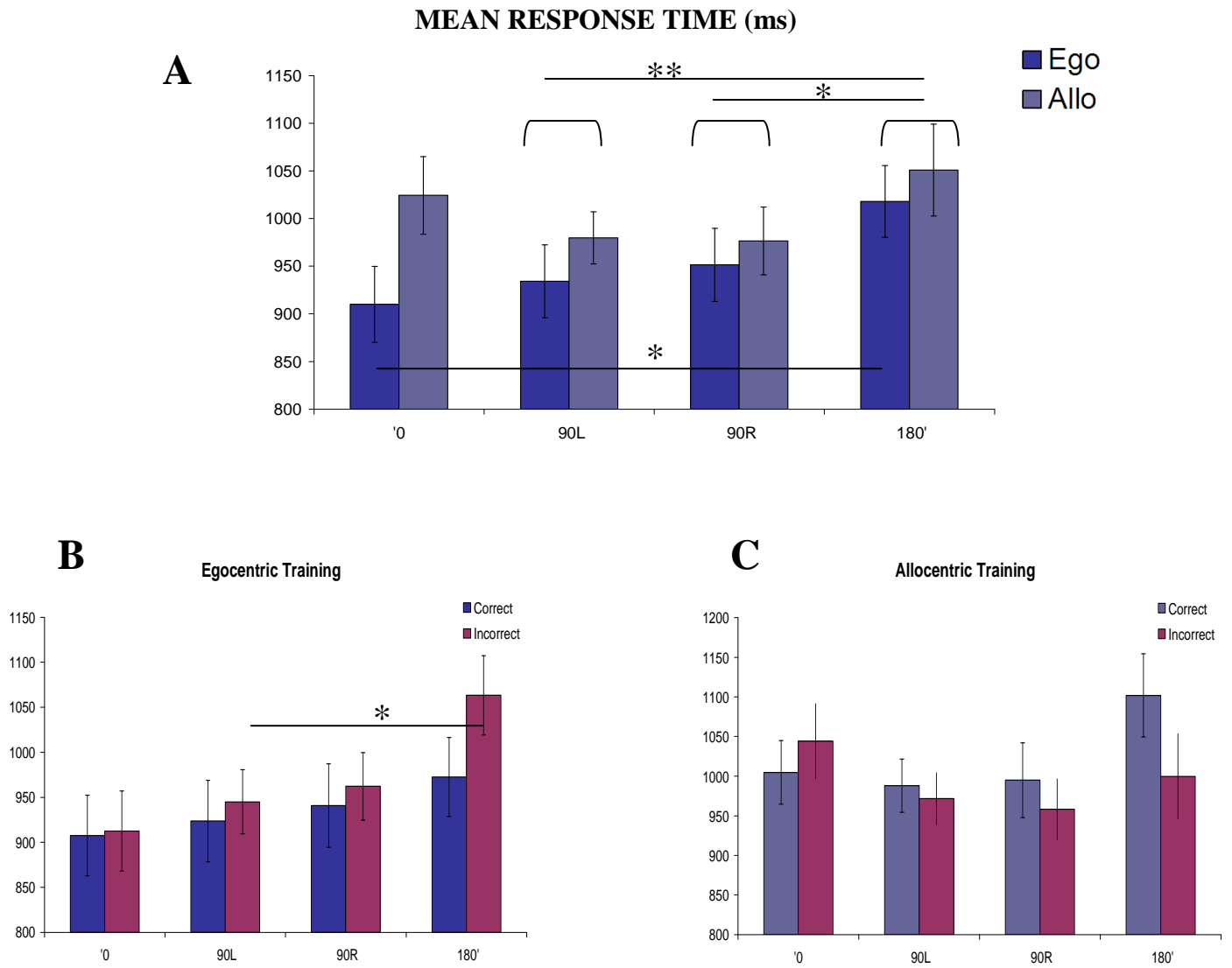


Figure 5.6 **a)** Mean Response times (\pm Standard Errors) across viewpoints for both the Egocentric and the Allocentric Groups **b)** RTs for the Egocentric Group on correct and incorrect location stimuli **c)** RTs for the Allocentric Group on correct and incorrect location stimuli

5.5 Discussion

The results of this study have shown that differential training regimes can produce subtle differences in performance on the Spatial Grid Task. The effect of viewpoint on the accuracy and reaction times for the egocentric group showed that they performed significantly better at 0° compared to 180° . This finding is similar to the differences seen in previous chapters; however here the effect has been shown after a shift of perspective between study and test blocks. This suggests that the *performance differences seen for the egocentric (study) viewpoint cannot be explained by scene recognition*. However, the difference between 0° and the rotated viewpoints was not as we have seen in previous experiments, where accuracy and reaction times were more evenly distributed across the novel viewpoints. Instead we see a linear gradient in performance for the egocentric group, where accuracy decreases and reaction time increases as one moves further from the 0° viewpoint.

However, this trend does not simply highlight a mental rotation effect. Since the study view was at a greater elevation than the test view, mentally rotating from the 90° and 180° viewpoints would require additional vertical translations. Comparing the mean reaction times in this experiment to those of Chapter 3, it is clear that participants in the egocentric group performed no slower for the 0° viewpoint (910ms compared to 905ms). In addition to this, in the current study there was no overall effect of ‘Group’ on performance. As the allocentric group had no ‘default’ viewpoint for which to mentally rotate towards (i.e. they had no 0°), and the egocentric group were responding at a similar speed to the allocentric group, then it can be assumed that *neither group was engaged in a mental rotation strategy*. Instead it is posited that, in an attempt to remove scene recognition confounds, the elevated study view assisted participants in the egocentric

group in using a more allocentric-type strategy. The current experiment gave the allocentric group less exposure to each viewpoint during study i.e. one run of the objects from four viewpoints. The egocentric group on the other hand received four runs of the objects from the one (survey-type) viewpoint. Unfortunately due to the low number of trials in this test, benefits of exposure across trials could not be assessed. However, a re-analysis of the response times from Chapter 3 looking for performance benefits of experience (judged by significant improvements over blocks of test trials) found that as the test progressed, participants improved with repeated exposures to all of the viewpoints (see Appendix 5).

As can be seen, difficulties arise whether one maintains the same ‘surface’ view during both the study and the test blocks, and get levied with scene recognition criticisms, or remove the participants from the surface view during study and possibly reduce the egocentric nature of the 0° viewpoint. People do not encode information in an egocentric manner by imagining a survey-type viewpoint; the lack of consistency is ecologically invalid. Consistency of viewpoints between encoding and retrieval therefore seems appropriate. Indeed, critics citing scene recognition could be taken as implicitly supporting a snap-shot model of spatial memory similar to Cartwright and Collett (1983). The downsides to such a shallow sensory representation have been discussed in the Introduction to this thesis (p. 10). However, consistency between study and test may be considered a training effect. For example, differential training exposures are used, in part, to test the levels-of-processing effect, identified by Craik and Lockhart (1972). Depth of processing in spatial memory has been identified as especially important for place recognition (Gillner & Mallot, 2008; Mallot & Baston, 2009). Similar to how landmark processing can be described along the shallow to deep processing continuum, perhaps

ego- and allocentric processing can also be thought of along a similar continuum. If so, then what the current experiment demonstrates (similar to depth of processing with context) is the importance of consistency between encoding and retrieval. The egocentric group were trained egocentrically and tested both ego- and allocentrically and performed best on the egocentric trials (as predicted). Conversely, the allocentric group were trained and tested allocentrically and showed no effect of viewpoint (also as predicted). This study therefore highlights *the importance of the training regime in relation to the task demands at retrieval*.

In conclusion, this study has shown that exposure to many perspectives of an array can stabilise performance for recognising object-locations, suggesting a representation that is viewpoint-independent. However, as mentioned, this result is not without its complications. As these confounds impede progress for investigations into spatial representation, we refocus attention on the interaction of the spatial system in object-location memory. The next experiments aim to assess how spatial information aids more general episodic memory.

6

Chapter VI

The effect of implicit spatial memory
on object recognition

This chapter has been published as Murphy, JS., Wynne, CE., O'Rourke, EM., Commins S. & Roche RAP. (2009) High-resolution ERP mapping of cortical activation related to implicit object-location memory, *Biological Psychology*, 82, 3, 234-245.

I would like to thank Ciara Wynne and Edel O'Rourke for their help in collecting the data for this chapter

6.1 Abstract

This study was undertaken to examine the influence of implicit spatial memory on explicit object recognition memory. High-density event related potentials (ERPs) were recorded during an object recognition task which involved task-irrelevant changes in the location of studied objects. Participants categorised objects as studied or novel while data were analysed to ascertain the effect of the location changes on performance and waveform topography. Results indicate that humans can classify objects faster and more accurately when using implicit spatial memory. Individual differences observed in object recognition proficiency were absent if objects were presented in their ‘correct’ location. In a second experiment we replicated the behavioural findings while manipulating viewpoint to discount scene recognition as an underlying factor. We propose a model which includes activation of the right medial temporal lobe prior to P300 elicitation to account for the facilitative effect of implicit processing on object recognition.

6.2 Introduction

Wang and colleagues (2002) found that object locations may be implicitly encoded relative to their surroundings. Despite instruction to learn and retrieve object-location associations using landmarks in a spatial array, participants performed successfully in a ‘fixed-no cue’ condition where the landmarks were not present. The experimenters concluded from reaction times and eye movement traces during the object-location retrieval tasks that encoding using a fixed external reference frame (screen-based representations of object locations) is equivalent to the encoding of fixed-landmark to object-location representations. The results indicate that a screen-based spatial representation may be *implicitly* encoded and stored, and that this representation may even be adopted to perform the fixed-landmark condition. In addition, during the encoding phase subjects were found to move their eyes back and forth between the currently presented object and the location of the previously displayed object suggesting that some form of object-based spatial relationships may also be encoded directly and quite early. Reaction time data and eye movement traces indicate that multiple forms of representations may be used to encode and retrieve object-locations.

Spatial relationships among objects have been shown to be important for object recognition in complex scenes (Chun & Marois, 2002; Ullman, 1996). Implicit spatial memory has been studied with regard to perceptual object recognition i.e. the contextual cuing paradigm (Chun & Jiang, 1998), in which participants were required to perform a visual search task wherein the spatial configuration of the array elements (a target ‘T’ and rotated ‘L’ distractors) was random or repeated across the experiment. Participants were found to respond faster to targets in repeated than in new configurations of the spatial array (e.g., Chun & Jiang, 1998; Chun, 2000; Olson & Chun, 2002). It is suggested that

participants learn the invariance between the locations of array elements and the target location in the repeated configurations.

The aim of the current study is to assess, both behaviourally and electrophysiologically, the effect of implicit spatial memory on object recognition and to identify sources that may underpin such memory. Here ‘implicit’ refers to incidental rather than inarticulable learning. To date there has been little work investigating the electrophysiological biomarkers of implicit spatial memory. The two experiments in the current study both utilized the Spatial Grid Task (based on the Milner paradigm; see Methods section 2.2.2) to test participants’ object recognition memory explicitly, while simultaneously testing implicit memory effects of object-location. Objects were encoded one at a time in a three-dimensional spatial grid, so that participants never saw the complete array, allowing for greater manipulation of conditions and processing demands at retrieval. All objects were presented in colour with 3D rendering, and encoded and retrieved from a stationary, oblique viewpoint which permitted an egocentric (person-centred) frame of reference. In the test phase, a studied or ‘target’ object was presented in its ‘correct’ (i.e. previous) location. Additionally, novel or ‘distractor’ objects were also presented in one of four random locations (i.e. neither a familiar object nor location). In Experiment 1 high-density, 128-channel EEG recordings were used to investigate the scalp waveform componentry and electrical dipole sources associated with object-location memory. ERP data were analysed and dipole source localisation carried out using BESA software. Experiment 2 was a behavioural experiment, utilising the same Spatial Grid task but with the addition of two new viewpoints from which participants had to respond in the test phase.

It is predicted that upon encoding object information participants will implicitly record the object locations due to the influence of habit (Caldwell & Masson, 2001) and that this influence will have a beneficial effect on performance. Thus, it is hypothesised that response latency will be faster and response accuracy will be greater upon presentation of target objects in their correct (i.e. previous) location than target objects in an incorrect location. It is also predicted that participants' performance will be similar from the altered viewpoints in Experiment 2 thereby eliminating scene recognition as a valid explanation for effects observed in Experiment 1. Specifically, in Experiment 1, we predict that retrieval should engage temporal and medial temporal lobe (MTL) areas (Roche *et al.*, 2005). Consistent with previous studies of spatial memory (e.g. Owen *et al.*, 1996; Johnsrude *et al.*, 1999), it is predicted that modelled dipoles will be lateralised in the MTL region, predominantly in the right MTL. Cortically, we predict that the dorso-lateral prefrontal areas will be active for all trials (Goldman-Rakic, 1987) in addition to the right posterior parietal lobe (Andersen *et al.*, 1985). Finally we predict task-based modulations of the amplitudes and/or latencies of ERP components associated with spatial processing, particularly increased parieto-occipital P300 for correct location presentations, consistent with the findings of Mecklinger *et al.* (1997).

Experiment 1

High-resolution ERP mapping of cortical activation related to implicit object-location memory

6.3 Methods

6.3.1 Participants

The participants consisted of an *ad-hoc* sample of 20 undergraduate volunteers. The ages of the participants ranged from 20-27 years (mean age = 21.6 years). Of these participants, 3 were removed for excessive EEG/EOG artifacts or head movements in their data or for misinterpreting the method of responding. Of the remaining 17 participants, 7 were females and 14 were right-handed. All participants had normal or corrected-to-normal vision and gave informed, written consent before participation. The experiment was conducted in accordance with the Code of Ethics of the World Medical Association and the ethical standards of the American Psychological Association (APA) as well as abiding by the NUI Maynooth University Ethics Code.

6.3.2 Stimuli

The Spatial Grid Task was used for this experiment – see General Methods section 2.2.2. All stimuli were presented using E-Prime on an Intel Pentium 4 Processor (3.00GHz CPU) and displayed on an LCD monitor. They consisted of 8 different objects. The task consisted of two computer-generated environments (Carpet and Grass) each with 8 different objects and 8 distractors. Although environments and the objects they contain were different, the task required the same memory functions, and as no significant

differences were noted between environments, the behavioural paradigm will be described in reference to a single environmental task. The particular set of objects presented (on Grass) included a bin, a bucket, a post-box, a road-cone, a fire hydrant, a tree, a tyre and a keg; distractors included a parasol, a microphone stand, a cactus plant, a blender, a fire extinguisher, a stool, a lamp and a cavity/cinder block.

6.3.3 Procedure

After the electrophysiological preparation (see next section for details), participants were seated 50cm from the LCD computer screen on their own in a darkened, electrically shielded and sound-attenuated testing cubicle (150cm x 180cm) with access to a mouse for responses. A study block preceded a test block. Instructions were presented on screen prior to these blocks.

STUDY BLOCK

During the study block participants were asked to study the objects that appeared one at a time in the environmental grid with two stationary landmarks and were told that they would need to remember the objects for a subsequent recognition test. *No reference was made to the location of the objects*, only that the objects themselves had to be learned. The study block consisted of 64 trials of object presentations. Each of the 8 objects was presented in isolation 8 times in a pseudo-randomised order so that consecutive presentations of the same object did not coincide. The temporal sequence of a trial remained the same as in the previous experiment and is displayed in Figure 3.1. A fixation cross was presented first for 750ms, followed by the spatial grid with landmarks (e.g. lamp-post and water fountain) for 1500ms and then the test stimulus was presented

on the grid and remained onscreen for 2000ms. This cycle was repeated for the 64 trials. Stimulus presentations were marked on the EEG recording by transistor-transistor logic (TTL) triggers.

TEST BLOCK

Following the 64 trials of object presentations, another set of instructions was provided. Participants were told to respond to previously studied (or ‘old’) objects that appeared during the test block by pressing the left mouse button with their index finger. If a ‘new’ object (i.e. not shown in the study phase) was presented, then the right mouse button should be pressed with their middle finger. For the Test block, the sequence of a single trial followed the same pattern as previously shown (Figure 3.1), with the stimulus duration as the response interval, <2000ms. This trial sequence was repeated for 128 trials of object presentations. Three test conditions were constructed using either the 8 ‘old’ (studied) objects or 8 ‘new’ (distractor) objects and were presented in a pseudo-randomised order, to test the implicit learning of object locations. The first condition (Target Object condition) involved the presentation of each of the 8 ‘old’ objects in their previously studied or ‘correct’ location a total of 4 times each (n=32 trials). The second condition (Target Object-Incorrect Location condition) involved the presentation of each of the 8 ‘old’ objects in 4 allocated ‘incorrect’ locations (n=32 trials). The third condition (Distractor condition) then presented 8 novel or distractor objects in 4 random locations that were unfamiliar to the participant; these 32 trials were each repeated twice (n=64 trials). Accuracy and reaction times were both recorded during the test phase of the experiment.

6.4 Results

6.4.1 Behavioural Data

As we found no significant difference between environment type (carpet and grass), the mean participant accuracy for both experimental environments were combined to give overall mean accuracy scores for each of the three stimulus conditions (target object, target object-incorrect location and distractor object condition). Overall, accuracy was high across the three conditions on both environments. Figure 6.1a shows the percentage mean accuracy for each of these stimulus types (Correct location targets: $97.6 \pm 0.79\%$, Incorrect location targets: $94.8 \pm 1.1\%$, and Distractors: $97.7 \pm 0.75\%$). A repeated-measures ANOVA was carried out to compare the mean accuracy across the three conditions. The within-subjects effect revealed that there was a significant main effect for Accuracy across stimulus types [$F(2, 34)=3.281$, $p=0.05$] but subsequent paired-samples t-tests found no significant differences between conditions. Reaction times (correct responses only) are shown in Figure 6.1b and can be seen to be quicker on average for Correct location targets ($737.8 \pm 67.8\text{ms}$) compared to Incorrect location targets ($788.2 \pm 88.4\text{ms}$) and Distractors ($774.6 \pm 80.1\text{ms}$). A second repeated-measures ANOVA was carried out to compare mean reaction time in the three conditions. Reaction times were found to differ significantly with stimulus type [$F(2, 36)=7.601$, $p=0.002$]. Bonferroni corrected t-tests found significant differences between Correct location targets and Incorrect location targets [$t(18)=4.250$, $p<0.005$] and Correct location targets and Distractors [$t(18)=3.261$, $p<0.05$]. A comparison of males' and females' performance revealed no significant differences in accuracy or reaction time.

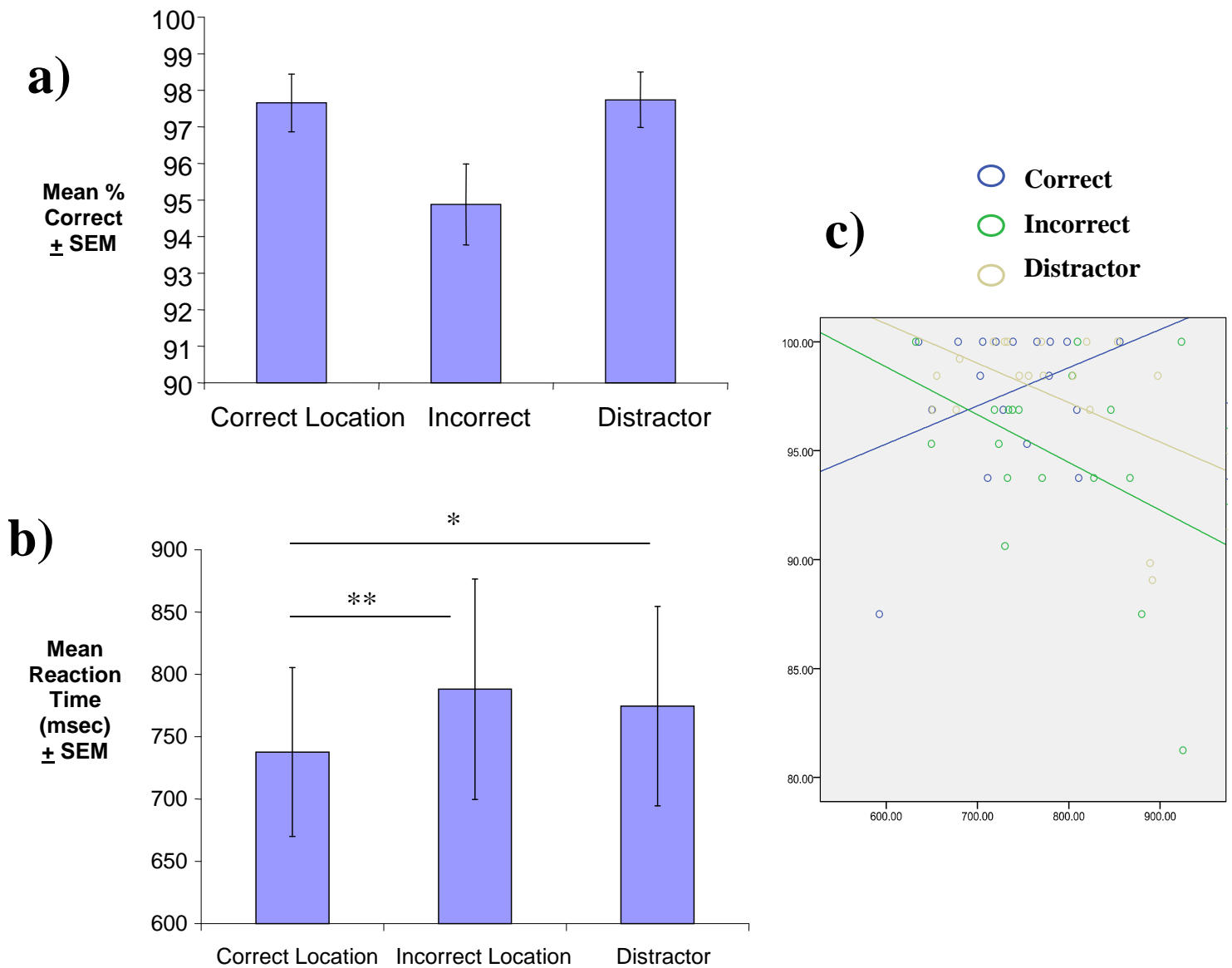


Figure 6.1 a) Mean Percentage Accuracy scores for each of the stimulus type conditions. Error bars display Standard Error of the Mean. **b)** Mean reaction times (correct responses only) for each of the stimulus type conditions. Error bars display Standard Error of the Mean. **c)** Scatterplot plotting individual performances i.e. accuracy/RT correlations for each stimulus type

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

An additional analysis of the reaction time data was performed to further assess the effect of task-irrelevant locational information on object recognition performance. This was conducted after a median split based on variance in reaction times for correctly and incorrectly located target objects resulting in two groups of participants, one with a small effect of object location on reaction time (Good Recognition Group) and one with a large effect (Poor Recognition Group). The Good group responded on average 17.59ms slower

to target objects incorrectly located versus an average 87.67ms delayed response for the Poor group. Testing whether the performance difference between the groups was significant, paired-samples t-tests revealed no significant difference in reaction times across stimulus-types for the Good group whereas differences were found for the Poor group for Correctly vs. Incorrectly located targets ($p < 0.001$) and Correct location targets vs. distractors ($p < 0.01$). Comparing reaction times between the groups using a mixed-factorial ANOVA (Stimulus-type x 3 and Group x 2), a significant effect of stimulus-type was found [$F(2, 28) = 10.206$, $p < 0.001$] as well as an interaction effect [$F(2, 28) = 4.699$, $p < 0.05$]. The between-subjects variable ‘group’ also yielded a significant effect [$F(1, 14) = 8.665$, $p < 0.05$] confirmed in the *post-hoc* Bonferroni test ($p < 0.05$). A series of independent-samples t-tests was used to compare the Good Recognition and Poor Recognition Groups on each stimulus-type. No significant difference was found for Correct location targets [Good Group $M = 712.9\text{ms}$, $SD = 78.4\text{ms}$; Poor Group $M = 771.9\text{ms}$, $SD = 35.9\text{ms}$ $t(14) = 1.936$, $p > 0.05$] but significant differences existed for both Incorrect location targets [Good Group $M = 730.5\text{ms}$, $SD = 87.5\text{ms}$; Poor Group $M = 859.6\text{ms}$, $SD = 46.3\text{ms}$ $t(14) = 3.687$, $p < 0.005$] and Distractors [Good Group $M = 738.9\text{ms}$, $SD = 69.2\text{ms}$; Poor Group $M = 816.1\text{ms}$, $SD = 64.3\text{ms}$ $t(14) = 2.311$, $p < 0.05$]. These results would suggest that performance differences in object recognition were removed with the aid of implicit spatial memory.

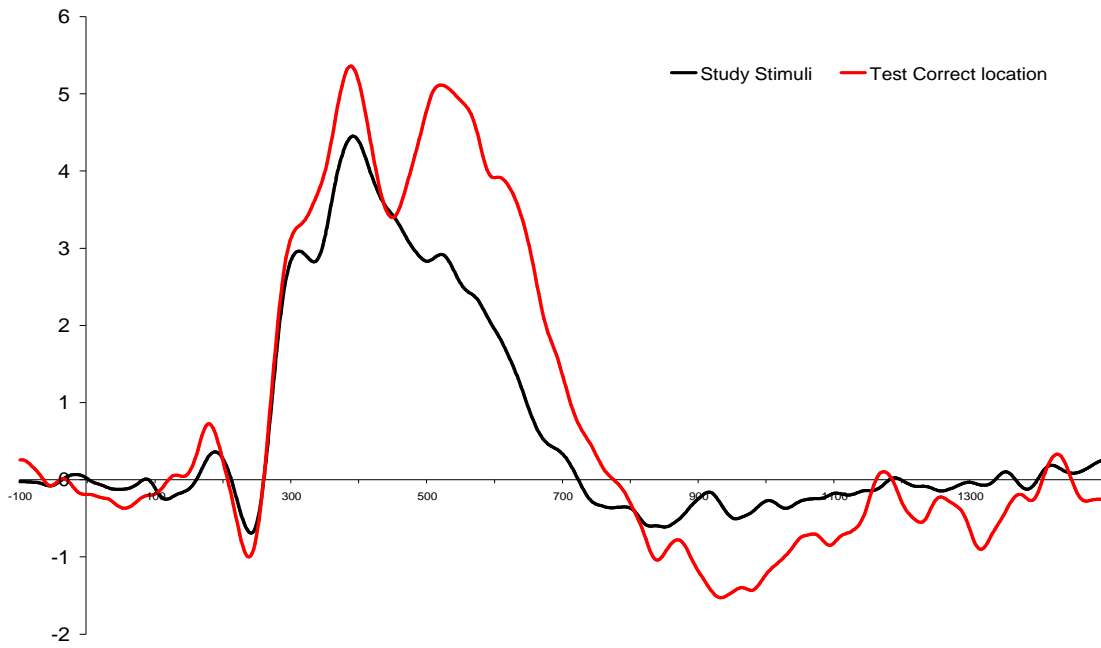
6.4.2 Electrophysiological data

Study vs. Correct location Test stimuli: Three waveform peaks were observed for Study stimuli, a P1, N2 and P3. Similar peaks were elicited for Test stimuli with additional post-P3 positivity (a P3b peak). The ERP waveforms for both the Study and Test stimuli

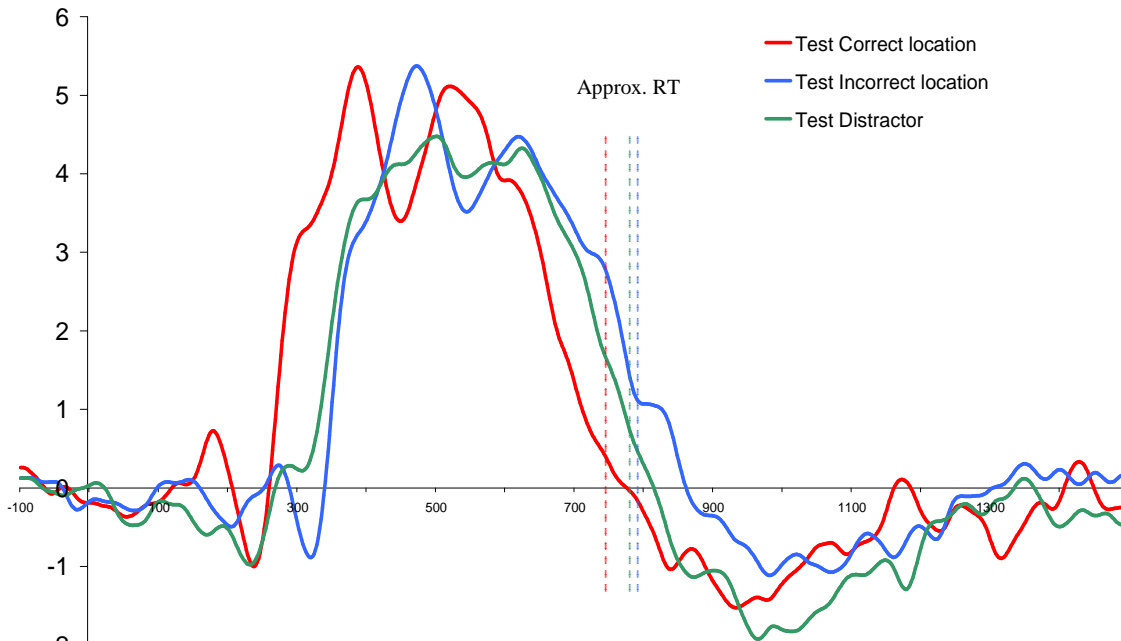
across parietal sites resembled those recorded at CPz (displayed in Figure 6.2a inset) where an extra late positivity was seen for the Test stimuli. To ascertain whether the waveforms differed significantly between 450-650ms, individual mean amplitudes were collated for both stimulus-types over this time interval and subjected to a paired samples t-test. The average mean amplitude elicited by the Study stimuli was $2.45\mu\text{V}$ compared to $4.22\mu\text{V}$ for Correct location Test stimuli. A significant difference was found [$t(16)=4.681$, $p<0.0005$] indicating the presence of a P3b component uniquely elicited by Test stimuli.

Test stimulus comparisons. After examining differences between ERPs related to the study and test blocks, Grand Mean Average waveforms were generated for the different stimulus-types presented in the test block (Correct location targets, Incorrect location targets and Distractors). These waveforms are presented in Figure 6.2b for site CPz. The latency difference seen here between correct location targets and the other stimuli was evident across centro-parietal scalp sites (i.e. CP'xx' electrodes). Analyses were conducted on the latencies of individual maximum peaks calculated between 0-1000ms from CPz (Mean latencies were 458.35ms, 525.41ms, 519.41ms for Correct location targets, Incorrect location targets and Distractors, respectively). These maximum peaks represented individual P300s and the averages show a delayed response to objects presented out of their studied locations. A repeated-measures ANOVA yielded significant differences in waveform latencies [$F(2, 32)=4.543$, $p=0.018$] and a series of paired-samples t-tests showed this difference existed between Correct location targets and Incorrect location targets [$t(16)=2.607$, $p=0.019$] and between Correct location targets and Distractors [$t(16)=2.438$, $p=0.027$].

a) CPz



b) CPz



c) CPz

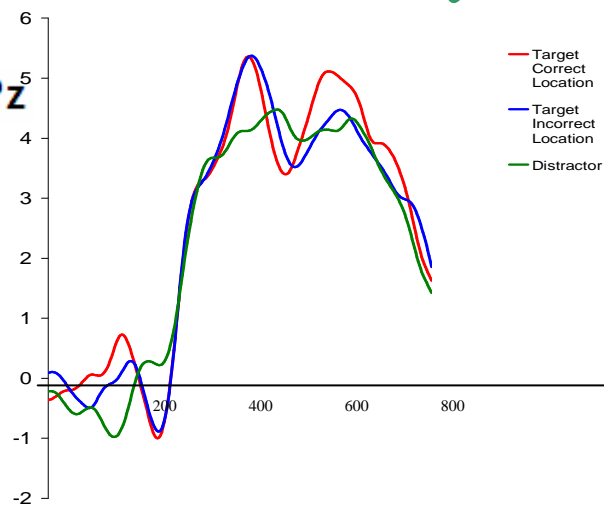


Figure 6.2 a) The ERP waveforms elicited by Study vs. Test stimuli illustrating the peaks in common and the P3b found for Test stimuli. b) The ERP waveforms elicited by Test stimuli illustrating a latency shift in response to incorrect objects and locations. c) The amplitude difference in the P3b after the shift was corrected for (not significant)

Figure 6.2c shows the waveforms after this latency difference has been removed. In order to correct for this difference and match the waveforms temporally, the ‘Correct location targets’ waveform was shifted 80ms in time. This figure now allows an amplitude difference in the P3b to be seen. However, an ANOVA using mean peak data from the corresponding time intervals (480-580ms for correct location targets and 560-660ms for the other stimuli), revealed that this difference was not significant [$F(2, 32)=0.797, p>0.05$].

The same latency difference can also be seen for the N2 as well as the P3, and appeared to be the consequent result of a P1 that was present for Correct location targets. An ANOVA testing differences in mean peaks of corrected waveforms over 150-200ms was conducted; although a polarity difference can be seen in the average mean peaks relating to these stimuli (Figure 6.3), the ANOVA did not reach significance [$F(2, 32)=2.109, p>0.05$].

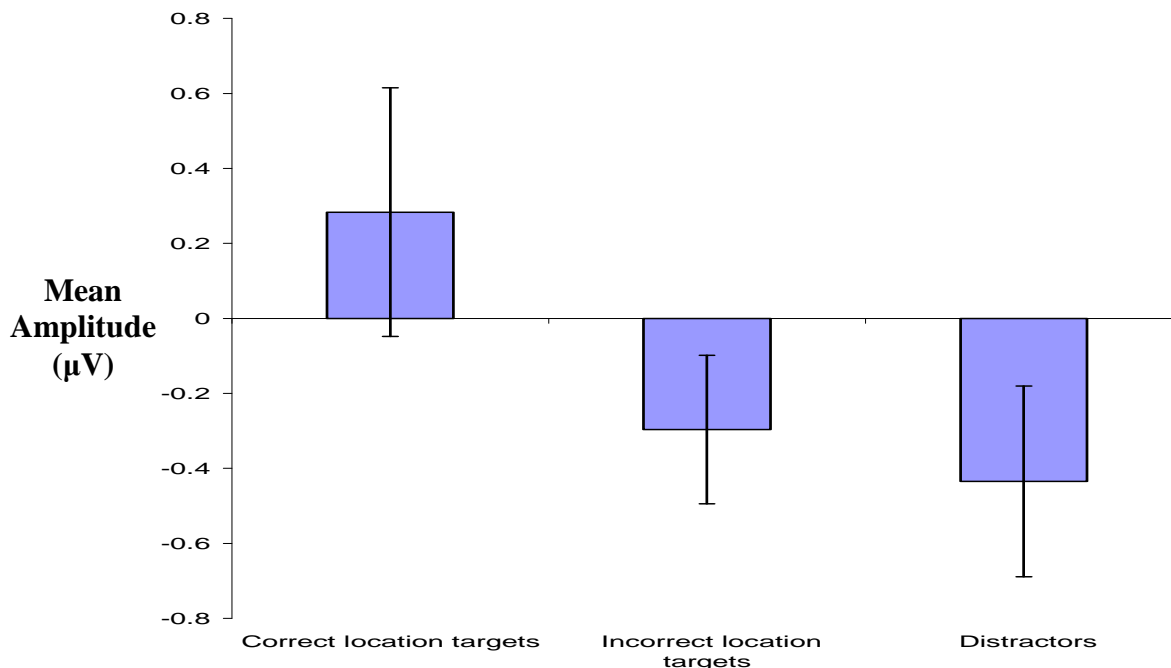
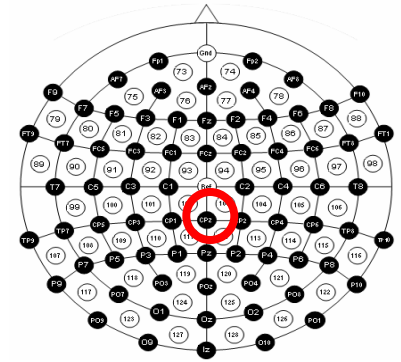
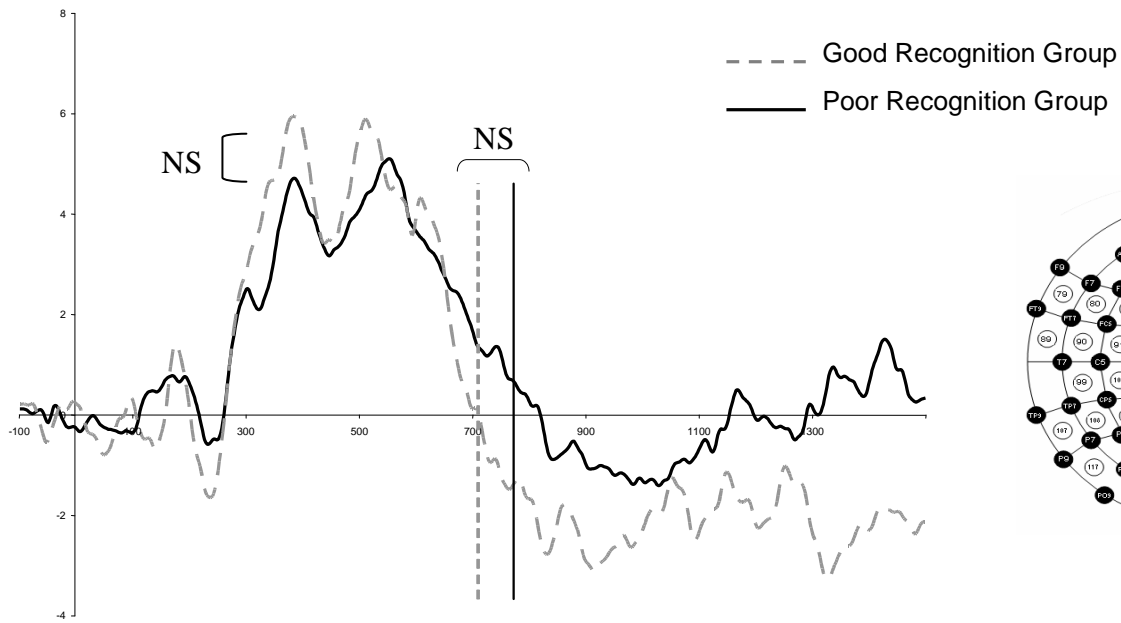


Figure 6.3. Histogram displaying the averages of the individual participants' mean peaks for each test stimulus type over the P1 time interval (150-200ms). Although a P1 seems to exist for Correct location targets the difference in amplitudes was not significant.

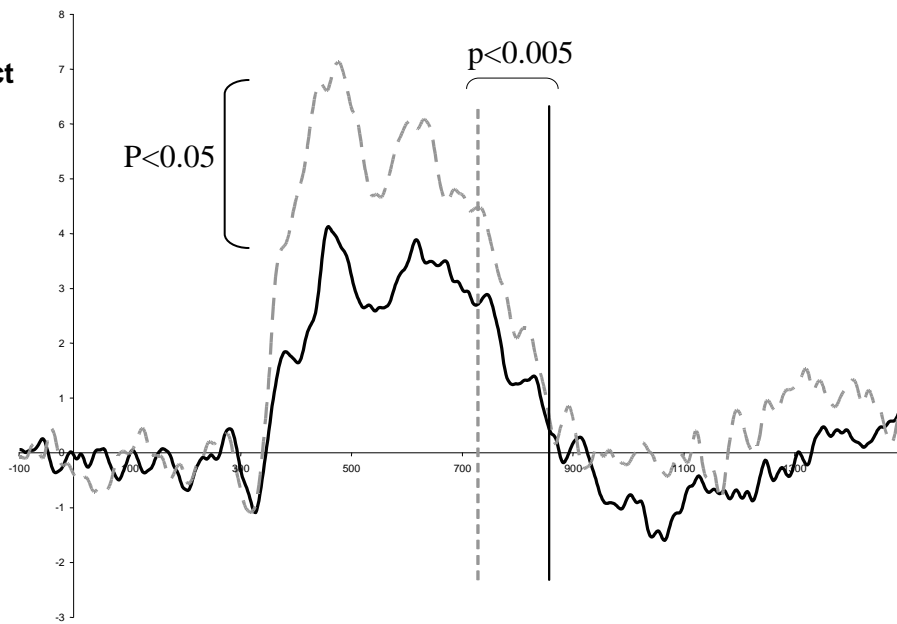
Good Recognition Group versus Poor Recognition Group

Using the median split of the data based on reaction times (see above), waveforms elicited by each of the stimulus-types were calculated for both the Good Recognition Group and the Poor Recognition Group. The latency difference in the rise of the P300 existed in both groups. This was confirmed with a mixed-factorial ANOVA (Stimulus-type x 3 and Group x 2) where a main effect of stimulus type was found [$F(2, 28)=3.820$, $p<0.05$] but the between-subjects 'group' variable had no significant effect on P300 max. peak latency. However, amplitude differences in the P300 were observed between the groups and tested for each of the stimulus-types. Mean amplitudes were calculated for the time interval 300-500ms for Study and Test stimuli for both groups. Independent-samples t-tests revealed significant differences in amplitudes between the groups for Incorrectly located objects and Distractors [$t(14)= 2.824$, $p<0.05$ and $t(14)=-2.966$, $p<0.05$ respectively]. Upon presentation of these stimuli, participants in the Poor Recognition Group showed significantly lower P300 amplitudes. Mean amplitudes for Correct location targets did not vary significantly between the groups (see Figure 6.4). The relationship between reaction times and mean P300 amplitudes was investigated using Pearson product-moment correlation coefficient. There was a moderate negative correlation between the two variables ($r=-.431$, $n=48$, $p<0.005$), with high amplitudes associated with lower reaction times.

a)
Correct location



b)
Incorrect location



c)
Distractor

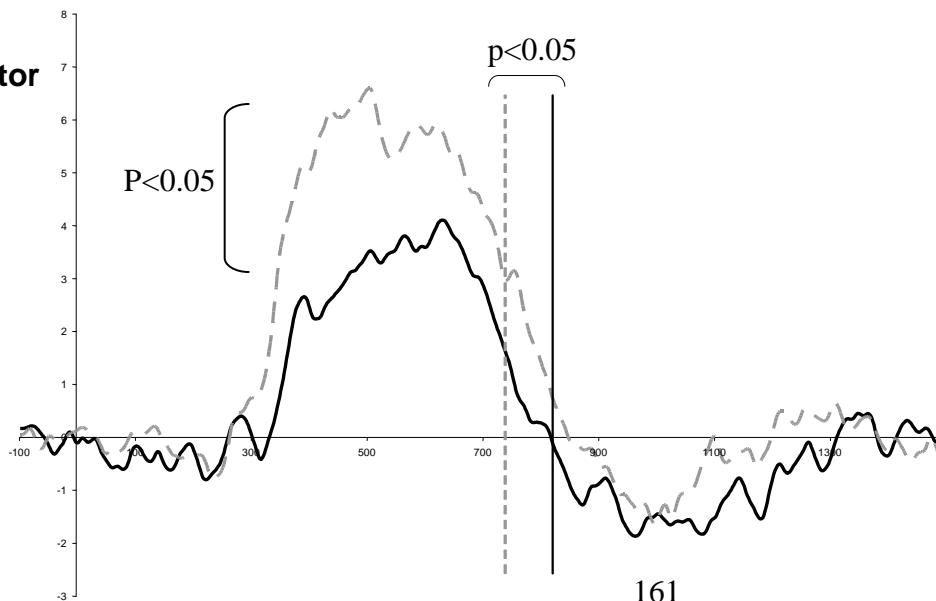


Figure 6.4 Averaged ERP waveforms for good and poor recognition groups elicited by **a)** correct location stimuli, **b)** incorrect location stimuli and **c)** distractors. The vertical lines show, approximately, the average reaction times for both groups. No significant behavioural or electrophysiological differences were found for object recognition when location was consistent with the study phase.

6.4.3 Dipole Source Analysis

Models were generated from the Global Field elicited for the Study stimuli and each of the three stimulus types from the test block. Table 6.1 shows the number of dipoles in each model, their Talairach co-ordinates and their approximate locations (supplied by the Talairach Daemon) and the Residual Variance (RV) of each model. Figure 6.5a shows the dipole model for the Study stimuli. The dipole solution for the Test stimuli (Correct location targets) can be seen in Figure 6.5b. The source waveforms shown illustrate each dipole's contribution to the models. Figure 6.5c shows the dipole model for the localisation of the P1 identified for Correct location targets moving down through brain space on the z-axis. In localising the P1, a six dipole model consisting of bilateral frontal and parahippocampal dipoles (along with an occipital dipole and left temporal source) accounted for ~90% of the variance. Like the solution for the correct location test stimuli above, the source waveforms relating to these generators show P1 activity for the correct location targets. No activity was seen when this solution was used for the other test stimuli. Source models were produced in a step-wise fashion by fitting sources with some constraints. In most cases bilateral constraints of symmetry were enforced with anatomical constraints used to represent medial temporal contribution to the models. Attempts to construct a model without fixed sources led to dipole migration from the head model, resulting in implausible solutions.

A comparison of the models in Table 6.1 revealed possible differential temporal lobe activations between study and test stimuli (superior temporal vs. middle temporal), and between correctly and incorrectly located stimuli where frontal differences were also observed (medial frontal vs. anterior cingulate). No differences were seen (at the structural level) between the models related to correct location objects and distractors. The

P1 localisation showed the greatest deviation from the other models with more frontal lobe involvement (bilateral dipoles).

Table 6.1 *Dipole model information for Study and Test stimuli solutions.*

| Condition | Dip. | Talairach Co-ordinates | | | Brodmann's Area | Structure | Figure 6.7 |
|---|------|------------------------|-------|-------|-----------------|-----------------------------|------------|
| Study Stimuli 300-600ms (R.V. – 2.91%) | 1 | -48.2 | -35.7 | 3.1 | BA22 | L. Sup. Temporal Gyrus | ● |
| | 2 | 48.2 | -35.7 | 3.1 | BA22 | R Sup. Temporal Gyrus | ● |
| | 3 | 22.1 | -78 | 25.6 | BA31 | R. Precuneus | ● |
| | 4 | -22.1 | -78 | 25.6 | BA31 | L. Precuneus | ● |
| | 5 | -1.6 | 44.7 | 22.4 | BA9 | L. Medial Frontal Gyrus | ● |
| | 6 | 21 | -20.1 | -5 | BA28 | R. Parahippocampal Gyrus | ● |
| | 7 | -21 | -20.1 | -5 | BA28 | L. Parahippocampal Gyrus | ● |
| Test Stimuli (Correct location target) 300-600ms (R.V. – 3.24%) | 1 | -51.1 | -43.9 | 9.4 | BA21 | L. Middle Temporal Gyrus | ● |
| | 2 | 51.1 | -43.9 | 9.4 | BA21 | R. Middle Temporal Gyrus | ● |
| | 3 | 18.1 | -75 | 29.3 | BA31 | R. Precuneus | ● |
| | 4 | -18.1 | -75 | 29.3 | BA31 | L. Precuneus | ● |
| | 5 | -16.5 | 40.4 | 12.2 | BA10 | L. Medial Frontal Gyrus | ● |
| | 6 | 21.3 | -19.9 | -4.7 | BA28 | R. Parahippocampal Gyrus | ● |
| | 7 | -21.3 | -19.9 | -4.7 | BA28 | L. Parahippocampal Gyrus | ● |
| Test Stimuli (Incorrect location target) 300-600ms (R.V. – 4.04%) | 1 | -52.9 | -39.7 | 10 | BA22 | L. Sup. Temporal Gyrus | ● |
| | 2 | 52.9 | -39.7 | 10 | BA22 | R Sup. Temporal Gyrus | ● |
| | 3 | 19.8 | -77.5 | 28 | BA31 | R. Precuneus | ● |
| | 4 | -19.8 | -77.5 | 28 | BA31 | L. Precuneus | ● |
| | 5 | -11.2 | 33.5 | 24.3 | BA32 | L. Anterior Cingulate Gyrus | ● |
| | 6 | 21.3 | -21 | -4.8 | BA28 | R. Parahippocampal Gyrus | ● |
| | 7 | -21.3 | -21 | -4.8 | BA28 | L. Parahippocampal Gyrus | ● |
| Test Stimuli (Distractors) 300-600ms (R.V. – 3.07%) | 1 | -51.1 | -43.6 | 9.3 | BA21 | L. Middle Temporal Gyrus | ● |
| | 2 | 51.1 | -43.6 | 9.3 | BA21 | R. Middle Temporal Gyrus | ● |
| | 3 | 18 | -74.9 | 29 | BA31 | R. Precuneus | ● |
| | 4 | -18 | -74.9 | 29 | BA31 | L. Precuneus | ● |
| | 5 | -16.8 | 40.4 | 12.2 | BA10 | L. Medial Frontal Gyrus | ● |
| | 6 | 22.2 | -22.1 | -4.9 | BA28 | R. Parahippocampal Gyrus | ● |
| | 7 | -22.2 | -22.1 | -4.9 | BA28 | L. Parahippocampal Gyrus | ● |
| P1 localisation (Correct location target) 160-200ms (R.V. – 9.61%) | 1 | 22.6 | -36.2 | -10.5 | BA36 | R. Parahippocampal Gyrus | ● |
| | 2 | -22.6 | -36.2 | -10.5 | BA36 | L. Parahippocampal Gyrus | ● |
| | 3 | 37.4 | 42.4 | 3.4 | BA- | R. Inferior Frontal Gyrus | ● |
| | 4 | -37.4 | 42.4 | 3.4 | BA- | L. Inferior Frontal Gyrus | ● |
| | 5 | -51.7 | -39.8 | 1.9 | BA22 | L. Middle Temporal Gyrus | ● |
| | 6 | 30.4 | -77.4 | 27.9 | BA19 | R. Cuneus | ● |

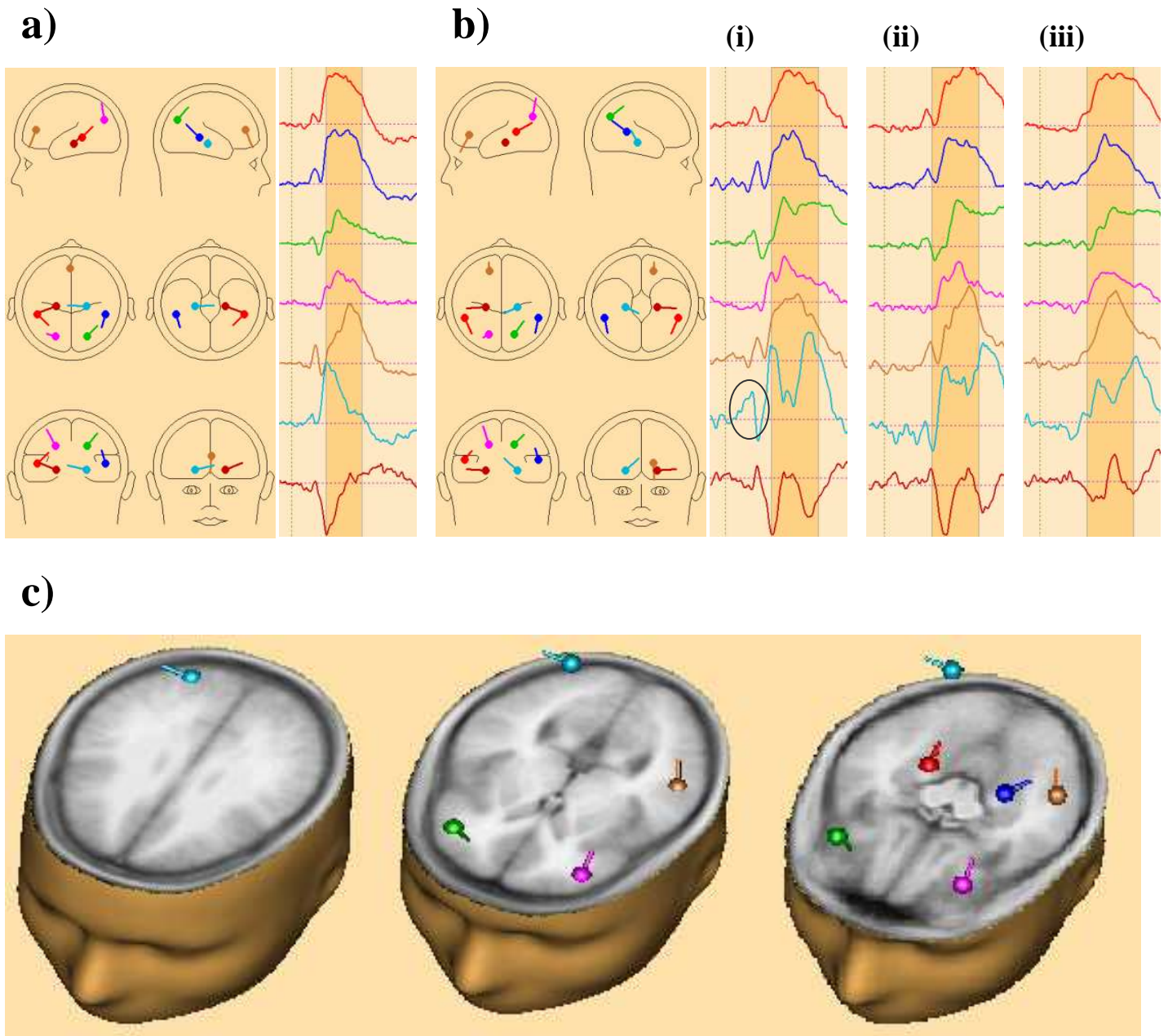


Figure 6.5 Dipole models of the neural generators involved in processing **a)** Study stimuli and **b)** Correct location Test stimuli. Models for other test stimuli are described in Table 1. Source waveforms showing each dipoles time course are shown for Study stimuli and (i) Correct location (ii) Incorrect location and (iii) Distractor stimuli. The fitting epoch for these models was 300-600ms (shown as the dark region in the source waveforms). **c)** Source localisation of the P1 for Correct location targets with dipole locations displayed over transverse MRI slices at different slice selections on the z-axis

Note: the circle over Correct location Test stimuli (b)-(i) identifies a peak in activation not seen for Incorrect location (ii) or Distractor (iii) stimuli. This 'P1' is most prominent for the right parahippocampal source but can be seen for all sources in the model.

6.4.4 Summary of electrophysiological results

In summary, the ERP data showed measurable differences in brain activity related to study and test stimuli, with additional prolonged test-related parietal activity indicating the presence of a P3b. A centro-parietal latency difference was observed for test stimuli, where correct location targets elicited faster peaking P300 components. This difference was preceded by earlier positive-going activity (possibly a P1) which was unique to the correct location targets. The latency difference was not related to behavioural performance, in that it was present even after a group split based on reaction times. Reaction time was instead found to have an effect on P300 amplitude with fast responders showing larger amplitudes. Finally, dipole models suggest that similar structures were involved across conditions with frontal, temporal, parietal and parahippocampal sources appearing in each model. However, differences in the temporal activation of these structures were observed. For instance, the source waveforms related to the fixed parahippocampal dipoles revealed the possible earlier involvement of this area for the correct location targets.

The findings of this experiment will be discussed at the end of this chapter alongside the results of the following experiment which was undertaken to account for the possible confounding influence of scene recognition.

Experiment 2

Behavioural investigation of implicit object-location memory using shifted-viewpoints

6.5 Methods

6.5.1 Participants

Twenty-three participants were chosen in an *ad-hoc* manner, all aged between 20-21 years (14 females). All participants had normal or corrected-to-normal vision and gave informed, written consent before participation. The experiment was conducted in accordance with the Code of Ethics of the World Medical Association and the ethical standards of the APA as well as abiding by the NUI Maynooth University Ethics Code.

6.5.2 Stimuli

The Spatial Grid Task was used for this experiment – see General Methods section 2.2.2. All stimuli were presented using E-Prime on an Intel Pentium 4 Processor (3.00GHz CPU) and displayed on an LCD monitor. They consisted of 8 different objects and 8 distractors. The particular set of objects presented were a bin, a bucket, a post-box, a road-cone, a fire hydrant, a tree, a tyre and a keg and distractors were a parasol, a microphone stand, a cactus plant, a blender, a fire extinguisher, a stool, a lamp and a cinder block.

6.5.3 Procedure

The Study Block in the procedure remained unchanged (See Experiment 1 above). The Test Block was also similar to Experiment 2 with 3 conditions 1) familiar objects presented in old (correct) location 2) familiar objects in novel (incorrect) location and 3) novel objects presented in random location. However, for this experiment we included a number of viewpoints with the addition of 90° left and 90° right. The test block consisted of a 12 trial practice from the studied viewpoint followed by 96 trials where participants performed the task as described above from the studied (0°) viewpoint as well as 90° left of the environment and 90° right of the environment. Each of the 8 study objects appeared twice in each viewpoint (once in their correct location and once in their incorrect location) and the 8 distractor objects appeared twice in each viewpoint. $(8 \text{ study objects} \times 2 \text{ locations} \times 3 \text{ viewpoints}) = 48 \text{ trials} + (8 \text{ distractors} \times 3 \text{ viewpoints} \times 2) = 96 \text{ trials}$. Response procedures did not change between experiments.

6.6 Results

6.6.1 Behavioural Data

Individual mean accuracy scores for each of the three stimulus conditions (target object, target object-incorrect location and distractor object) for each of the viewpoints (study, 90° left, 90° right) were collated for comparison. Overall, accuracy was high across the three conditions regardless of the viewpoint from which participants were tested. Figure 6.6a (top panel) shows the percentage mean accuracy for each of these stimulus types scored from the Study viewpoint (Correct location targets: $98.4 \pm 1.2\%$; Incorrect location targets: $91.3 \pm 3.4\%$; Distractors: $98.1 \pm 0.72\%$) and the novel viewpoints (Correct location targets: $95.1 \pm 1.7\%$; Incorrect location targets: $92.4 \pm 3.2\%$; Distractors: $97.6 \pm 0.75\%$). A repeated-measures ANOVA was carried out to compare the mean accuracy in the three conditions across the three viewpoints. The within-subjects comparisons revealed no main effect of stimulus-type or viewpoint but a significant interaction effect was found for stimulus x viewpoint [$F(4, 88)=4.135$, $p<0.005$]. Subsequent Bonferroni-corrected paired-samples t-tests found a significant difference between Correct and Incorrect location targets for the Study viewpoint [$t(22)=3.026$, $p<0.05$] (see Figure 6.6a top panel). The change in viewpoint to the novel view only significantly affected performance for Correct location targets, with accuracy significantly lower for the new view trials [$t(22)=3.761$, $p<0.01$]. When paired-samples comparisons were made between stimulus-types regardless of viewpoint, accuracy was found to be significantly diminished for the Incorrect location condition compared to Correct location [$t(68)=3.187$, $p<0.05$] and Distractor stimuli [$t(68)=2.918$, $p<0.05$] - Bonferroni-corrected (see Figure 6.6a-bottom panel).

Reaction times (from accurate trials) are shown in Figure 6.6b (top panel) and can be seen to be quicker on average for Correct location targets ($653.43 \pm 22.86\text{ms}$) compared to Incorrect location targets ($721.91 \pm 22.43\text{ms}$) and Distractors ($715.72 \pm 13.71\text{ms}$) from the Study viewpoint, and Correct location targets ($702.19 \pm 24.26\text{ms}$) compared to Incorrect location targets ($744.44 \pm 31.72\text{ms}$) but not Distractors ($694.15 \pm 15.14\text{ms}$) from the novel viewpoints. Figure 6.6b (bottom panel) shows mean reaction time grouped by stimulus-type (Correct location targets $685.94 \pm 14.51\text{ms}$; Incorrect location targets $736.93\text{ms} \pm 17.51$; Distractors $701.34 \pm 8.94\text{ms}$). A repeated-measures ANOVA revealed that reaction times differed significantly with stimulus-type [$F(2, 44)=4.821, p<0.05$] but no main effect was found for viewpoint. An interaction effect of stimulus x viewpoint was also found [$F(4, 88)=9.423, p<0.001$]. Bonferroni corrected t-tests comparing reaction times in trials from the Study view found significant differences between Correct location targets and Incorrect location targets [$t(22)=4.356, p<0.01$], and between Correct location targets and Distractors [$t(22)=3.398, p<0.05$]. Participants were also found to respond significantly faster on the novel view trials when the target object was correctly (versus incorrectly) positioned [$t(22)=2.895, p<0.05$]. Participants' reaction times were slower, on average, for the novel viewpoints compared with the study viewpoint, significantly so for Correct location targets [$t(22)=2.657, p<0.05$] and Distractors [$t(22)=2.810, p<0.01$] but not for Incorrect location targets. Comparing stimulus-type regardless of view (Fig 6.6b-bottom panel) revealed a significant difference between Correct and Incorrect location targets [$t(68)=4.858, p<0.01$] – Bonferroni corrected.

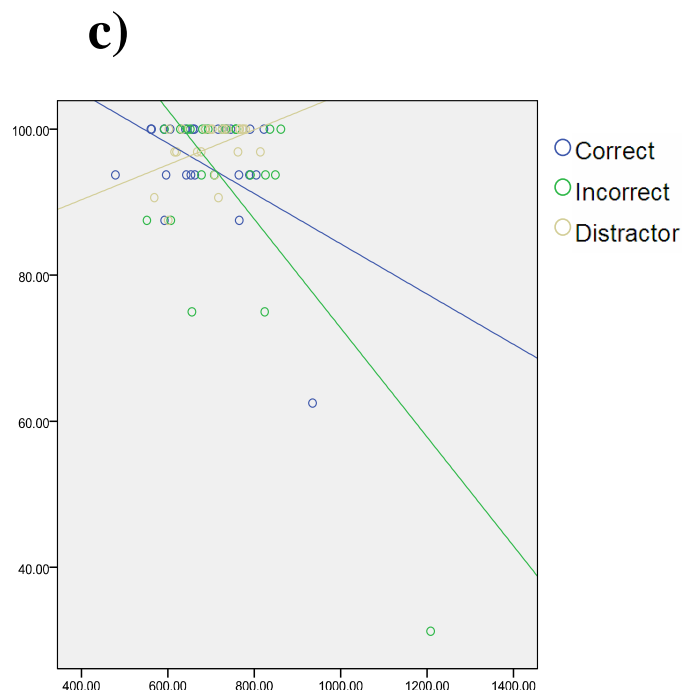
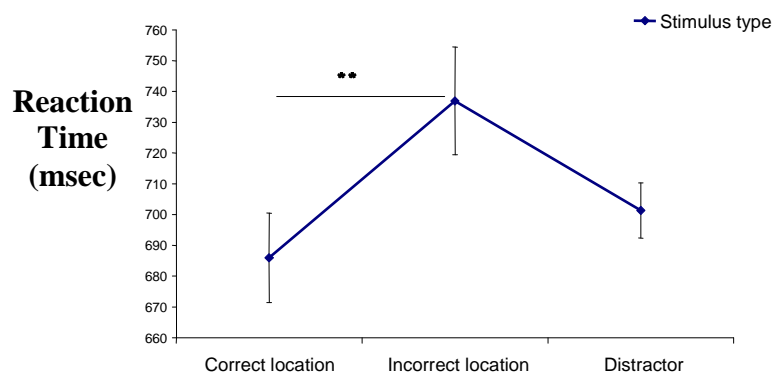
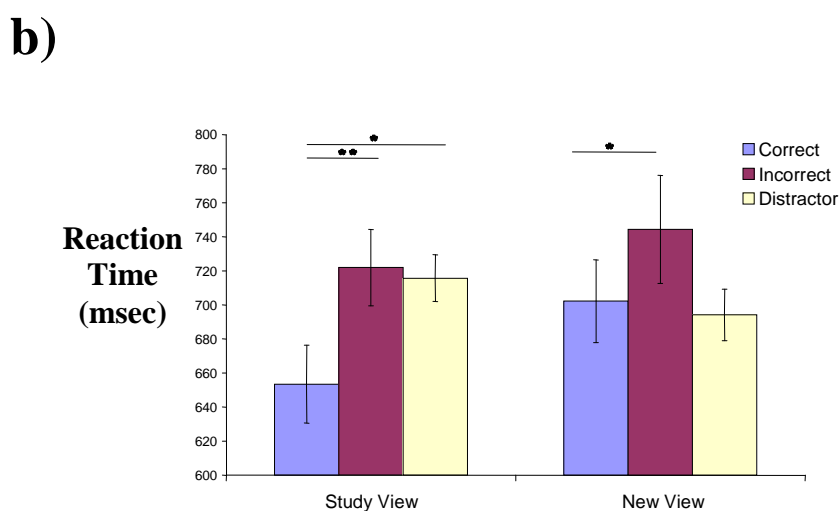
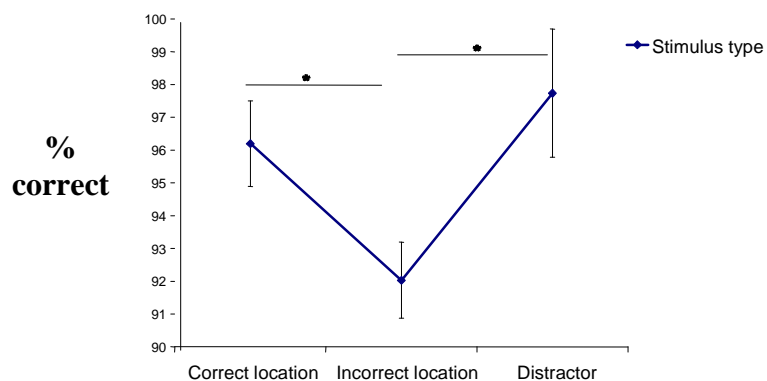
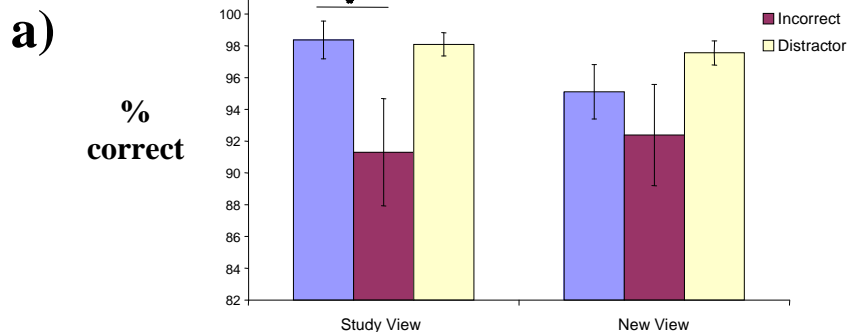


Figure 6.6 a) Mean accuracy for each of the stimulus type conditions for the different viewpoints tested (left and right views collated into 'new' view condition). Mean accuracy for each of the stimulus type conditions regardless of viewpoint is also displayed. Error bars display Standard Error of the Mean.

b) Mean reaction times for each of the stimulus type conditions for the different viewpoints tested (left and right views collated into 'new' view condition). Mean reaction times for each of the stimulus type conditions regardless of viewpoint are also shown. Error bars display Standard Error of the Mean. **c)** Scatterplot plotting individual performances i.e. accuracy/RT correlations for each stimulus type (with viewpoints collapsed)

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

6.7 General Discussion

Behaviourally, it was expected that in both experiments response accuracy would be greater and response latency would be faster upon presentation of studied or target objects in their correct location than target objects in an incorrect location. The pattern of accuracy data found was similar to item-context association tasks (Rugg *et al.*, 1998) where accuracy was greater for target objects in their correct location than those placed in an incorrect location. Accuracy data from Experiment 1 were found to differ significantly after an ANOVA was performed but subsequent non-significant t-tests provided no clarification. Reaction times differed significantly as predicted, with correct targets being identified the fastest. Experiment 2 was undertaken to allay criticisms that the effects observed in both the behavioural and the ERP data from Experiment 1 were due to simple scene recognition. Specifically, trials where the test object appeared in its correct or studied location would be recognized as a scene compared to trials in which object or object location had changed from the study phase. On review of the behavioural data from both experiments it can be argued that, although scene recognition may play a role, the effect of viewpoint on memory differs from the effect of stimulus location. The viewpoint changes in Experiment 2 lead to some decreases in overall performance but the pattern of performance across stimulus-types was similar in the old and new viewpoints. In addition, reaction times differed significantly with stimulus-type but no main effect was found for viewpoint. In both experiments there was no difference in accuracy scores between targets and distractors, suggesting that the participants clearly understood the instructions of the task. The reaction time data are a more useful measure of whether implicit learning occurred and based on the data reported there is a strong argument this was the case. Indeed, in the alternative analysis after the median split (in Experiment 1),

reaction times were shown to differ significantly for the object recognition task but these differences were nullified when the object was presented in its original location. Among the characteristic differences between explicit and implicit memory, outlined by Reber (1993), is the low variability (individual differences) in implicit learning and memory compared to explicit learning and memory. The variance between the ‘Good Recognition Group’ and ‘Poor Recognition Group’ seemed to be dependent on whether the objects’ spatial location was (re)presented. This variance was also seen in the ERP findings where amplitude differences observed between the groups were not present when objects appeared in their correct locations. The results from ERP and source data will be discussed separately in subsections relating to stimulus processing and stimulus type. A more general discussion will follow including an elaboration on the sex differences identified.

Encoding. The processing of the Study stimuli elicited a P300 identified over parietal scalp electrodes. The P300 component is thought to be composed of several parts that reflect an information processing cascade when attentional and memory mechanisms are engaged (Polich, 2007). The model described by Polich (2007) posits that “the P300” comprises an early attention process stemming from a frontal working memory representational change to produce the P3a. The attention-driven stimulus signal is then transmitted to temporal and parietal structures related to P3b. Dipole source analysis revealed a distributed network involving frontal, parietal, temporal and medial temporal sources. With an RV of <3%, the model generated to account for the scalp pattern recorded for Study stimuli includes regions that may be involved in processing verbal attributes of the objects (frontotemporal) as well as spatial aspects of the environment (medial-temporal and parietal).

Retrieval. Differences between the ERP waveforms elicited by Study and Test stimuli could be seen in the extended duration of P300 positivity for Test stimuli most likely indicating additional stimulus evaluation processing and response selection. The processing of the Test stimuli led to a latency difference in the elicitation of a parietal P300, dependent on object-location variance from the encoding phase. P300 latency is thought to index classification speed, which is proportional to the time required to detect and evaluate a target stimulus (Kutas *et al.*, 1977; Magliero *et al.*, 1984). The latency difference was significant, where earlier positive-going fluctuations were recorded for Correct location Targets. So in addition to the reaction time data, participants physiologically classified test objects more quickly when they were presented in their studied location. Source analysis showed the same (or similar) neural generators were involved in retrieval of test objects regardless of stimulus type. Therefore the latency difference reveals an earlier activation of an underlying process or network which recruits the same areas. These areas, namely frontal (BA10, 32) and temporal gyri (BA21, 22), precuneus (BA31) and parahippocampus (BA28) were also active for the encoding of the Study stimuli. Before discussing possible neural generators, it must again be noted as it has been in previous chapters, that the dipole models reported here are approximations of source activity and as such they are merely suggestive of a structures possible involvement.

BA28 denotes a specific area of the parahippocampus, the entorhinal cortex (EC). The EC provides the critical input pathway in this area of the brain, linking the association cortices to the hippocampus. It also provides the pathway for signals returning from the hippocampus to the association cortices. Due to its role as a major convergence zone, both for object information arriving from perirhinal cortex and spatial information

arriving from parahippocampal cortex, its function in object-location memory has been tested in numerous studies in rats (Parron & Save, 2004; Parron *et al.*, 2006), primates (Insausti *et al.*, 1987; Suzuki & Amaral, 1994; Suzuki *et al.*, 1997) and humans (Haist, Bowden & Mao, 2001; Miller, Lai & Munoz, 1998).

BA31, which is positioned between the cingulate and splenial sulci, includes both posterior cingulate (a.k.a. retrosplenial) and precuneate cortices. The precuneus has been implicated in spatial attention (Le *et al.*, 1998), allocentric spatial memory (Frings *et al.*, 2006), mental navigation (Ghaem *et al.*, 1997), real-world navigation (Suzuki *et al.*, 1998) and visual imagery in episodic memory recall (Buckner *et al.*, 1995; Fletcher *et al.*, 1996; Halsband *et al.*, 1998). The principal extraparietal corticocortical connections of the precuneus are with the frontal lobes (Cavanna & Trimble, 2006). The precuneus has reciprocal projections to the pre-frontal cortex as well as superior temporal sulci, areas also included in the dipole models.

Frontal regions, such as mid-prefrontal area (BA10) and anterior cingulate cortex (ACC- BA32) are posited to be involved in a cognitive control network for processing context and monitoring performance (Gutchess *et al.*, 2007; Ridderinkhof *et al.*, 2004) and working memory in general. The shift in frontal activations to the ACC during Incorrect location Target processing may indicate a task-difficulty increase or an increase in self-monitoring or error processing. Behaviourally most errors occurred for these stimuli. Activation of the ACC has recently been shown for errors made with and without awareness (Hester *et al.*, 2005).

Temporal activations were more superior than expected for object processing. Dipoles were located bilaterally either in middle or superior temporal gyri (BA21/22). The inferior temporal gyrus is one of the higher levels of the ventral stream of visual

processing and there are an extensive number of studies highlighting this area's role in object representation (Gross, 1994; Wachsmuth et al., 1994). However, Duzel *et al.* (1999) conducted a PET and ERP co-registration study to distinguish between the neural correlates of task-related (episodic/semantic) and item-related (old/new) processes of memory retrieval. They reported temporal lobe activation in BA21 for the semantic retrieval task. This co-occurred with left frontal activations similar to those found in the current study. The easily accessible semantic properties of the unambiguous objects used in the current study may have been responsible for the unpredicted temporal lobe activations.

As mentioned above, processing of test stimuli recruited very similar brain areas leaving the latency difference to be explained. Although significance was not reached in the comparison of P1 amplitudes across stimulus types, it is posited that the earlier activation which occurred for Correct location Targets was associated with a P1, specifically related to same-location facilitation. This component can be seen in the source waveforms relating to the dipole models but is only evident for the model pertaining to Correct location Targets. In particular, putative activation of the right parahippocampal gyrus can be seen to occur when the test object was presented in its 'correct' location (Fig. 6.5b-(i)). Localising the P1 for Correct location Targets separately, bilateral sources were found in BA36 (parahippocampal cortex), the area that relates spatial information on to the EC. Frontal and temporal generators were again identified. A source in the cuneus suggests processing earlier in the visual system before the parietal processing documented in the precuneus. When this model was applied to the other test stimuli over the same fitting interval (160-200ms), the RV was >50%, a further indication of the importance of these activations for the latency effect to occur dependant

on implicit location memory. Activations of the hippocampus would suggest the involvement of explicit memory. The MTL dipoles contradict previous research which has shown a differentiation in terms of brain areas involved in explicit and implicit memory, with activations of the medial temporal lobes for explicit and the basal ganglia for implicit (Honda *et al.*, 1998; Poldrack *et al.*, 2001). However, some argue that MTL pathology produces implicit memory impairment that often goes undetected (Ostergaard & Jernigan, 1993; Ostergaard, 1999; Jernigan *et al.*, 2001) and a number of functional magnetic resonance studies have reported medial temporal lobe activation in implicit learning (see for review, Forkstam & Petersson, 2005).

Here, we demonstrate, both behaviourally and physiologically, that humans can classify objects more quickly when using implicit spatial memory. As the task was an object recognition task with reaction time being an explicit measure of performance, the P300 amplitudes may represent task proficiency, as mean amplitudes correlated significantly with reaction time. Differences observed in object recognition proficiency were absent if objects were presented in their correct location. Correct location presentations implicitly aided object recognition as they removed both behavioural and electrophysiological performance differences. A network of structures was identified in frontal, parietal and temporal areas with subdivisions of the parahippocampus playing a crucial role in the implicit recognition of location and its facilitation of concurrent explicit object recognition. In conclusion, we propose an electrophysiologically based model of implicit spatial memory which demonstrates the influence of object-location memory on P300 latency and amplitude, and the importance of this component as well as earlier spatially-related components for object recognition.

7

Chapter VII

Electrophysiological correlates of
object and spatial memory:
Dissociations and interactions

7.1 Abstract

Exactly how are objects and locations bound together in the brain to form coherent object-location memories? This question is central to an enduring debate, underway not only in the spatial cognition literature, but also affecting research into general episodic memory. This final chapter outlines a study which probed this question using a cueing paradigm assessing memory for objects and locations. Both behavioural and electrophysiological responses to these events were also compared to those from uncued blocks of object-location pairs. Cued locations were found to engage frontal and temporal cortices along with more posterior and parahippocampal areas, the recruitment of which may have aided performance on these trials. Similarly, cued objects engaged frontal and temporal cortices but no medial temporal activity was seen during these trials. Performance on the paired stimuli was found to be dependent on the congruence of the pairs. These stimuli engaged a subset of the areas seen for the separate location and object presentations. These areas, localised to within the frontal cortex and around the temporoparietal junction, are posited to be involved in the binding of objects and locations, bridging the separate processes carried out in the dorsal and ventral streams. The findings are discussed in relation to qualitative differences in the questions effectively posed by the cues – namely ‘what goes here?’ versus ‘where does this go?’

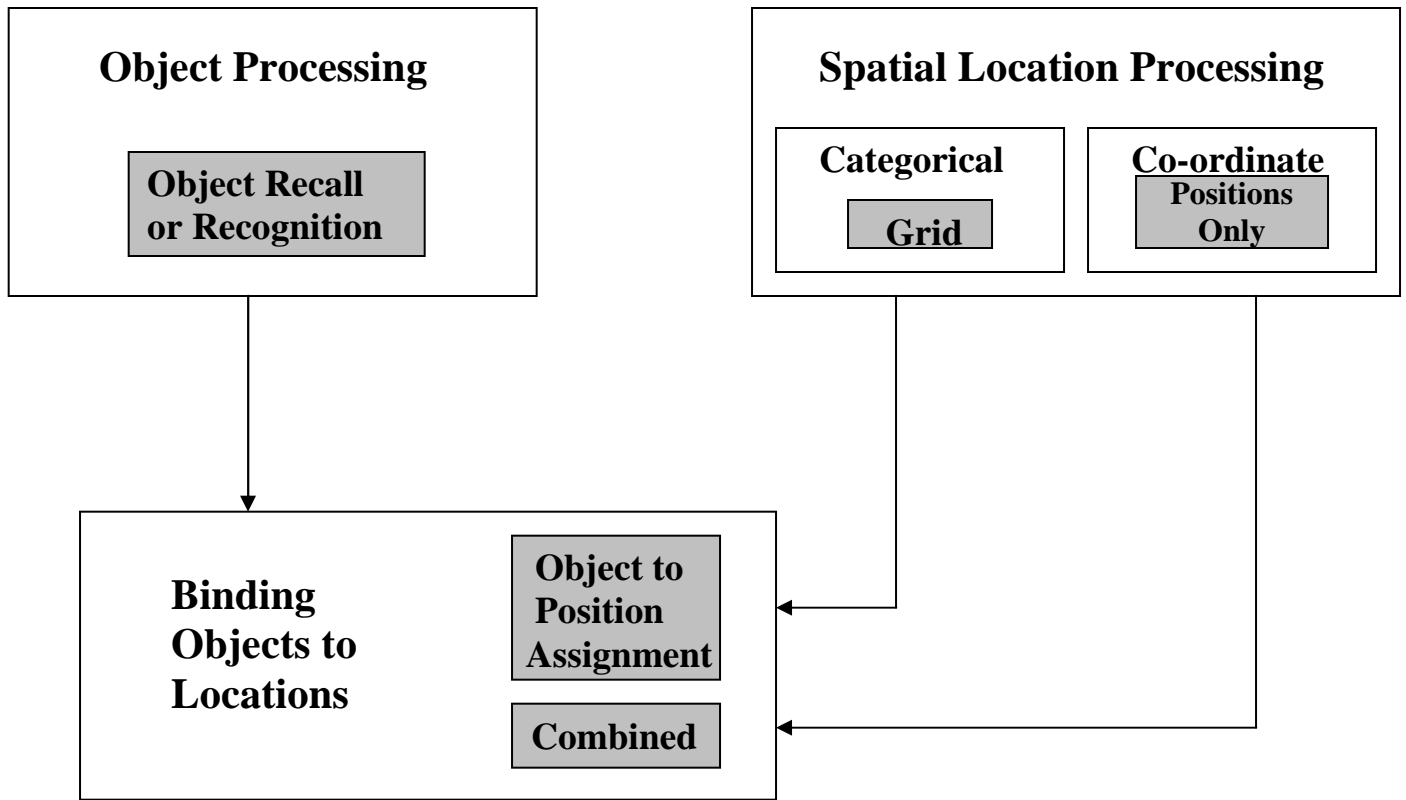
7.2 Introduction

The Spatial Grid Task has been demonstrated to be a useful tool for investigations into small-scale spatial memory. Specifically, it is useful for studies of object-location memory. The experiments presented so far have probed the spatial side of this relationship while largely ignoring the ‘object’ element of these memories. Knowing ‘what is where’ concerns the question of how features are bound together to form complex memories (Chalfonte, Verfaellie, Johnson & Reiss, 1996). A study of spatial representation is not complete without an analysis of how representations deal with binding spatial and object memory in the brain.

Locations are remembered for their utility, usually because what they contain is of interest or importance. Every location has a physical property and every object has a spatial component. Object-location memory reflects the multi-attribute nature of the visual world. As we navigate, we use locational information as both the guide and the goal but object-location memory differs from the kind of spatial memory used for navigation in a number of ways. It has no need for a stored temporal order or sequence of information; it is merely a description of where things are in space, not how to get to them (Postma, Kessels & van Asselen, 2005). Object-location memory depends on a variety of component processes such as object processing, spatial-location processing (or memory for the locations of individual items) and memory for the binding of objects in occupied locations (Puglisi, Park, Smith & Hill, 1985). These three component processes (object, spatial, binding) are included in the functional analysis of object-location memory (shown in Figure 7.1a) presented by Postma, Kessels and van Asselen (2004). Since the initial dissociation of the ventral and dorsal streams by Ungerleider and

Mishkin (1982), a large number of studies have sought to separate these object, spatial and binding processes into the ‘what’ and ‘where’ pathways (Figure 7.1b).

a)



b)

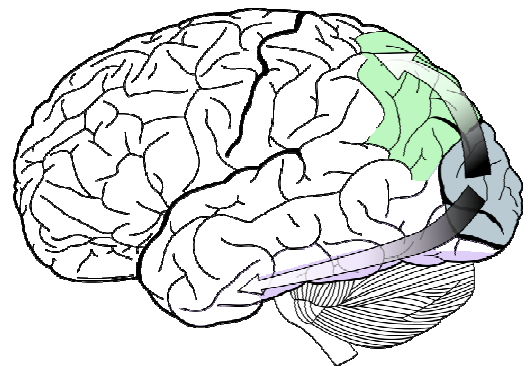


Figure 7.1 a) A functional analysis of object-location memory proposed by Postma, Kessels and van Asselen (2004). Rectangular shapes depict processing components. Grey boxes show the tasks presumed to assess these components **b)** Propagation of the ventral (what) and dorsal (where) streams from primary visual areas first identified by Ungerleider and Mishkin (1982). More recently it has been argued that certain forms of spatial processing recruit both streams (Milner & Goodale, 1995)

Smith *et al.* (1995) observed that object working memory activated left parietal and temporal areas, whereas spatial working memory activated right-sided occipito-parietal and prefrontal areas. Vandenberghe *et al.* (1996) reported consistent deactivation by familiar (compared with novel) images in a 'stream' stretching from the lateral occipital gyrus along ventral temporal cortex to the hippocampus. Other human imaging studies also suggest that the more 'cognitive' stages involved in object identification activate more anterior and ventral areas in the brain. Studies involving ERP (Allison *et al.*, 1994), PET (Sargent, Ohita & MacDonald, 1992) and fMRI (Puce *et al.*, 1995) have all reported selective activation in response to objects and faces in the ventral stream. More recently, Reddy and Kanwisher (2006) described the coding of objects (based on familiarity) in a sparse, clustered manner by the ventral stream.

A hemispheric dissociation has also been suggested in recognising objects from familiar and novel views but debate continues as to whether right hemispheric structures hold exemplar representations (Burgund & Marsolek, 2000; Marsolek, 1999) or allow the processing of non-canonical views (Layman & Greene, 1988; McAuliffe & Knowlton, 2001; Warrington & James, 1986; Warrington & Taylor, 1973, 1978). Laeng and colleagues (1999) argue that the left hemisphere performs superiorly for encoding objects in novel, contorted poses, whereas the right hemisphere is better in encoding familiar, conventional poses of objects. In a recent review of object-location memory studies, Postma, Kessels and van Asselen (2008) conclude that object memory is most likely underpinned by ventral cortical areas and prefrontal dorsolateral areas. They also suggest that the debate about lateralization patterns may be complicated by the fact that object identities can often be memorized by means of verbal codes and this may lead to the left-hemispheric contributions observed by some researchers (see Stewart *et al.*, 2001).

The dorsal contributions to spatial memory have been discussed throughout this thesis. Egocentric and allocentric coding engage different neural circuitries and it is the viewer-centered, egocentric encoding of space that has been shown to recruit a fronto-parietal network along the dorsal stream (Committeri *et al.*, 2004; Galati *et al.*, 2000; Wilson, Woldorff & Mangun, 2005). Smith and Jonides (1997) and Wilson *et al.* (1993) both reported that encoding locations in memory relies predominantly on the posterior parietal cortex implicating the dorsal stream. Spatial location processing along the dorsal stream has been assessed by experiments testing both coordinate (e.g. Postma & De Haan, 1996) and categorical (e.g. Kessels *et al.*, 2004) position memory. Kessels *et al.* (2002) and more recently van Asselen *et al.* (2008) tested groups of stroke patients with lesions in the temporo-occipito-parietal area. Both studies observed that right-hemisphere damage adversely affected exact positional reconstruction.

Despite the general agreement regarding the roles of the individual object and spatial processing pathways, the degree to which these ‘streams’ are interconnected and the possible areas involved in the resulting convergent processing are still topics of debate. We revert back to Figure 7.1a and the lower box which encapsulates the binding problem. Baddeley (2000) proposed an episodic buffer in working memory that acts as an extension of the central executive (CE) in integrating information from a number of different sources into coherent episodes. Although the episodic buffer is anatomically ill-defined, it does suggest the involvement of higher-order prefrontal CE mechanisms in the binding of information. Neuropsychological evidence for the involvement of the frontal lobes in information binding has been reported by a number of researchers (e.g. Mitchell *et al.*, 2000; Piekema *et al.*, 2006; Prabhakaran *et al.*, 2000). Prabhakaran and colleagues (2000) reported greater activation in dorsolateral prefrontal cortex (DLPFC) for retention

of letter-location bindings than for separate retention of letters and locations. Other previous investigations have instead reported strong evidence for posterior parietal involvement in encoding and maintenance of object-location relationships (Piekema *et al.*, 2006; Todd & Marois, 2004; Xu & Chun, 2006). Researchers investigating multi-sensory integration using functional imaging (Calvert *et al.*, 2001; Lewis *et al.*, 2000; Miller & D'Esposito, 2005) and electrophysiological techniques (Molholm *et al.*, 2006) have also reported contributions from the parietal lobes for the binding of information.

In addition to frontal and parietal involvement, Piekema *et al.* (2006) suggested the right hippocampus participates in short-term memory maintenance of object-location associations. The relational view of memory suggests that the hippocampus is particularly important in linking previously unrelated pieces of information, such as the relationship between an item or event and the learning context, or between different elements that make up an event (Eichenbaum & Cohen, 2001; Rudy & Sutherland, 1995; Sutherland & Rudy, 1989). It is generally agreed that structures in the MTL play a critical role in forming long-term relational memory representations (Eichenbaum *et al.*, 1994). Evidence implicating the hippocampus in short-term retention of relational memory is, however, also mounting in the neuropsychological literature (e.g. Hannula *et al.*, 2006; Hartley *et al.*, 2007; Kan *et al.*, 2007; Olson *et al.*, 2006). For example, Kan *et al.* (2007) tested hippocampally damaged patients and controls with a recognition test where items were cued correctly or incorrectly based on previously learned cue-target presentations. Only the controls benefited from the associative information provided by the correct cues supporting the role of the hippocampus in short-term relational memory.

Van Asselen *et al.* (2008) have argued that two binding mechanisms might be distinguished based on the locational processing involved, suggesting coordinate and

categorical binding processes. With this in mind, Postma, Kessels and van Asselen (2008) updated their earlier functional model of object-location memory (Postma, Kessels & van Asselen, 2004 – Figure 7.1a) assigning anatomical regions to the proposed processes. Figure 7.2 is a reproduction of their model. They highlight dissociations across hemispheres as well as visual processing streams and implicate the hippocampus as crucial for object-location binding.

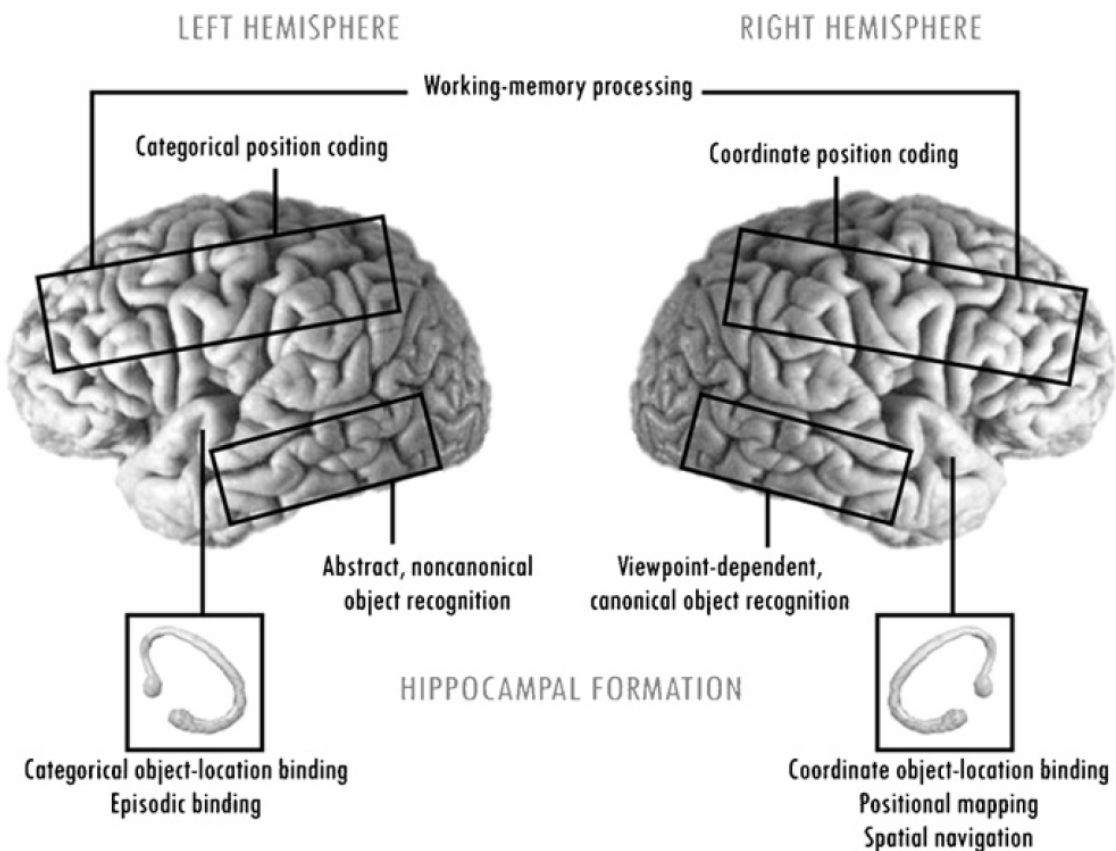


Figure 7.2 The neurocognitive model of object-location memory proposed by Postma, Kessels and van Asselen (2008)

Many studies have investigated attentional mechanisms across the two visual processing pathways. There is now clear evidence from spatial cueing studies supporting the idea of a space-based system of attention (e.g. Downing, 1988; Martinez *et al.*, 2006;

Muller & Findlay, 1987; Posner, 1980) and another object-based component (see Scholl, 2001; also Cave & Bichot, 1999, for reviews) with evidence coming from cued detection and cued discrimination tasks (e.g. Brawn & Snowden, 2000) and negative priming studies (e.g. Tipper, Brehaut & Driver, 1990). However, it is not clear how both systems can work in an integrated way within the visual system. In a PET study, Fink *et al.* (1997) found that object-based and space-based attention share common neural mechanisms in the parietal lobes, in addition to task specific mechanisms in early visual processing areas of the temporal and occipital lobes (see also Arrington, Carr, Mayer & Rao, 2000). Soto and Blanco (2004) recommend that, in order to study adequately both attentional components, at least four experimental conditions should be compared within a single task. The four experimental conditions suggested are cued vs. uncued location, and cued vs. uncued object. In their experiment, Soto and Blanco (2004) found that both spatial and object cueing effects (i.e. attention) were focused by both location and perceptual gestalts. Responses were faster when targets were cued correctly, with selection by location being primary over object-based selection.

The current electrophysiological study is designed to assess object-location memory using cued presentations similar to those in the selective attention literature (see also Kan *et al.*, 2007). In this study, however, objects are used to cue location recognition (BLOCK 1) and locations are used to cue object recognition (BLOCK 2). This allows for comparisons of responses to correctly and incorrectly cued locations and objects. Participants' performance on paired object-location recognition trials is also assessed (BLOCK 3). The three-block design of the experiment enables investigation into object-location processing compared to processing of isolated objects and locations. This investigation involves the calculation and assessment of super- or subadditivity in the

ERP responses (see Stanford *et al.*, 2005). This method is routinely used in multi-sensory integration studies, where responses elicited by bi-sensory stimuli are compared to the sum of the responses elicited by the uni-sensory constituents of the bi-sensory experience (e.g. Foxe *et al.*, 2000; Molholm *et al.*, 2002). In order to investigate binding in object-location memory, the current study will assess additivity by comparing behavioural and electrophysiological responses to locations with responses to objects as well as responses for paired stimuli (i.e. object-in-location presentations).

It is predicted that responses to objects and locations will be dissociable along the ventral and dorsal processing streams, respectively. Recognition of correctly cued objects and locations is predicted to involve frontal, parietal and medial temporal processing, as one element (i.e. test stimulus) is evaluated with the other (i.e. cue) in mind. The associative information provided by the correct cues is predicted to recruit the hippocampus and enhance recognition of targets compared to the misinformation provided by incorrect cues. The presentation of paired stimuli is predicted to have a beneficial effect on the recognition of its constituent parts (i.e. object and location). The lateralisation of the electrophysiological responses may be informative regarding the type of locational processing involved in object-location memory (right-hemispheric coordinate or left-hemispheric categorical) and hence shed light on the binding mechanisms involved in the Spatial Grid Task. Based on previous results it is predicted that responses will be right lateralized, indicating the use of a coordinate strategy.

7.3 Methods

7.3.1 Participants

The participants consisted of an *ad-hoc* sample of 12 undergraduate volunteers (4 females). The ages of the participants ranged from 21-27 years (mean age = 23.75years). After data screening, one participant's data was removed from ERP analysis due to excessive EEG artifacts. All participants were right handed, had normal or corrected-to-normal vision and gave informed, written consent before participation. The experiment was conducted in accordance with the Code of Ethics of the World Medical Association and the ethical standards of the American Psychological Association (APA) as well as abiding by the NUI Maynooth University Ethics Code.

7.3.2 Stimuli

The Spatial Grid Task was used for this experiment – see General Methods Section 2.2.2. All stimuli were presented using E-Prime on an Intel Pentium 4 Processor (3.00GHz CPU) and displayed on an LCD monitor. They consisted of 8 Target objects and 8 distractors. The particular set of objects presented included a bin, a bucket, a post-box, a road-cone, a fire hydrant, a tree, a tyre and a keg and distractors included a parasol, a microphone stand, a cactus plant, a blender, a fire extinguisher, a stool, a lamp and a cavity block.

7.3.3 Procedure

After the electrophysiological preparation (see Chapter 2 for details), participants were seated 50cm from the LCD computer screen on their own in a darkened, electrically shielded and sound-attenuated testing cubicle (150cm x 180cm) with access to a mouse for responses. A study block preceded a test block. Instructions were presented on screen prior to these blocks.

STUDY BLOCK

Participants learned eight objects and their locations in a computer generated environment during a study block (32 trials). Each of the 8 objects was presented in isolation 4 times in a pseudo-randomised order so that consecutive presentations of the same object did not coincide. The temporal sequence of a trial was the same as previous experiments (see for example Chapter 3, Figure 3.1). A fixation cross was presented first for 750ms, followed by the spatial grid with two landmarks (e.g. lamp-post and water fountain) for 1500ms, and then the study stimulus was presented on the grid, remaining onscreen for 2000ms. This cycle was repeated for the 32 trials.

TEST BLOCK

For the test block participants were either cued with an object and required to respond to a location (**LOC**), or cued with the location and required to respond to the object (**OBJ**). There were 112 trials in each block where the object or location was correct or incorrect with reference to the cue i.e. 56 matches and 56 mismatches. Presentation of blocks LOC and OBJ were randomised. Finally participants were required to respond to both object and location after seeing a paired presentation (**PAIR – (obj), (loc)**) – 64 trials. The trial sequence for the test blocks can be seen in Figure 7.3.

A fixation cross was presented for 750ms, followed by the spatial grid with landmarks for 1500ms. Then the **cue** was presented in the LOC and OBJ trials for 1000ms. The landmarks then appeared for 750ms before the **probe** stimulus (object or location) was presented for 2000ms – this was the response interval and a response terminated the trial. In the PAIR trials, a fixation cross was presented for 750ms, followed by the spatial grid with landmarks for 1500ms and then the **pair** stimulus was presented for 1000ms before participants responded to the questions (obj – OBJECT?) and (loc – LOCATION?), each presented for 1000ms. The presentation of the questions (obj) and (loc) was randomised and counter-balanced.

7.3.4 Data Analysis

For the cue-probe trials ANOVAs were used to assess differences in performance with the variables Cue Type (2 levels: obj + loc) and Match (2 levels: match + mismatch). Match refers to the stimulus type for which responses were made i.e. whether participants were responding to a stimulus that was a correct match for the cue or a mismatch. Participants' performance was examined for the pair trials using an ANOVA with the factors Pair Type (4 levels) and Response Question (2 levels: Object + Location). The pairs were 1) Responding to a correct stimulus from a correct pair (CC), 2) Responding to a correct stimulus when its paired stimulus was incorrect (CI), 3) Responding to an incorrect stimulus when its paired stimulus was correct (IC) and 4) Responding to an incorrect stimulus from an incorrect pair (II). Data were taken from responses to the first question (either 'object?' or 'location?') as these responses were not primed.

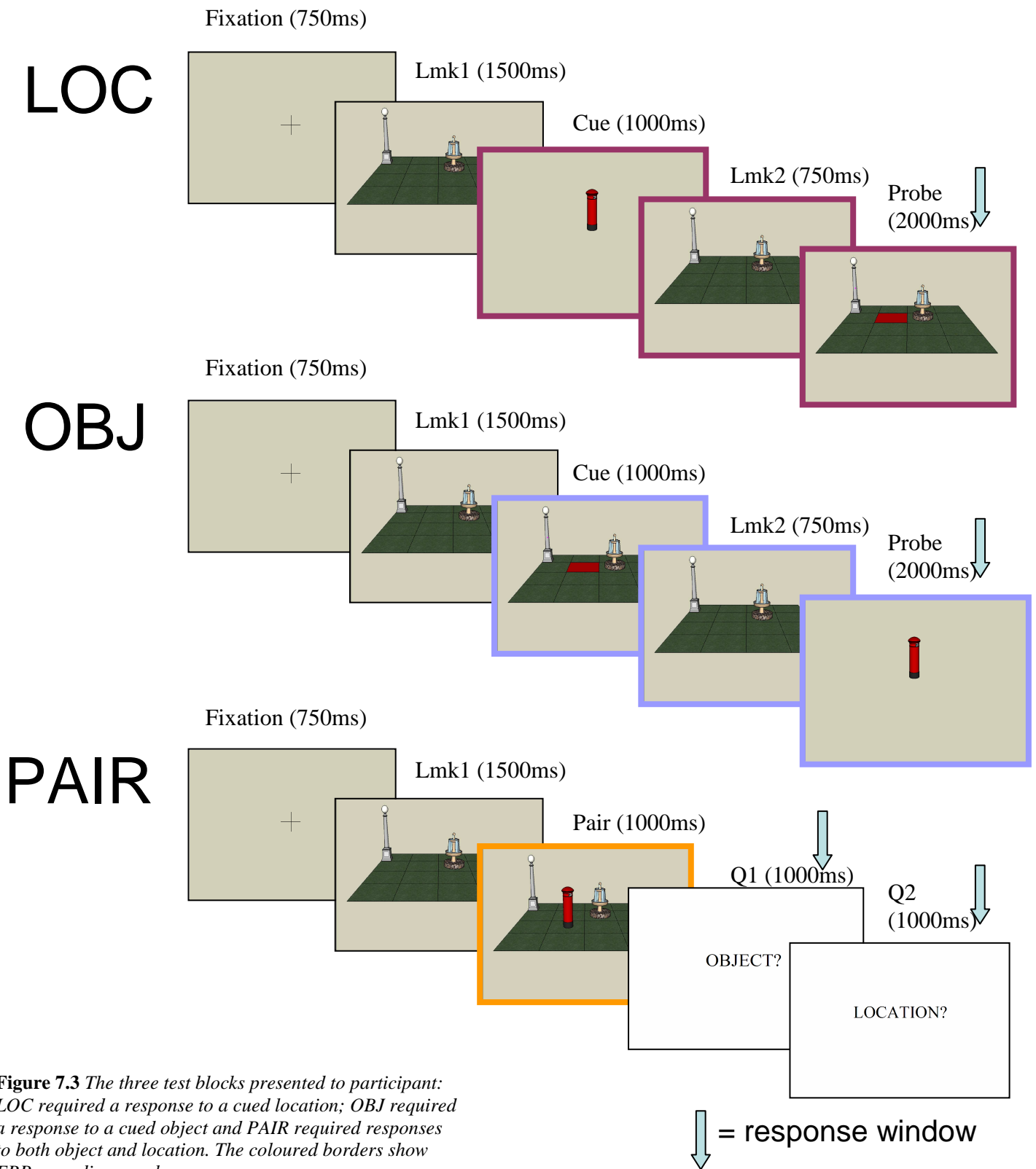


Figure 7.3 The three test blocks presented to participant: LOC required a response to a cued location; OBJ required a response to a cued object and PAIR required responses to both object and location. The coloured borders show ERP recording epochs.

7.4 Results

7.4.1 Behavioural Data

Cueing effects - LOC vs. OBJ:

The effect of cueing objects versus locations was investigated for accuracy scores and reaction times. Accuracy was not significantly different across cueing conditions or for matches and mismatches. When response times were analysed for cued locations (LOC) and cued objects (OBJ), significant main effects for Cue Type (LOC, OBJ) [$F(1, 11)=10.686$, $p<0.01$] and Match (match, mismatch) [$F(1, 11)=26.082$, $p<0.001$] were found (Figure 7.4). Locations were recognised significantly faster than objects and correct matches bore significantly faster response times. Bonferroni corrected paired-samples t-tests were significant for correct match LOC vs. correct match OBJ $t(11)=-4.756$, $p<0.005$, correct match LOC vs. mismatch LOC $t(11)=-3.830$, $p<0.05$ and correct match OBJ vs. mismatch OBJ $t(11)=-3.767$, $p<0.05$ (shown in Figure 7.4). Differences between mismatched locations and mismatched objects did not reach significance $t(11)=-2.168$, $p>0.05$.

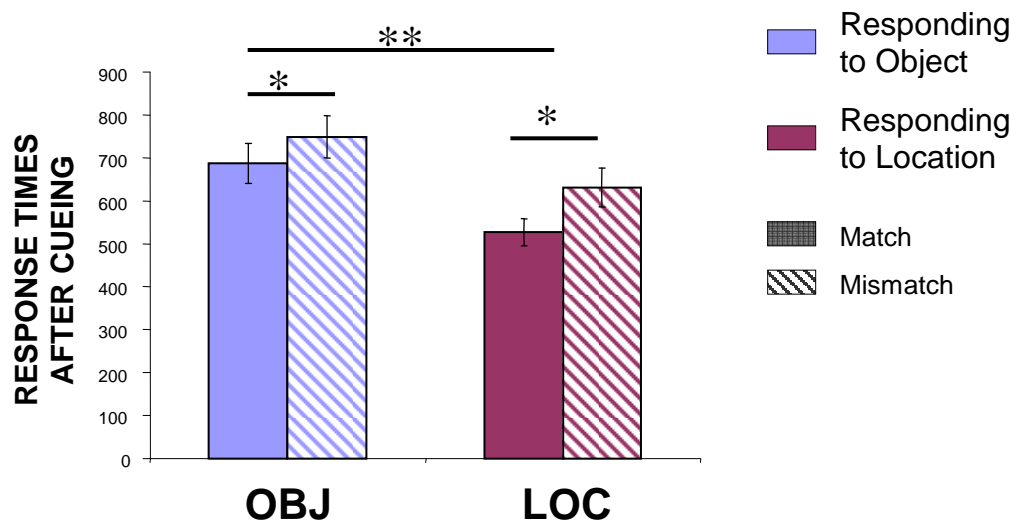


Figure 7.4 Comparison of mean response times \pm SEM from the first two test blocks where subjects were responding to a cued object (OBJ) or cued location (LOC). Responses were made for stimuli matching the cue i.e. for stimuli that completed a studied pairing, or for mismatches.

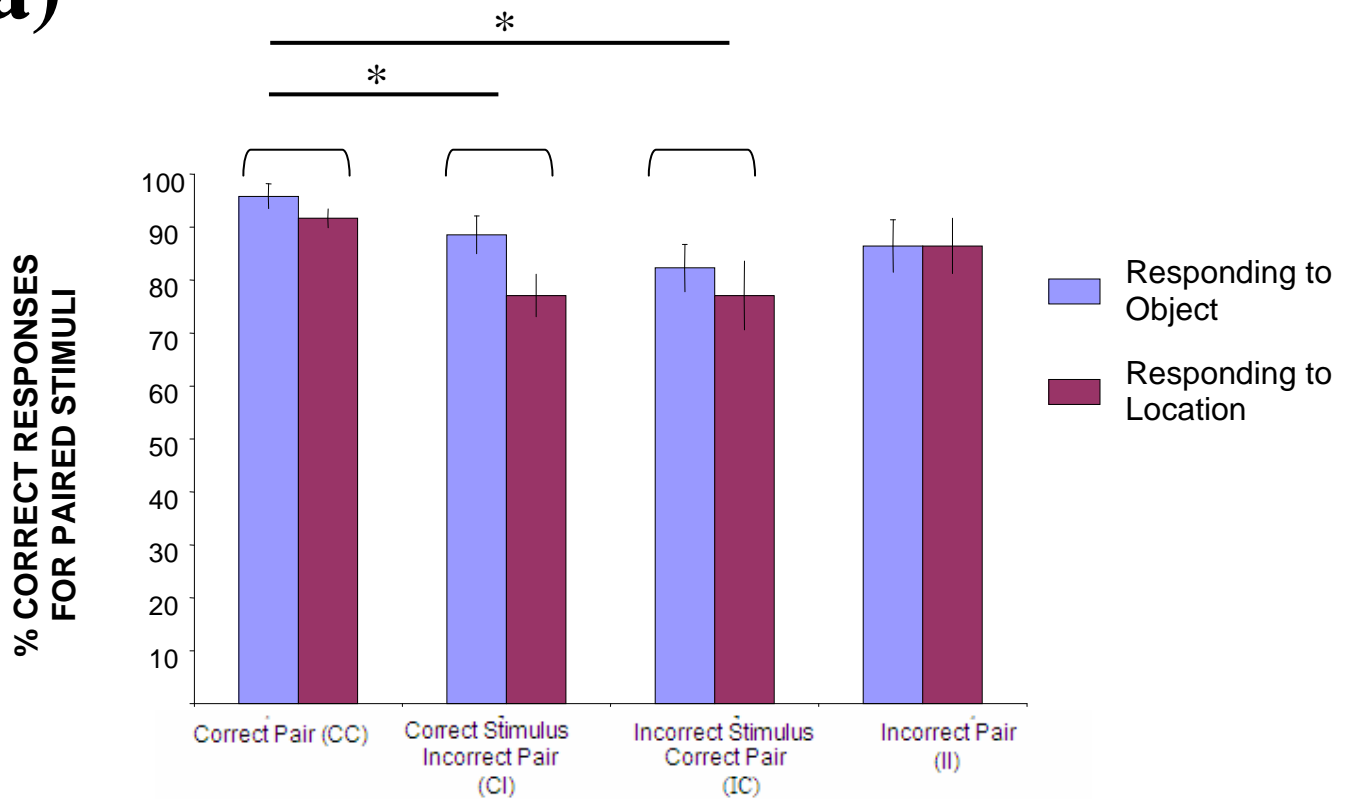
Pairing effects - PAIR(loc) vs. PAIR(obj):

An analysis of the accuracy data revealed a significant main effect of Pair Type (i.e. CC, CI, IC, II) on accuracy [$F(3, 33)=5.138$, $p<0.005$]. Participants showed significantly higher accuracies for correctly paired stimuli (Figure 7.5a). Bonferroni corrected t-tests confirmed this, highlighting significant differences between CC vs. CI pairs $t(23)=3.599$, $p<0.05$ and CC vs. IC pairs $t(23)=3.288$, $p<0.05$. The response times for each pair type are shown in Figure 7.4b. An ANOVA revealed a significant main effect of Pair Type on response time [$F(3, 33)=8.167$, $p<0.005$] and an interaction effect of Pair Type*Response Question [$F(3, 33)= 3.682$, $p<0.05$]. Bonferroni corrected paired-samples t-tests showed significantly faster responses when responding to CC vs. CI pairs $t(23)=-5.006$, $p<0.001$ or responding to CC vs. IC pairs [$t(23)=-4.300$, $p<0.001$]. Responses on II trials were also found to be significantly faster than CI trials $t(23)=3.211$, $p<0.05$ – see Figure 7.5b.

Paired vs. Cued stimuli:

A comparison of accuracy scores can be seen in Figure 7.6a below. Analysing differences in accuracy revealed a significant drop in the correct identification of locations during the paired compared to the cued locations $t(11)=3.838$, $p<0.05$, and cued objects $t(11)=4.064$, $p<0.05$. Figure 7.6b shows the mean reaction times for responses to cued objects and locations and pairs. Results from a set of Bonferroni corrected t-tests showed that participants performed significantly slower when recognising objects after being cued with a location compared to recognising a location cued with an object $t(11)=3.269$, $p<0.05$ or recognising the object/location elements of a pair $t(11)=5.605$, $p<0.001$ and $t(11)=5.715$, $p<0.001$ – see significance bars in Figure 7.6b.

a)



b)

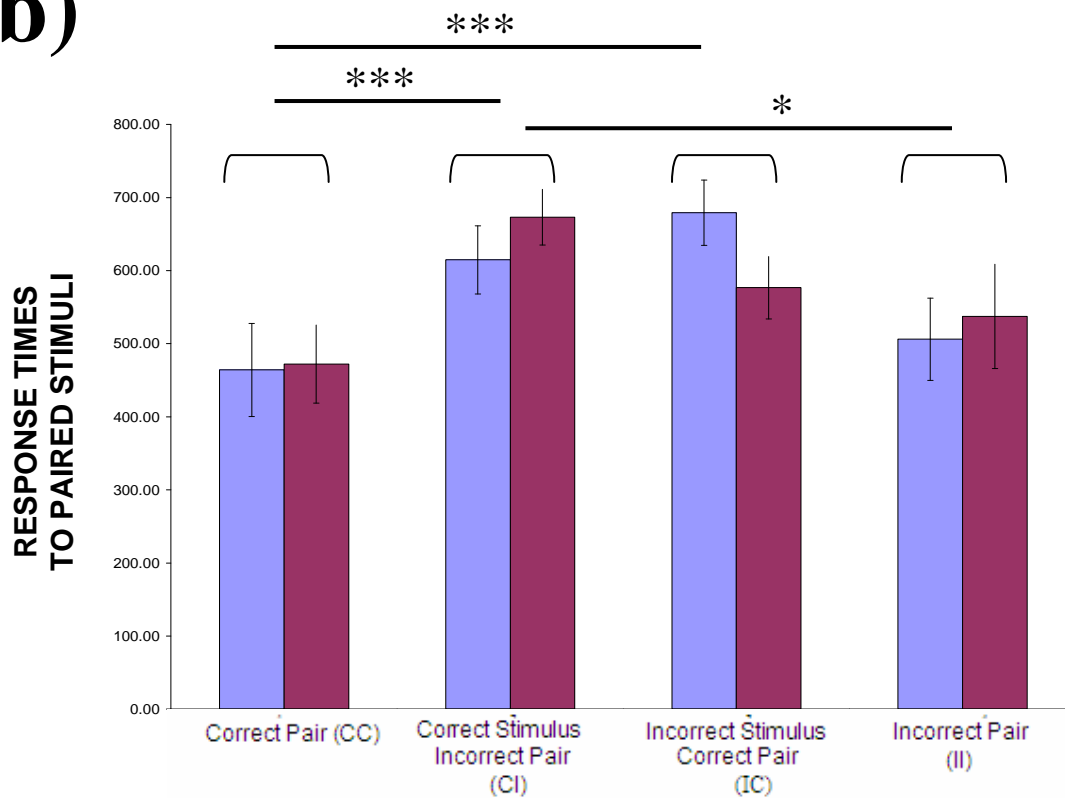
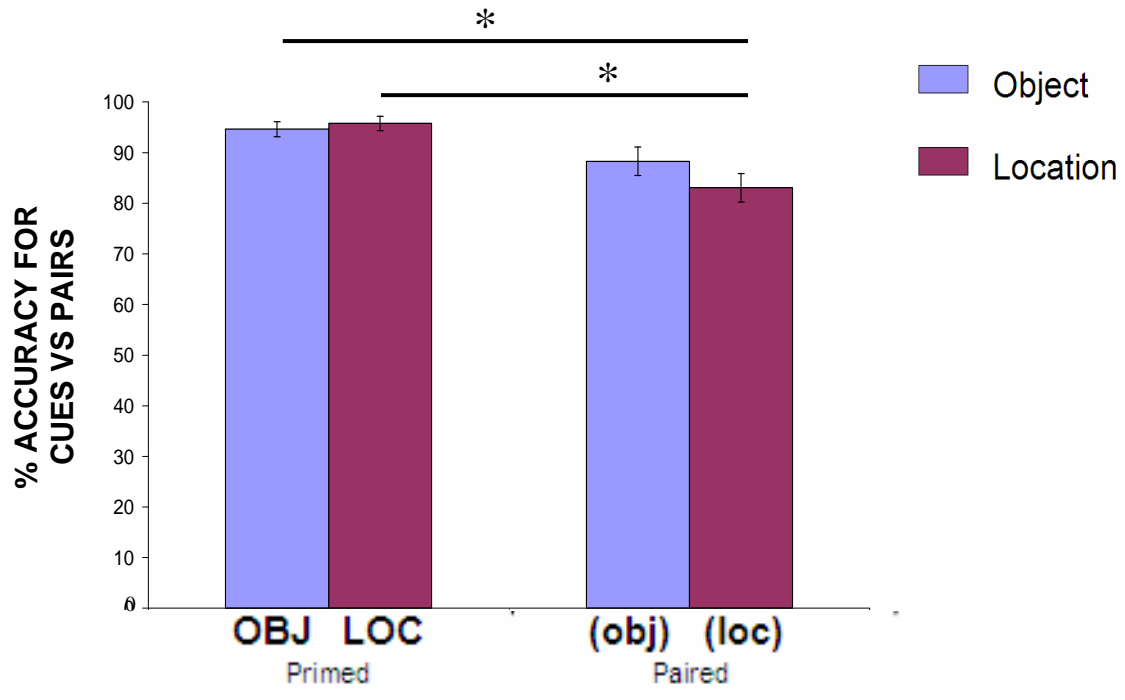


Figure 7.5 a) Mean accuracy scores \pm SEM for responses made to the object and location questions relating to the paired stimuli (PAIR) **b)** Response times for paired stimuli showing differences between recognition of elements in correct and incorrect pairings. Significance bars relate to comparisons across Pair-types, collapsing for response (represented by brackets)

a)



b)

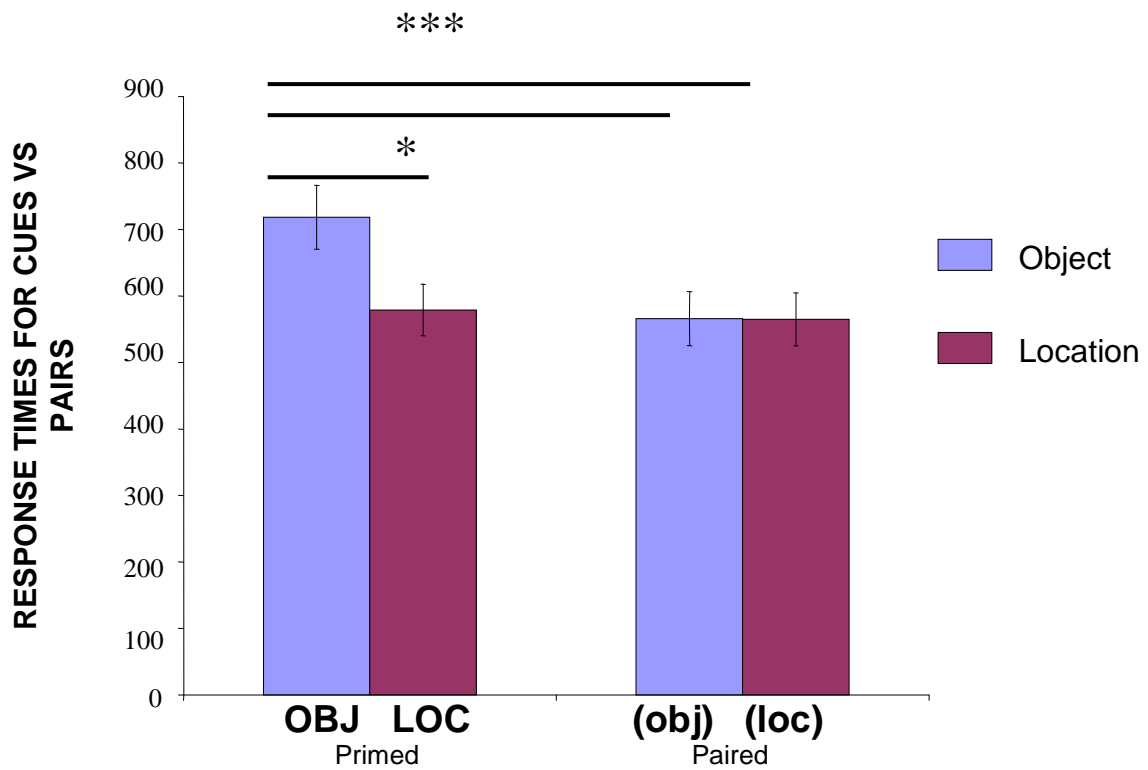


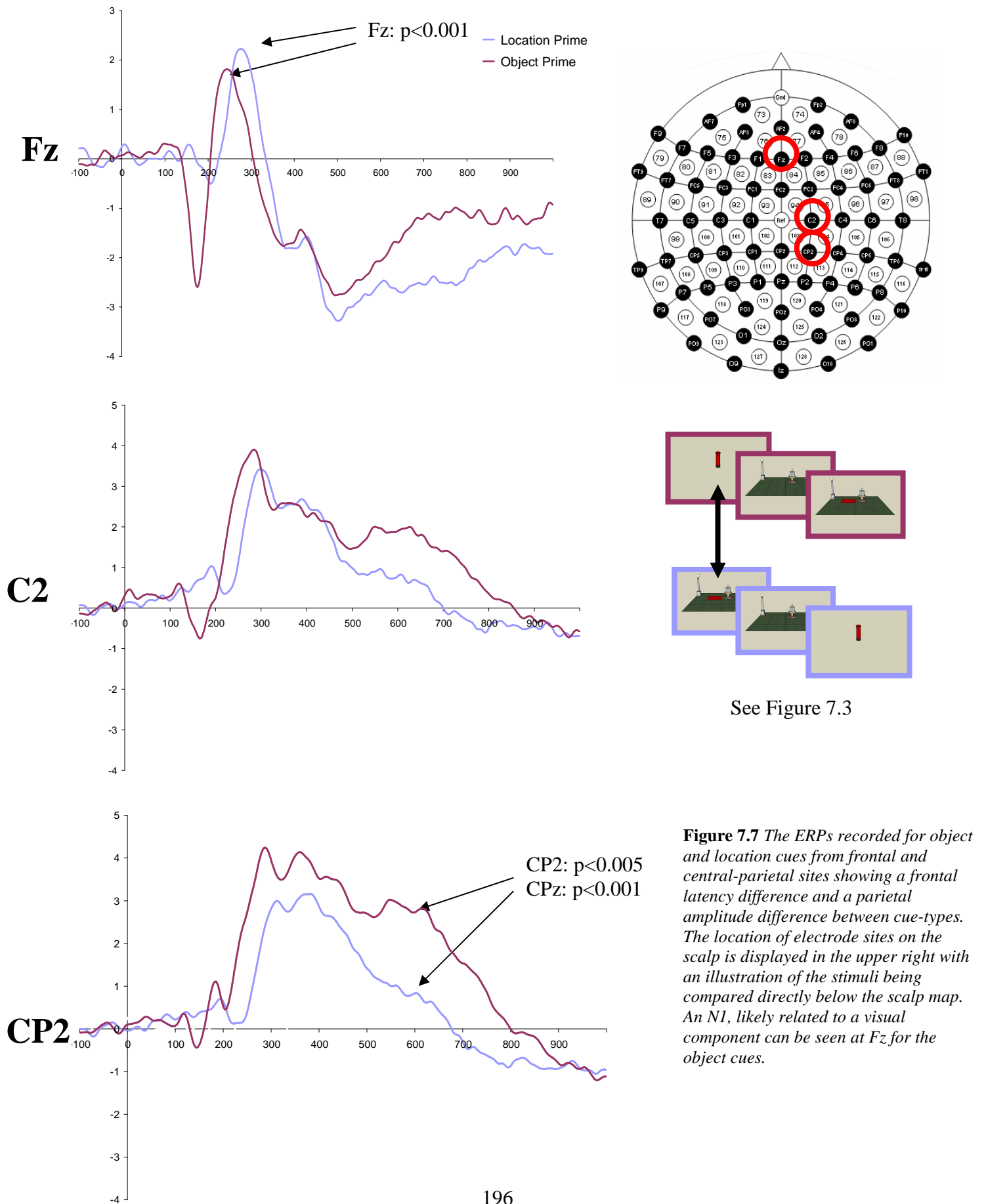
Figure 7.6 a) Accuracy scores for objects and their locations in cued vs. paired trials **b)** Comparison of the response times for objects and their locations in cued vs. paired trials

7.4.2 Electrophysiological data

Object cues vs. Location cues:

The initial ERP analysis compared the electrophysiological responses to the cueing stimuli (Figure 7.7). When locations appeared as cues they elicited positive deflections which reached maximal amplitudes at Fz circa 280ms (3.63 μ V) and spread in a posterior direction over the right hemisphere [C2 (3.3 μ V – 310ms); CP2 (3.05 μ V – 360ms)]. Bilateral parietal activity was present after 360ms and dissipated by 600ms (<1 μ V). When objects appeared as cues they elicited a P1 maximal at site PO3 (3.22 μ V – 178ms). Maximal amplitudes circa 280ms were recorded over right central-parietal scalp sites (CP2 – 4.17 μ V and C2 – 3.86 μ V). This activity was maintained and moved slightly posteriorly by 360ms (CP2 – 4.12 μ V and Pz – 3.90 μ V). Bilateral parietal activity was present after 360ms with maximal amplitudes >2.5 μ V still present after 550ms at site Pz. Figure 7.7 plots the activity time-course from frontal to right central-parietal sites for both location cues and object cues. A latency difference between location and object cues was evident ~200ms in the positive-going deflections. This was assessed by comparing the individual maximum peak latencies of the P2 (150-400ms) recorded from site Fz. Maximum peak latencies obtained for object (M=212.7ms, SD=76.6ms) and location (M=328.2ms, SD=84.7ms) cues were subjected to a paired-samples t-test which revealed the P2 elicited by the object cues was significantly faster in reaching maximal amplitude [$t(10)=-4.409$, $p<0.001$]. A second paired-samples t-test was used to compare mean amplitude differences for object and location cues over parietal scalp (CPz and CP2) between 500-700ms. The average of the individual mean amplitudes from

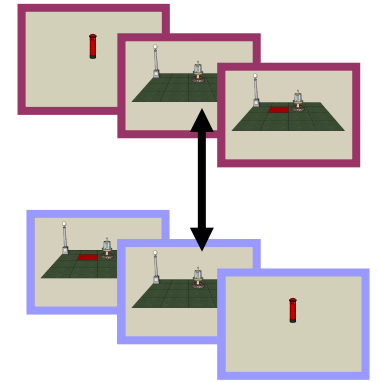
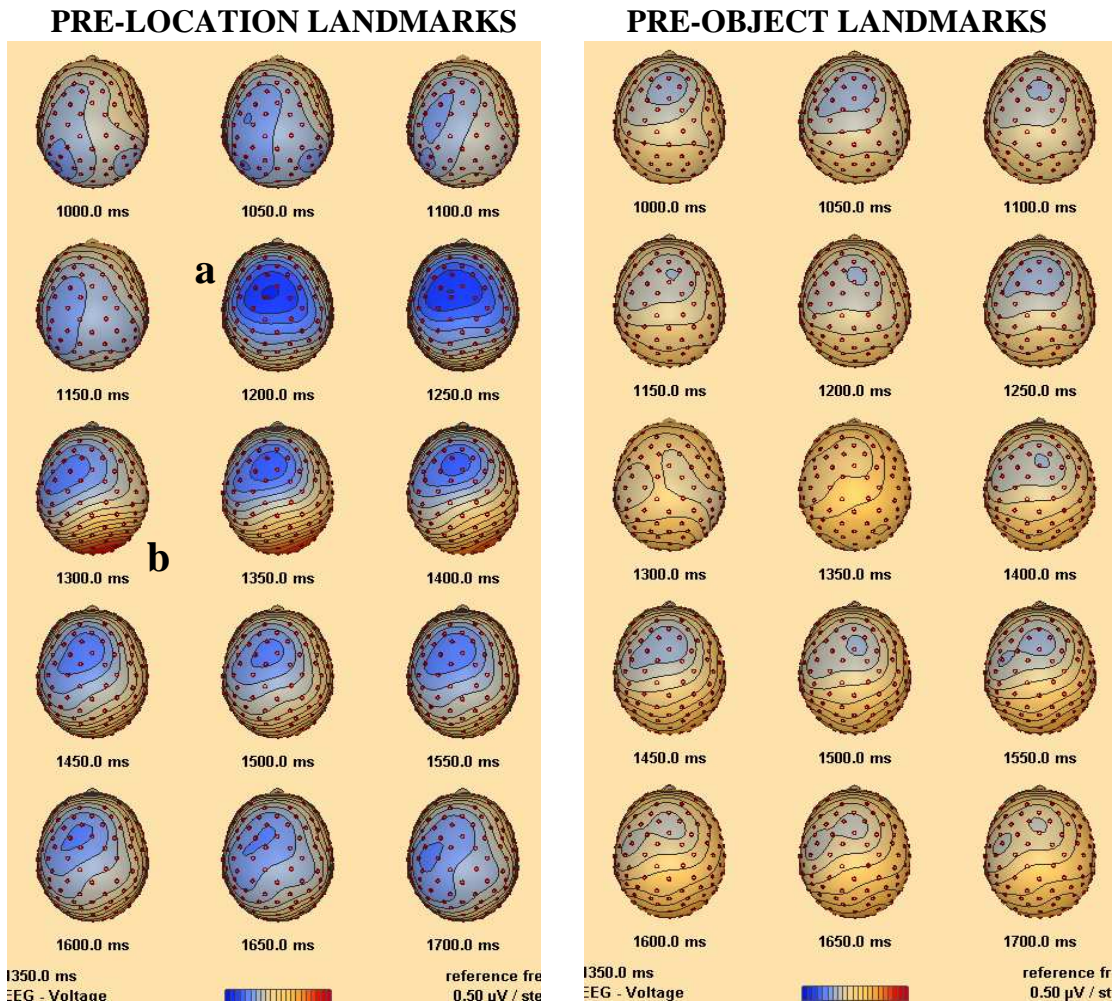
CUE-RELATED ACTIVITY FROM FRONTAL AND RIGHT CENTRAL-PARIETAL SITES



CPz was $2.4\mu\text{V}$ for object cues ($\text{SD}=1\mu\text{V}$) compared to $0.74\mu\text{V}$ for location cues ($\text{SD}=1\mu\text{V}$). The mean amplitudes for object cues over this time period were found to be significantly larger than for location cues [$t(10)=4.380$, $p<0.001$]. The mean amplitudes recorded from CP2 for object cues ($M=2.46\mu\text{V}$, $\text{SD}=1.6\mu\text{V}$) were also found to be significantly greater than for location cues ($M=0.64\mu\text{V}$, $\text{SD}=1\mu\text{V}$ - $t(10)=4.189$, $p<0.005$). Overall, therefore, the object cues elicited significantly earlier and more sustained fronto-parietal activity.

Landmarks prior to Probe presentation:

The second ERP analysis compared activity during the landmarks i.e. after the cues but *before the probe stimuli* were presented (Figure 7.3 – Lmk2). During this time (750ms) the stimulus presented was the same but participants had seen different cues and were awaiting either an object or location probe stimulus. The time series in Figure 7.8 suggested that amplitude differences in frontal negativity existed in the recordings over this time period as well as a possible difference in parieto-occipital positivity. Mean amplitudes at frontal sites (FCz, E94) over the time period 200-450ms were $-3.22\mu\text{V}$ for pre-location landmarks and $-1.26\mu\text{V}$ for pre-object landmarks. Frontal activity was found to differ significantly with greater negativity during pre-location landmarks $t(10)=-4.744$, $p<0.001$ (Figure 7.8a & Figure 7.9 – left). For parietal sites (PO4, E120) the mean amplitudes were $2.17\mu\text{V}$ and $0.11\mu\text{V}$ for pre-location and pre-object landmarks, respectively. The additional parieto-occipital positivity seen for pre-location landmarks (Figure 7.8b) was also found to be significantly greater than for the pre-object landmarks [$t(10)=4.654$, $p<0.001$ - Figure 7.9 – right].



See Figure 7.3

Figure 7.8 Time-series for the first 700ms of the 750ms that landmarks appeared on screen prior to the presentation of probe stimuli for evaluation. Additional negative fronto-central activity (a) and positive right parietal activity (b) is visible for the pre-location landmarks on the left.

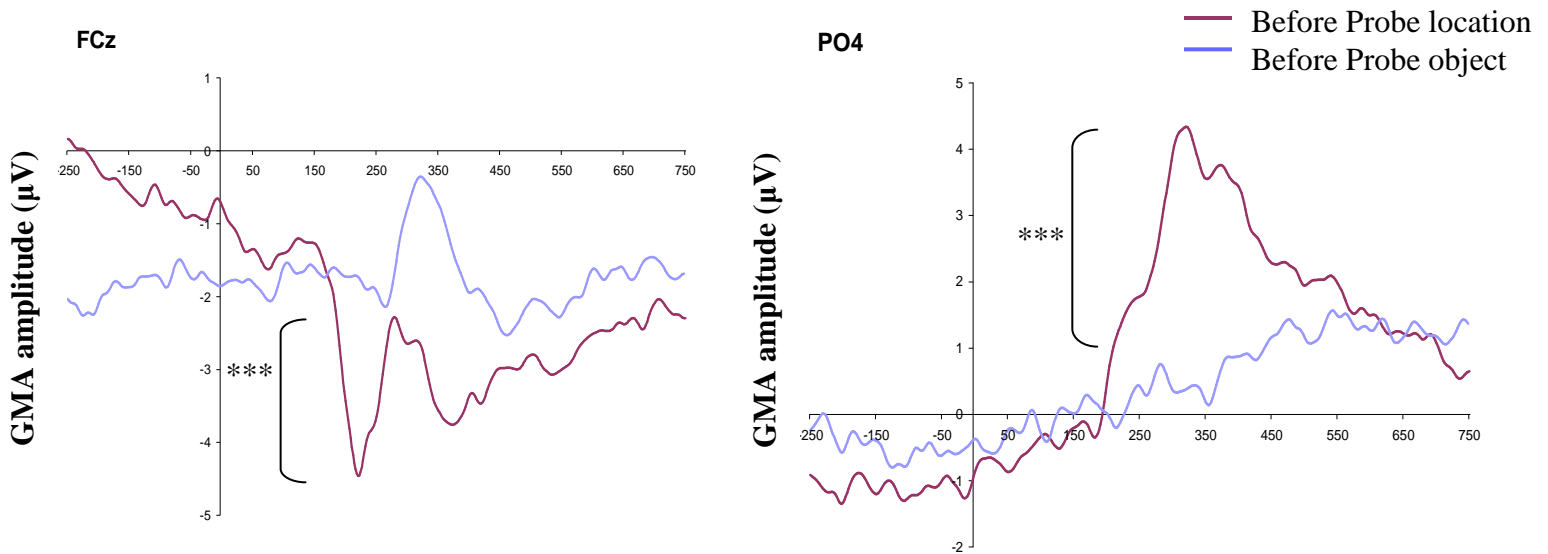
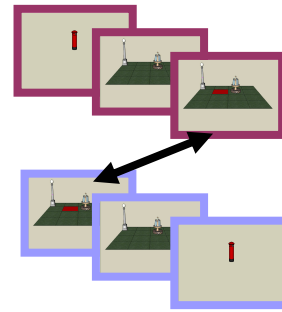
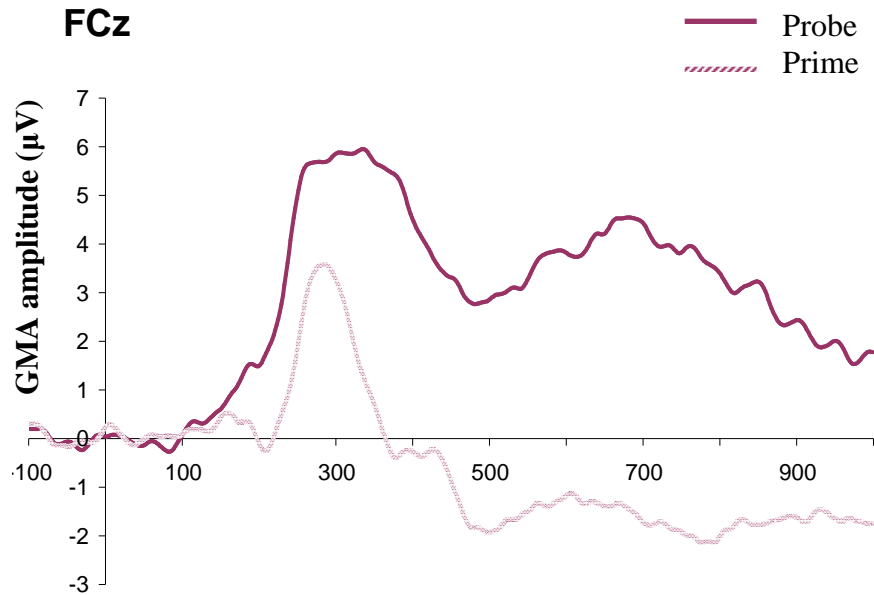


Figure 7.9 Grand Mean Average ERP waveforms recorded from site FCz and PO4 after cues disappeared during pre-location and pre-object landmarks. Significant differences in mean amplitudes were found with pre-location landmarks showing additional frontal negativity (see Fig. 7.8a) and parietal positivity (see Fig. 7.8b)
*** = $p < 0.001$

Cues vs. Probes:

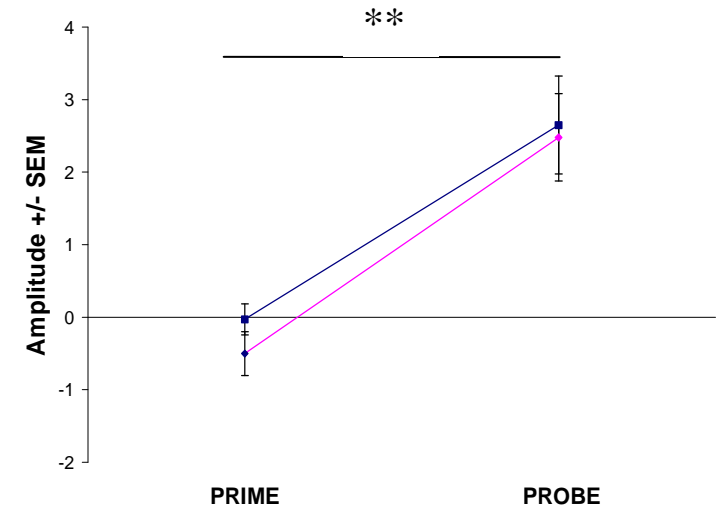
A third set of ERP analyses assessed differences between the visual processing of the stimuli (when they appeared as cues) and the assumed higher level associative processing involved in object and location recognition and response selection when the stimuli appeared as probes. Viewing Figure 7.3, this analysis corresponds with a comparison of the electrophysiological responses to LOC Cue vs. OBJ Probe (both object presentations) and OBJ Cue vs. LOC Probe (both location presentations). As can be seen in Figure 7.10, there was a large difference in recorded frontal and central amplitudes between the cues and probes. This difference was assessed by means of a repeated-measures ANOVA comparing mean amplitudes between 0-1000ms with Stimulus Type (location, object) and Presentation Type (cue, target) as variables. No significant main effect of Stimulus Type was found [$F(1, 10)=1.520$, $p>0.05$] but Presentation Type yielded a significant difference [$F(1, 10)=18.495$, $p<0.005$] with greater mean amplitudes elicited by the probes ($M=2.56\mu V$, $SD=2.11\mu V$) compared to cues ($M=-0.27\mu V$, $SD=0.85\mu V$). This difference can be seen in Figure 7.11a. A second ANOVA assessed whether differences existed in the mean amplitude of the frontal P2 by comparing data from a shorter and more specific time window (200-400ms). Presentation Type again yielded a significant difference [$F(1, 10)=10.184$, $p<0.01$] with greater mean amplitudes elicited by the probes ($M=3.58\mu V$, $SD=2.69\mu V$) compared to cues ($M=1.08\mu V$, $SD=1.1\mu V$). A significant interaction effect of Stimulus Type*Presentation Type was also found [$F(1, 10)=14.505$, $p<0.005$] – see Figure 7.11b. Bonferroni corrected paired-samples t-tests revealed significant differences in P2 amplitudes for location cues vs. location probes [$t(10)=3.853$, $p<0.01$] but the correction removed the difference ($p=0.39$) for object stimuli [$t(10)=2.371$, $p>0.05$].

RESPONSES TO LOCATION

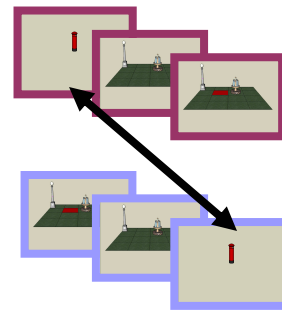
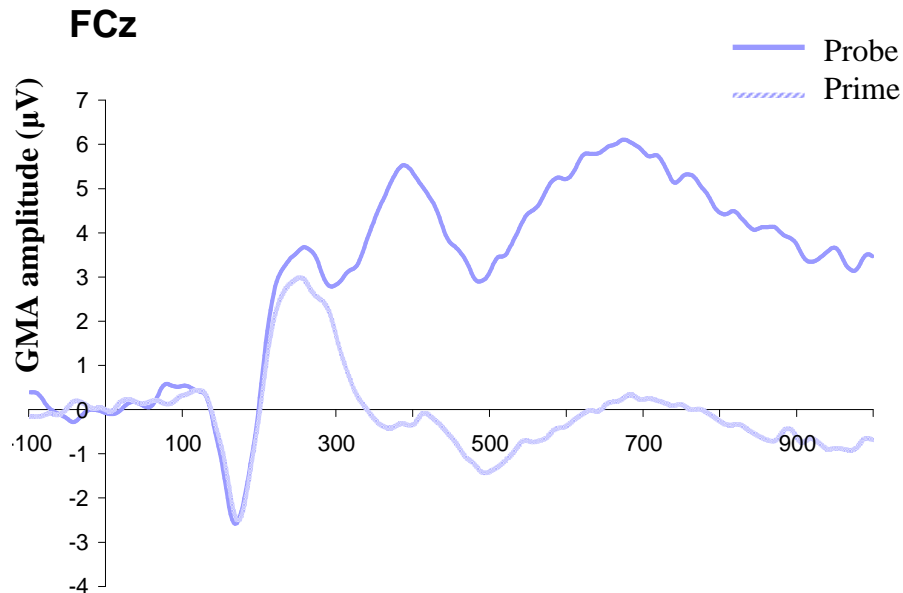


See Figure 7.3

a) MEAN AMPLITUDES OVER WHOLE EPOCH



RESPONSES TO OBJECT



See Figure 7.3

b) MEAN AMPLITUDES FROM 200-400ms

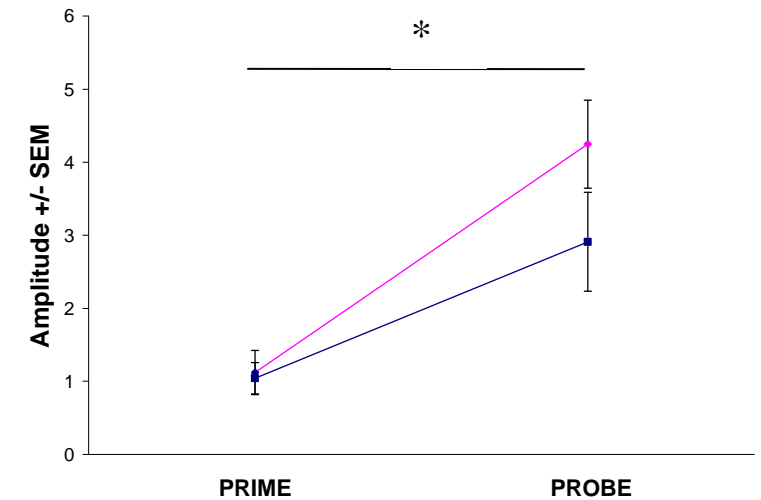


Figure 7.10 Comparison of the waveforms recorded from frontal site FCz illustrating the additional positivity generated by the stimuli when they appeared as probes compared to cues.

Figure 7.11 Graphs of the average mean amplitudes recorded from FCz for locations and objects when they were presented as cues and targets **a)** shows an increase in the average mean amplitudes for probes over the whole epoch i.e. from 0-1000ms **b)** specifically compares the frontal P2 and shows an increase in average mean amplitudes for probes during 200-400ms

Cueing effects - LOC vs. OBJ Probes:

A comparison of the electrophysiological responses elicited by the cued locations and cued objects (for the correctly cued stimuli) began with an examination of the topographic maps and event-related potentials relating to each condition. These showed possible differences in voltage distribution over the scalp and highlighted areas for further analysis. Differences over frontal scalp electrodes were observed where probe locations appeared to elicit a larger and more sustained frontal P2 compared to object probes (Figures 7.12a and 7.12b). This difference can also be seen in the waveforms and the topographic difference map shown in Figure 7.13. To assess this difference in amplitude, individual mean amplitudes were taken for each participant from 200-350ms for frontal electrodes FCz and F1, Fz, F2 (not illustrated). Mean amplitudes were calculated for both probe location and probe object presentations separately. These individual electrode amplitudes were then averaged to give collated mean amplitudes over frontal scalp for each participant for both location and object probe stimuli. The average mean amplitude elicited by the location probes was $3.89\mu\text{V}$ compared to $2.42\mu\text{V}$ elicited by the object probes. This difference was found to be significant when compared using a paired-samples t-test $t(10)=3.585, p<0.005$.

This early difference in frontal P2 preceded another observed difference over right central-parietal electrodes where the latency to maximum peak for a P300 was seen to differ for the electrophysiological response to locations and objects. This can be seen in the topographic maps displayed in Figure 7.12 (c & d) and the related waveforms recorded from site C2 shown in Figure 7.13. Individual recordings were assessed for electrode site C2 and latency times were taken for the maximum amplitude reached between 300ms and 500ms. The average latencies were 353.8ms to P3 peak for locations

compared to 392.3ms for objects. This difference (~40ms) was found to be significant when compared using a paired-samples t-test $t(10)=-3.349$, $p<0.01$.

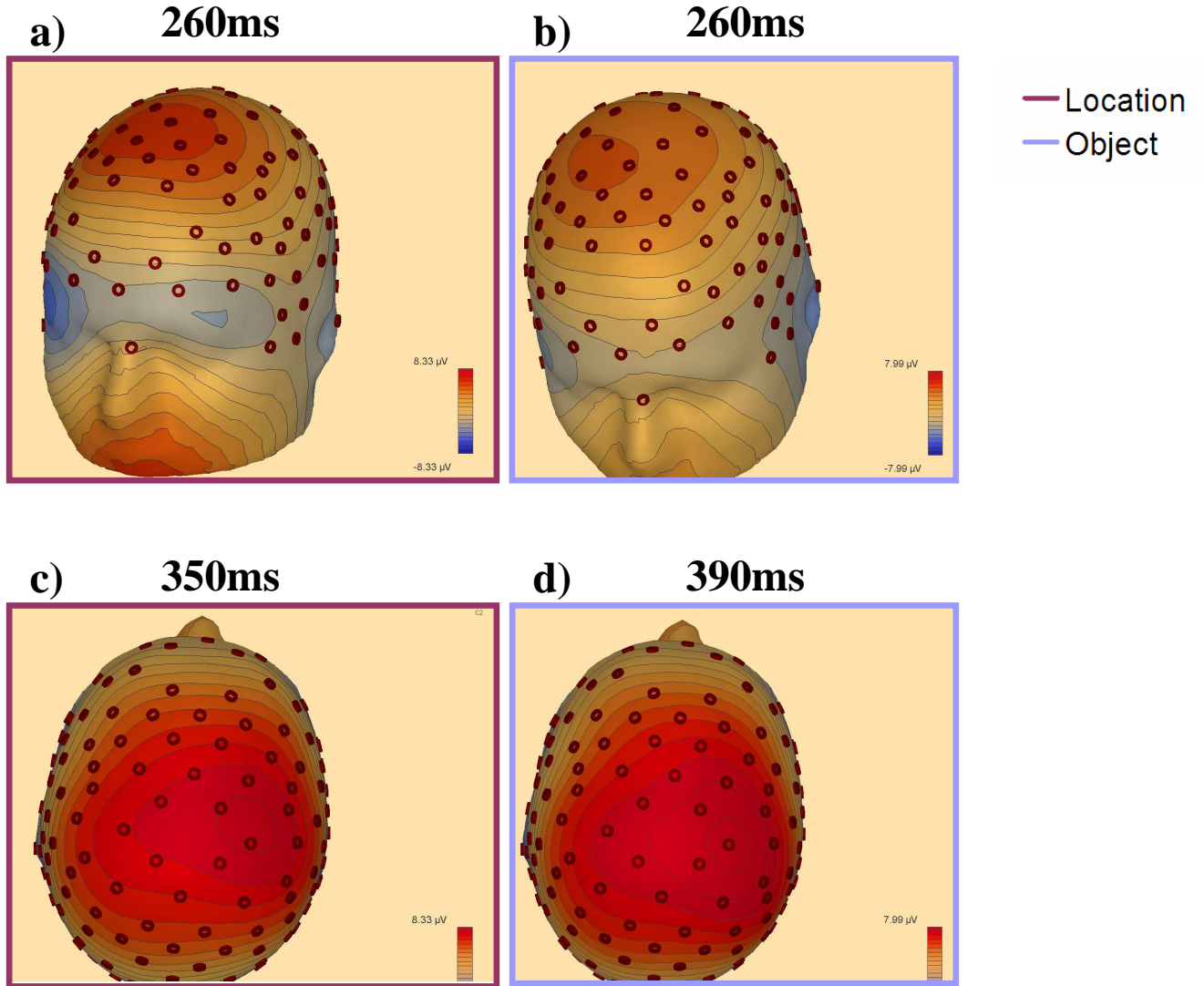
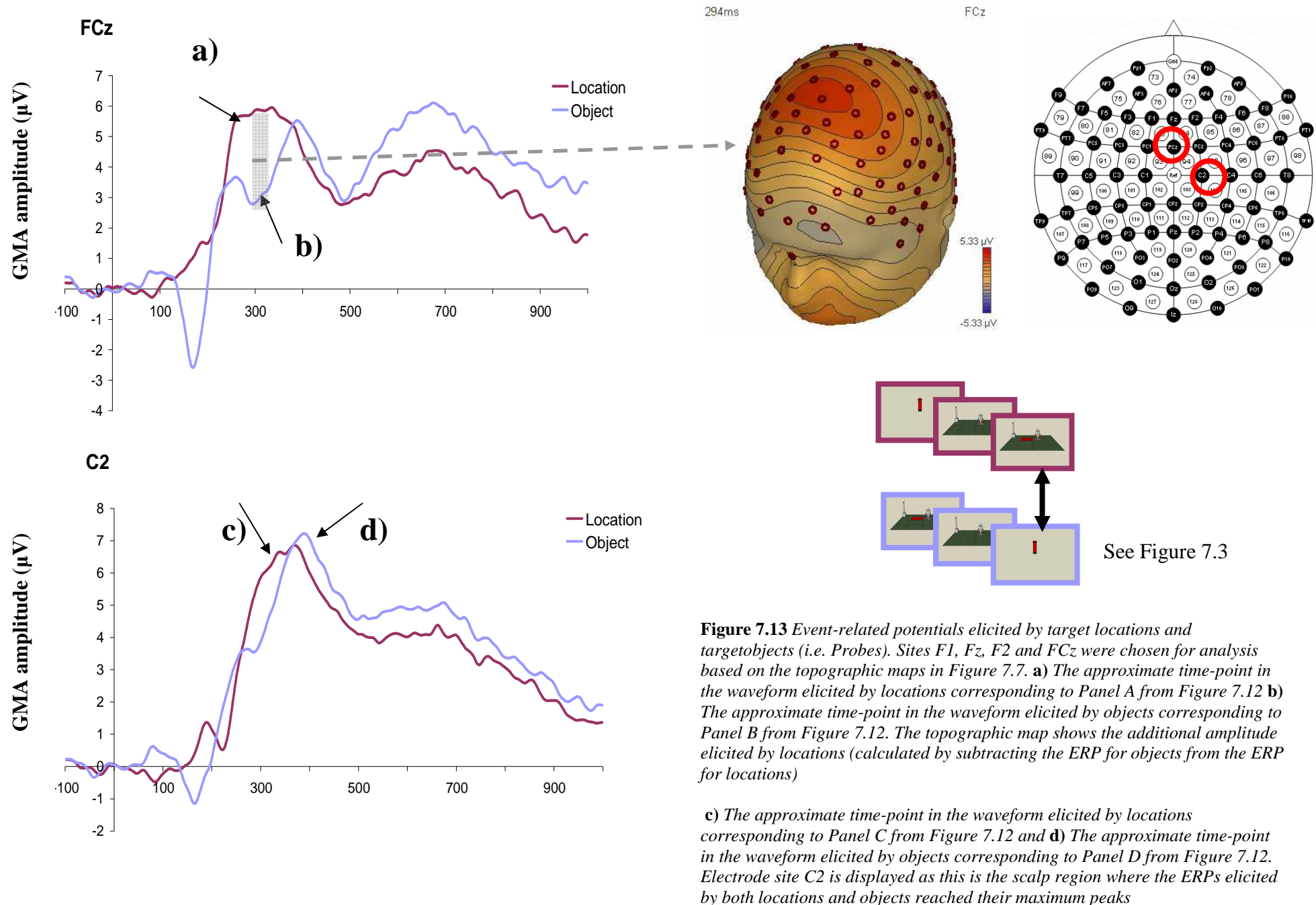


Figure 7.12 (a & b) Topographic maps showing the electrophysiological responses to locations vs. objects over frontal scalp electrodes at 260ms (c & d) Topographic maps showing right central-parietal areas where both ERP waveforms reached maximum amplitudes at differing times (~350ms for locations and ~390ms for objects)

ERPs for Probe LOCATIONS vs. Probe OBJECTS



Matches vs. mismatches:

As participants were found to perform significantly slower recognising the probes when they were presented with a mismatch (or false cue – see Figure 7.4), we assessed whether differences would manifest in the ERP waveforms relating to both matches and mismatches. We compared electrophysiological responses for both cued locations and cued objects. Waveforms elicited by location probes were not found to differ for frontal P2 amplitudes or latency (Figure 7.14 – Electrode Fz). The latency of the P3 was assessed for electrode site C2 for matched and mismatched locations. Individual peak latencies were calculated over the time period 250-500ms. These latencies ($M=350.5\text{ms}$, $SD=36.4\text{ms}$ for matched locations; $M=388.8\text{ms}$, $SD=69\text{ms}$ for mismatched locations) were found to differ significantly after being exposed to a paired-samples comparison [$t(10)=-2.407$, $p<0.05$]. The right central P3 elicited by mismatched (or incorrectly cued) locations was delayed nearing peak amplitude compared to the matched locations (Figure 7.14 – Electrode C2).

ERPs for matched and mismatched Probe LOCATIONS

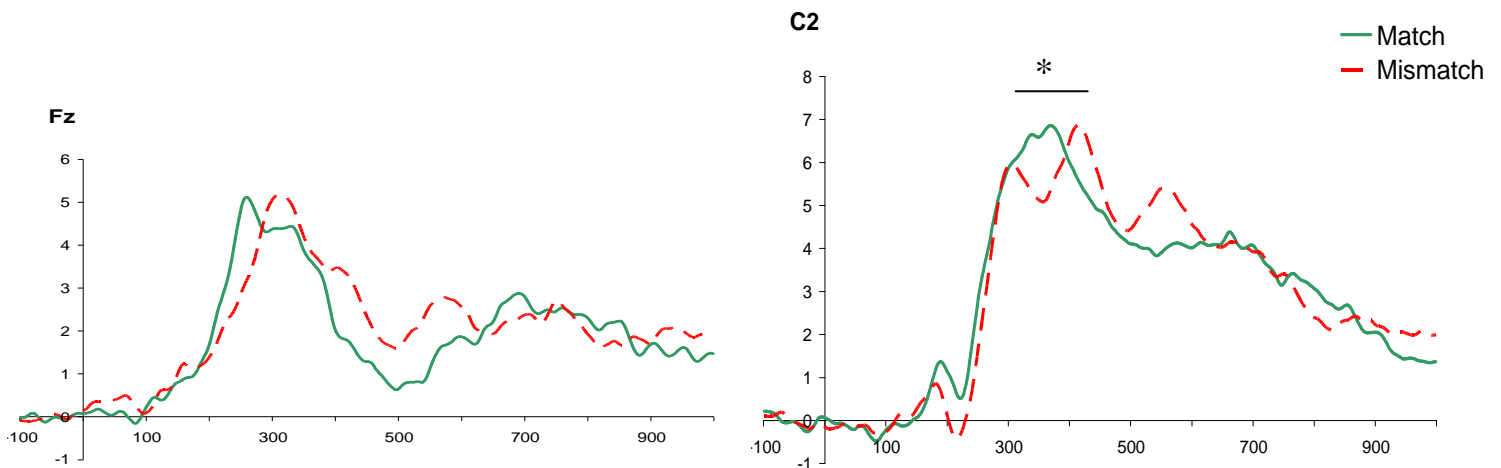


Figure 7.14 The electrophysiological response recorded from Fz (left) and C2 (right) for correctly cued locations (Match) and incorrectly cued locations (Mismatch). A P2 is visible in the topography of the waveform recorded from Fz whereas a P3 was identified over right central electrodes as evidenced by the C2 waveforms.

A comparison of the waveforms elicited by object probes revealed possible amplitude differences for both the P2 and P3 components (Figure 7.15). Individual mean amplitudes were calculated over the time period 250-400ms from site Fz to assess differences in the frontal P2, and between 300-500ms from site C2 to assess P3 differences. Both P2 amplitudes ($M=2.86\mu V$, $SD=2.28\mu V$ for matched objects; $M=1\mu V$, $SD=1.23\mu V$ for mismatched objects), and P3 amplitudes ($M=5.63\mu V$, $SD=2.62\mu V$; $M=4.21\mu V$, $SD=2.42\mu V$) were found to differ significantly. T-tests revealed significantly larger amplitudes were elicited for objects that matched their cue compared to mismatches for both P2 [$t(10)=3.790$, $p<0.005$] and P3 components [$t(10)=3.962$, $p<0.005$] respectively.

ERPs for matched and mismatched Probe OBJECTS

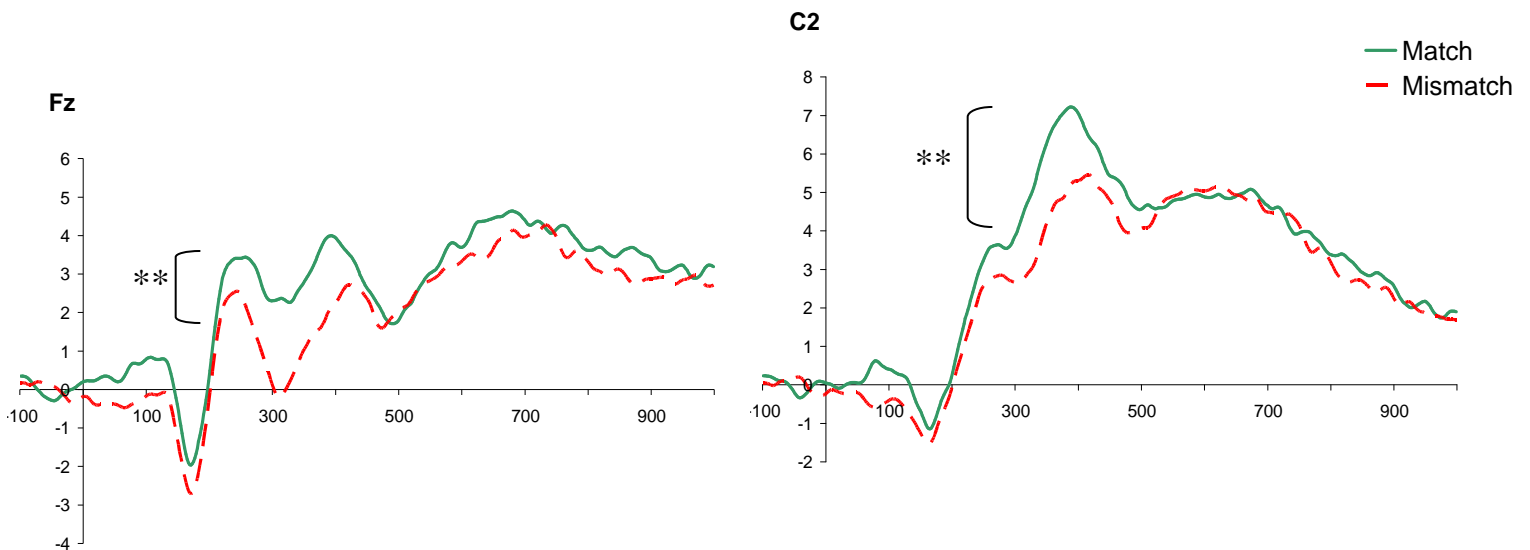


Figure 7.15 The electrophysiological response recorded from Fz (left) and C2 (right) for correctly cued objects (Match) and incorrectly cued objects (Mismatch). Objects were not seen to elicit a frontal P2 as pronounced as that elicited by locations and an amplitude drop-off occurred ~300ms. A P3 is visible in the waveform recorded from C2. Amplitudes of the componentry were significantly larger when the test objects were cued correctly by locations.

Paired vs. Cued stimuli:

Individually, there were not enough trials for the stimulus pairs to be meaningfully compared with each other. Therefore, the electrophysiological responses to the **paired** stimuli were combined for comparison with the **cued** stimuli rather than compared with one another. The mean amplitudes elicited by the paired stimuli were compared with the average mean amplitude generated by the cued stimuli (LOC + OBJ combined) over two time periods: 230-290ms and 300-500ms (Figure 7.16). This revealed a possible difference in frontal activations. Repeated-measures ANOVAs found a significant main effects for stimulus-type [$F(1, 10)=88.320$, $p<0.000$; $F(1, 10)=30.779$, $p<0.000$] for the first and second time periods, respectively. Recorded scalp sites were not found to be significant for the first time period [$F(1, 10)=4.594$, $p>0.05$] but a strong interaction effect was found [$F(1, 10)=35.771$, $p<0.000$]. An effect of scalp area was found for the second time period [$F(1, 10)=5.870$, $p<0.05$], as well as an interaction effect [$F(1, 10)=8.139$, $p<0.05$]. Bonferroni corrected t-tests revealed differences in frontal activity for both time periods where the combined stimuli elicited greater amplitudes – 230-290ms: [$t(10)=8.587$, $p<0.001$]; 300-500ms: [$t(10)=4.402$, $p<0.01$]. Parietal differences did not reach significance. The cued stimuli elicited more frontal activity between 230-290ms ($t(10)=4.269$, $p<0.05$), with no differences between 300-500ms. By contrast, the paired stimuli showed no difference between frontal and parietal activations for the early time period, whereas they elicited greater parietal amplitudes between 300-500ms ($t(10)=-5.576$, $p<0.001$). These parietal activations were found to be maximal at ~400ms at E113 ($3.49\mu\text{V}$) and Pz ($3.35\mu\text{V}$) for the paired stimuli whereas maximal amplitudes around this time were found at site C2 for the cued targets. These differences are displayed in Figure 7.16 and can be seen in the topographic maps shown in Figure 7.17.

Average Mean Amplitudes elicited by Combined Probes vs. Combined Paired stimuli recorded from Frontal vs. Parietal sites

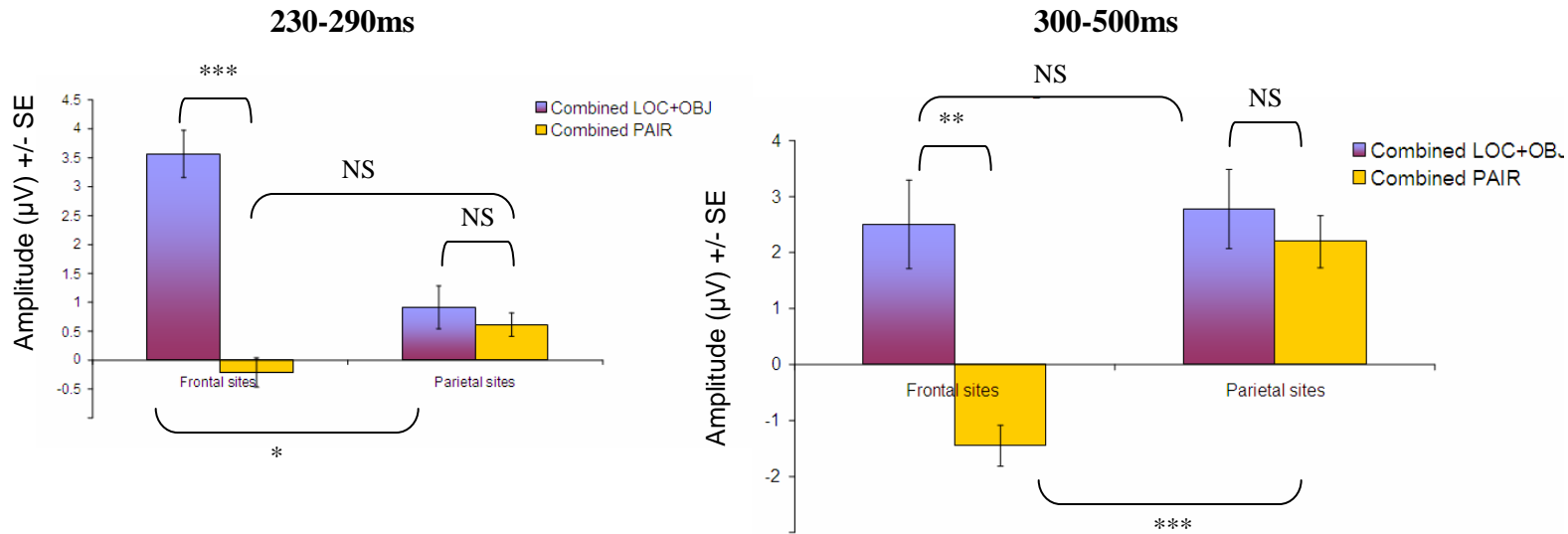
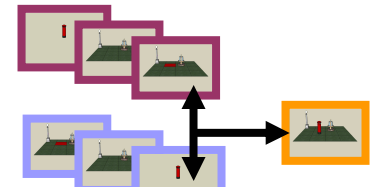


Figure 7.16 Comparison of the average mean amplitudes recorded from frontal (F1, Fz and F2) and parietal (P1, Pz and P2) sites after participants were presented with cued probe stimuli (combined) and paired stimuli (combined) during the recognition tests. The cued stimuli engaged frontal cortex at an early stage and both frontal and parietal cortices after 300ms. The paired stimuli however showed no frontal activity and engaged parietal cortex after 300ms. Significant differences in mean amplitudes are displayed above and below the graph.

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$



See Figure 7.3

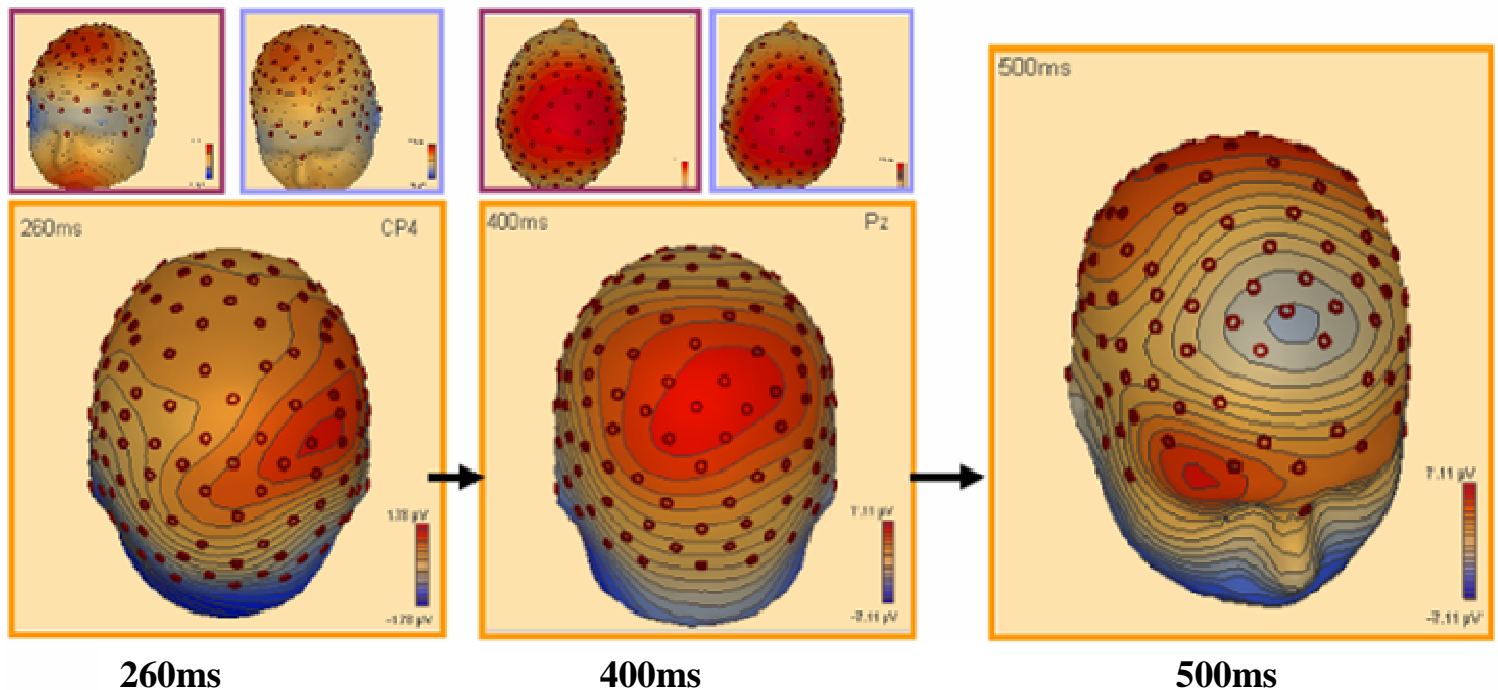


Figure 7.17 Topographic maps showing the distribution of voltage across the scalp in response to the paired stimuli at 260ms, 400ms and 500ms. A comparison with the distributions related to locations and objects can be seen for in the purple and blue boxes respectively. Note the propagation of activity in posterior regions and the absence of frontal recruitment for the paired stimuli

Summary of Electrophysiological Responses to Test conditions:

Similarities in the electrophysiological responses were found after a comparison of the data across both cues and cued stimuli and between cued stimuli and pairs. The cues resulted in frontal and parietal peaks between 200-300ms with a slower drop-off in posterior amplitudes. The cued probe stimuli elicited frontal P200 activity and right-central P300s were observed with maximal amplitudes at site C2. Parietal activity was also observed in response to the paired stimuli. However, large differences in global scalp topographies and in more specific localised peak latencies and amplitudes were found to exist due to the type of recognition test administered. When objects were used to cue locations, it resulted in faster-peaking frontal components and more sustained parietal activity during the object cue presentation itself compared with the location cue. In addition to this, greater frontal amplitudes and a faster peaking P300 were found over right-central scalp site C2 during the processing of target locations. Processing the paired stimuli resulted in more posterior parietal fluctuations (e.g. Pz) but more importantly, no significant frontal activity was found. This can be seen clearly in the time-series topographies shown in Figure 7.18. Processing probe locations engaged frontal regions to a greater extent compared to the probe objects. Both of the probe (cued) stimuli engaged frontal and then right-central-parietal areas whereas more bilateral and posterior central-parietal activity was seen in relation to processing the paired stimuli. The next section will examine the underlying neural generators related to these observed similarities and differences.

TIME-SERIES OF SCALP ACTIVITY DISTRIBUTIONS (300ms – 440ms)

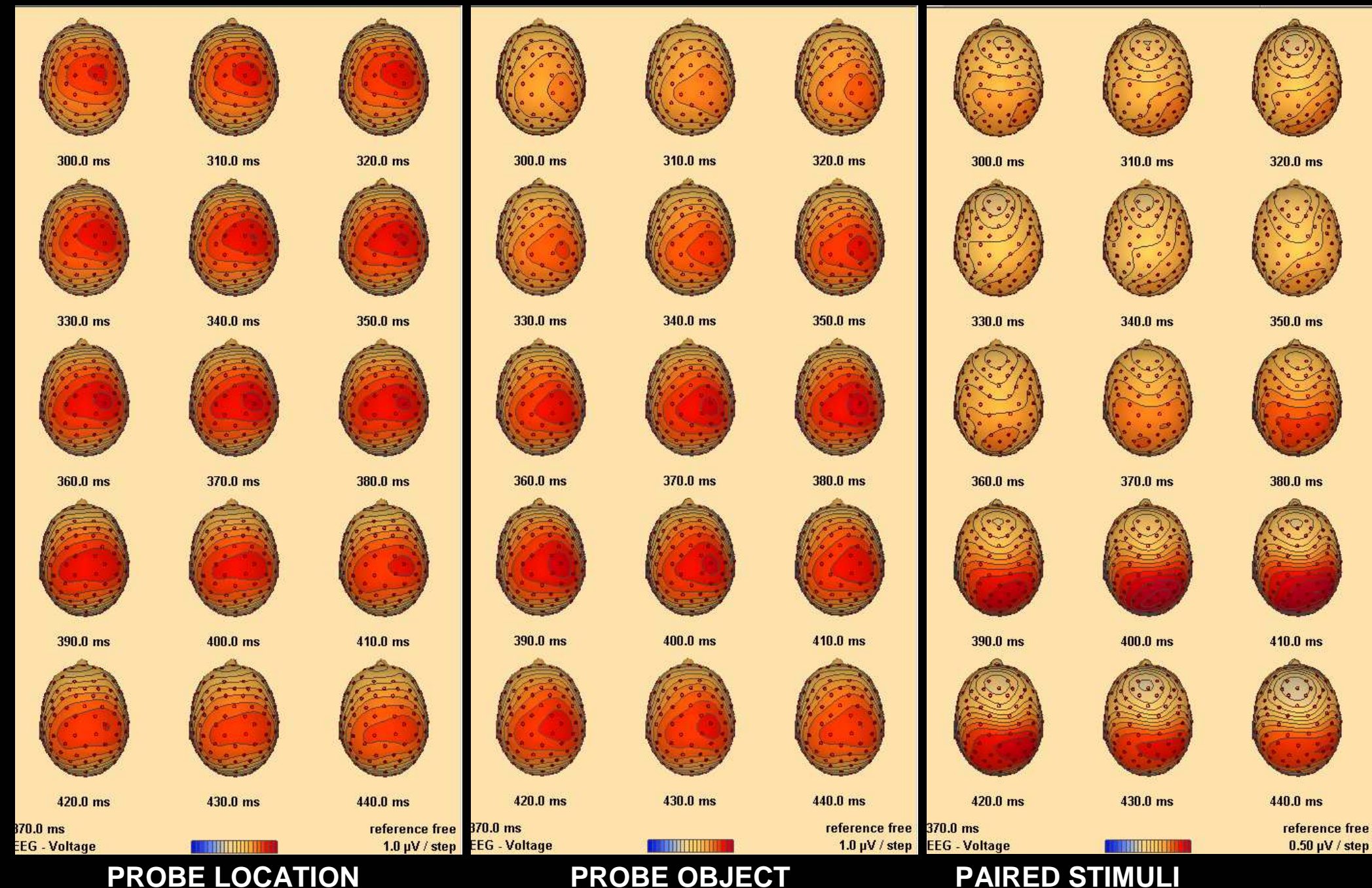


Figure 7.18 Activity distributions from 300-440ms shown for both cued locations and objects and for paired stimuli.

ERP/Behavioural correlations

Various measures of the waveform topographies were subjected to a correlational analysis investigating their relationship to mean reaction times to target stimuli. The only significant correlations found were related to peak latencies recorded for the object and location cues. These negative correlations are shown in Table 7.1 and suggest that individuals who responded faster had a later peaking frontal P2 when presented with the cues. Reaction times for both target stimuli were positively correlated.

Table 7.1 Pearson Correlations for P2 peak latency recorded for cues and subsequent reaction times for target stimuli.

| | | Cue Peak Latency (Object) | Cue Peak Latency (Location) | RT Target Location | RT Target Object |
|-------------|---------------------|---------------------------|-----------------------------|--------------------|------------------|
| RT Location | Pearson Correlation | -.626(*) | -.279 | 1 | .687(*) |
| | Sig. (2-tailed) | .039 | .406 | | .014 |
| | N | 11 | 11 | 12 | 12 |
| RT Object | Pearson Correlation | -.656(*) | -.653(*) | .687(*) | 1 |
| | Sig. (2-tailed) | .029 | .029 | .014 | |
| | N | 11 | 11 | 12 | 12 |

* Correlation is significant at the 0.05 level (2-tailed).

7.4.3 Dipole Source Analysis

Dipole models were generated for both cue types (object and location) across four time windows (100-200ms, 200-300ms or 250-350ms, 300-450ms and 450-800ms). The pre-target landmarks (0-1000ms) and the target stimuli (cued locations, cued objects, and paired stimuli) were also submitted for dipole source analysis. Two time windows (230-290ms and 300-450ms) were chosen for the target stimuli to localise the frontal P2 and parietal P3 components seen in the scalp data.

The structure of the models generated along with residual variance measures can be seen in Tables 7.2-7.4. These tables present information on each dipole and their corresponding location. Table 7.2 lists the neural generators purported to underlie cue-to-

target processing in the LOC trials. Table 7.3 lists the same data for the OBJ trials and Table 7.4 lists possible neural correlates for the PAIR trials. The models relating to cues, pre-probe landmarks and probes are displayed for comparison in Figures 7.19, 7.20 and 7.21 respectively. A summary of the brain areas involved in the study and the frequency of their engagement throughout the trials is shown in Table 7.5.

Table 7.2 *Talairach coordinates of dipoles in source models and corresponding Brodmann's Areas for LOC trials*

| | Time-period | Dip. | Talairach | (BA) | Nearest Gray Matter |
|-------------------------------|--|-------------|------------------|-------------|--|
| Object CUE | 100-200ms (RV~2.5%) | 1 | 34, 54, 19 | 10 | Bilateral Middle Frontal Gyrus |
| | | 2 | -34, 54, 19 | 10 | |
| | | 3 | 38, -46, 7 | - | Bilateral Middle Temporal Gyrus |
| | | 4 | -38, -46, 7 | - | |
| | | 5 | 33, -38, -11 | 37 | Bilateral Parahippocampal Gyrus |
| | | 6 | -33, -38, -11 | 37 | |
| | | 7 | -9, -10, 44 | 31 | Left Cingulate Gyrus |
| | 200-300ms (RV~7%) | 1 | 21, -23, 39 | 31 | Right Cingulate Gyrus |
| | | 2 | 13, -44, 5 | 30 | Right Parahippocampal Gyrus |
| | | 3 | -36, -79, -3 | 19 | Left Inferior Occipital Gyrus |
| | 300-450ms (RV~4%) | 1 | -5, 45, 24 | 9 | Left Medial Frontal Gyrus |
| | | 2 | 37, -46, 16 | 13 | Right Superior Temporal Gyrus/Insula |
| | | 3 | -37, -46, 16 | 22 | Left Superior Temporal Gyrus |
| | 450-800ms (RV~8%) | 1 | 11, -49, 35 | 31 | Right Precuneus |
| | | 2 | 51, -40, 5 | 22 | Bilateral Middle Temporal Gyrus |
| | | 3 | -51, -40, 5 | 22 | |
| | | 4 | -6, 46, 34 | 9 | Left Superior Frontal Gyrus |
| | | 5 | 34, 52, 20 | 10 | Right Superior Frontal Gyrus |
| Pre-Location Landmarks | Awaiting Location Presentation 0-750ms (RV<6.5%) | 1 | 30, 36, 27 | 9 | Bilateral Middle Frontal Gyrus |
| | | 2 | -30, 36, 27 | 9 | |
| | | 3 | 54, -39, -3 | 21 | Bilateral Middle Temporal Gyrus |
| | | 4 | -54, -39, -3 | 21 | |
| | | 5 | -11, -43, 7 | 29 | Left Posterior Cingulate Gyrus |
| | | 6 | -16, -77, 16 | 18 | Left Occipital Lobe, Cuneus |
| Target Locations | 230-290ms (RV~11%) | 1 | 29, 23, 40, | 8 | Right Middle Frontal Gyrus |
| | | 2 | 15, -42, -4 | 30 | Right Parahippocampal Gyrus |
| | | 3 | -33, -10, 44 | 6 | Left Middle Frontal/Precentral Gyrus |
| | 300-450ms (RV~4%) | 1 | 47, 24, 21 | 45 | Right Inferior Frontal Gyrus |
| | | 2 | 35, -40, 16 | 13 | Bilateral Superior Temporal Gyrus/Insula |
| | | 3 | -35, -40, 16 | 13 | |

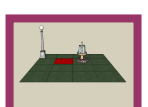
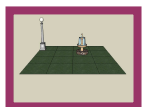


Table 7.3 Talairach coordinates of dipoles in source models and corresponding Brodmann's Areas for OBJ trials

| | Time-period | Dip. | Talairach | (BA) | Nearest Gray Matter |
|----------------------|---|------|--------------|------|--|
| Location CUE | 100-200ms (RV~8%) | 1 | 50, 14, -5 | 22 | Bilateral Superior Temporal Gyrus |
| | | 2 | -50, 14, -5 | 22 | |
| | | 3 | 42, -82, 13 | 19 | Bilateral Middle Occipital Gyrus |
| | | 4 | -42, -82, 13 | 19 | |
| | | 5 | 20, 55, 31 | 9 | Right Superior Frontal Gyrus |
| | | 6 | 39, -11, 40 | 6 | Right Precentral Gyrus |
| | | 7 | -30, -55, 56 | 7 | Left Superior Parietal Lobule |
| | 250-350ms (RV~5%) | 1 | 32, -35, 35 | 40 | Right Inferior Parietal Lobule |
| | | 2 | 37, -18, 16 | 13 | Right Insula |
| | | 3 | -48, -27, 4 | 41 | Left Superior Temporal Gyrus |
| | | 4 | -35, -80, 7 | 19 | Left Middle Occipital Gyrus |
| | | 5 | 0, 43, 33 | 9 | Left Medial Frontal Gyrus |
| | 300-450ms (RV~10%) | 1 | -4, 47, 41 | 8 | Left Medial Frontal Gyrus |
| | | 2 | 39, -31, 12 | 41 | |
| | | 3 | -39, -31, 12 | 41 | Bilateral Superior Temporal Gyrus |
| | 450-800ms (RV~9%) | 1 | 38, 50, 28 | 9 | Bilateral Middle Frontal Gyrus |
| | | 2 | -38, 50, 28 | 9 | |
| | | 3 | 45, -36, 1 | 22 | Bilateral Superior Temporal Gyrus |
| | | 4 | -45, -36, 1 | 22 | |
| | | 5 | 2, -67, 26 | 31 | Right Precuneus |
| | | 6 | 12, 20, 52 | 6 | Right Superior Frontal Gyrus |
| Pre-Object Landmarks | Awaiting Object Presentation 0-750ms (RV<12%) | 1 | 10, 43, 42 | 8 | Bilateral Superior Frontal Gyrus |
| | | 2 | -10, 43, 42 | 8 | |
| | | 3 | -36, -62, 12 | 19 | Left Middle Occipito-temporal Gyrus |
| | | 4 | -38, 14, 29 | 9 | Left Middle Frontal Gyrus |
| | | 5 | 49, -33, -4 | 21 | Right Middle Temporal Gyrus |
| Target Objects | 230-290ms (RV~6%) | 1 | 29, 16, 37 | 8 | Right Middle Frontal Gyrus |
| | | 2 | 45, -42, 10 | 41 | Right Superior Temporal Gyrus |
| | | 3 | -45, -32, 19 | 13 | Left Insula |
| | 300-450ms (RV~3%) | 1 | 45, 12, 20 | 9 | Right Inferior Frontal Gyrus |
| | | 2 | 39, -44, 13 | 13 | |
| | | 3 | -39, -44, 13 | 13 | Bilateral Superior Temporal Gyrus/Insula |

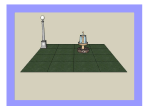
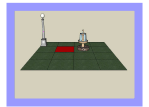
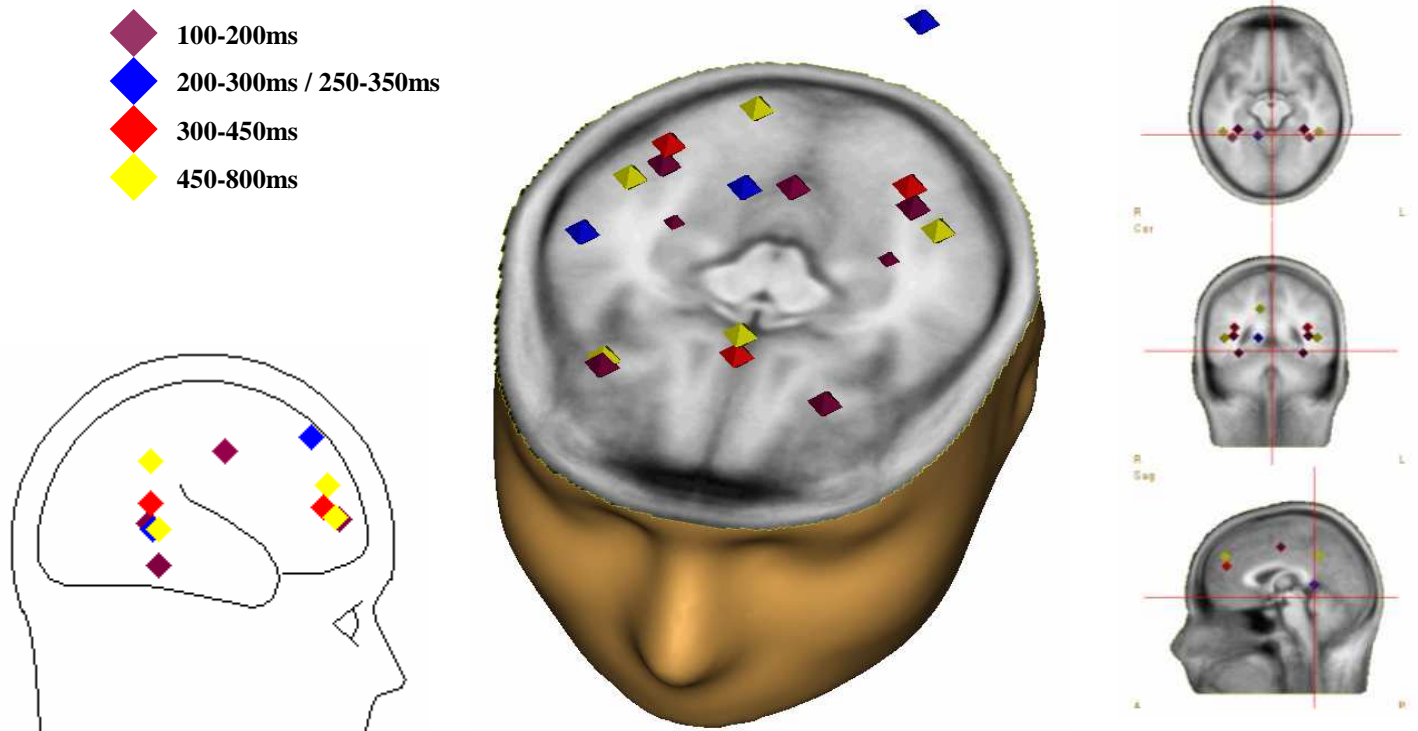


Table 7.4 Talairach coordinates of dipoles in source models and corresponding Brodmann's Areas for PAIR trials

| | | | | | |
|----------------|----------------------|---|--------------|----|-----------------------------------|
| Paired Stimuli | 300-450ms (RV~6%) | 1 | 43, -38, 7 | 41 | Bilateral Superior Temporal Gyrus |
| | | 2 | -43, -38, 7 | 41 | |
| | | 3 | 28, 55, 28 | 9 | Bilateral Superior Frontal Gyrus |
| | | 4 | -28, 55, 28 | 9 | |
| | | 5 | -22, -90, 16 | 18 | Left Middle Occipital Gyrus |



OBJECT AS CUE



LOCATION AS CUE

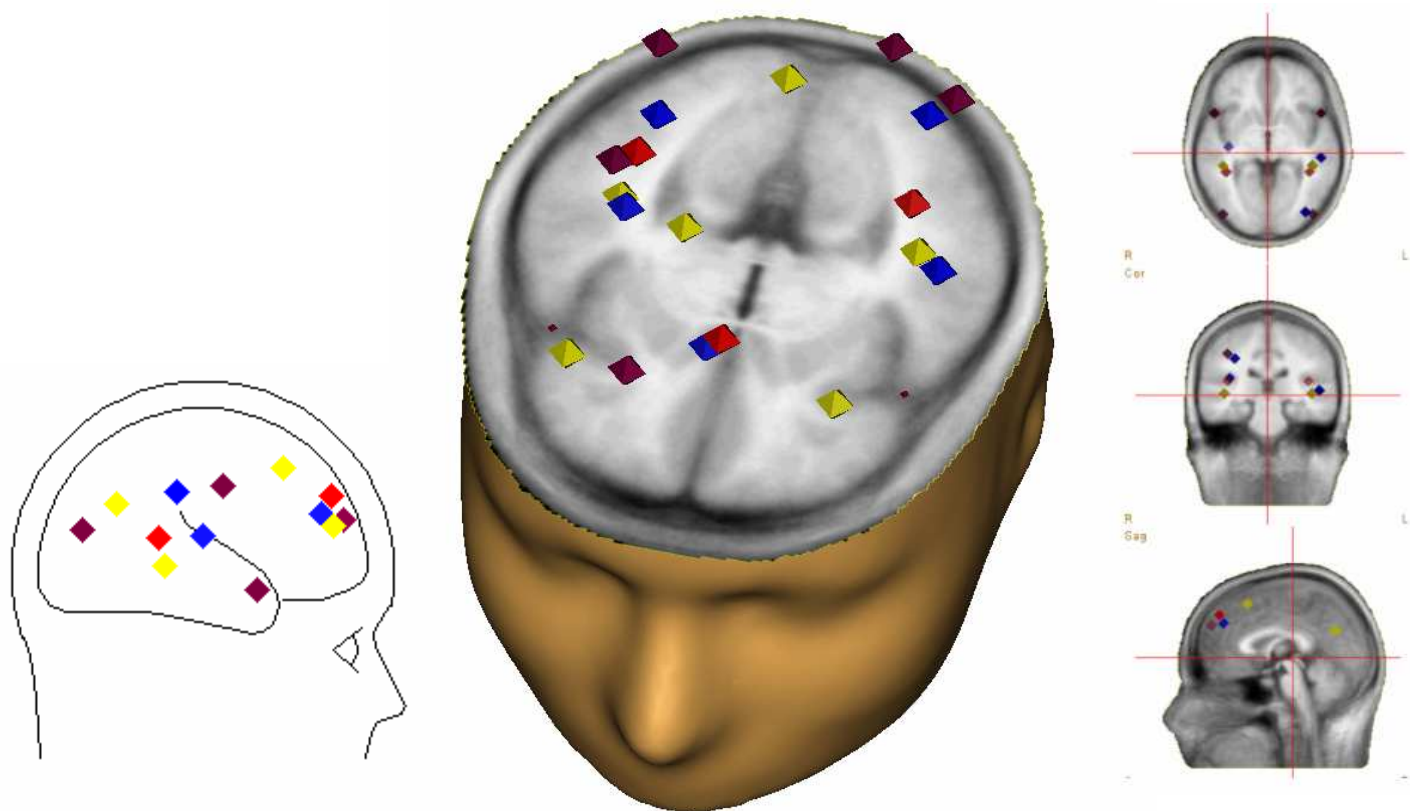
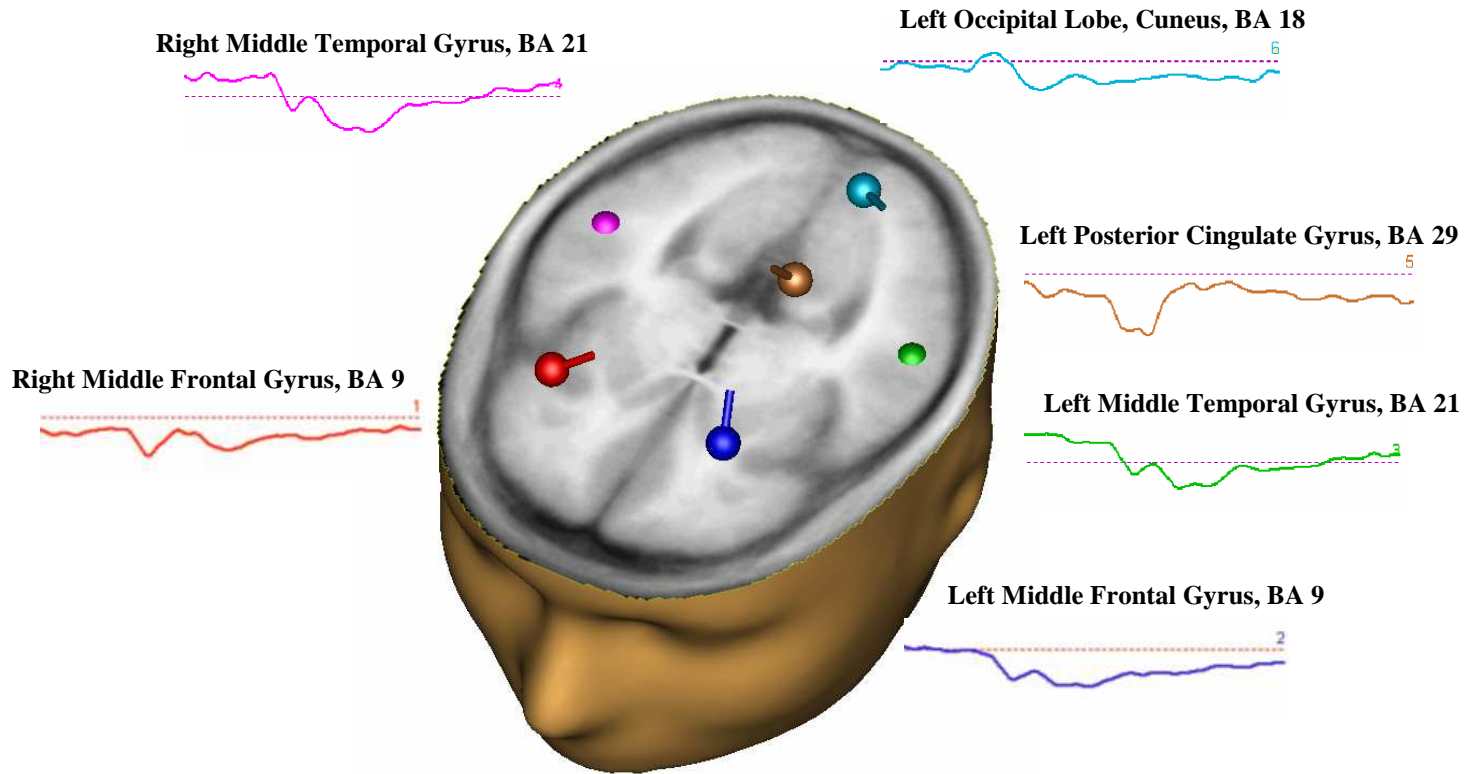


Figure 7.19 Source localisation for the electrophysiological response to the cues. The differing colours of the dipoles relate to their differing temporal activation across the presentation period.

PRE-LOCATION LANDMARKS



PRE-OBJECT LANDMARKS

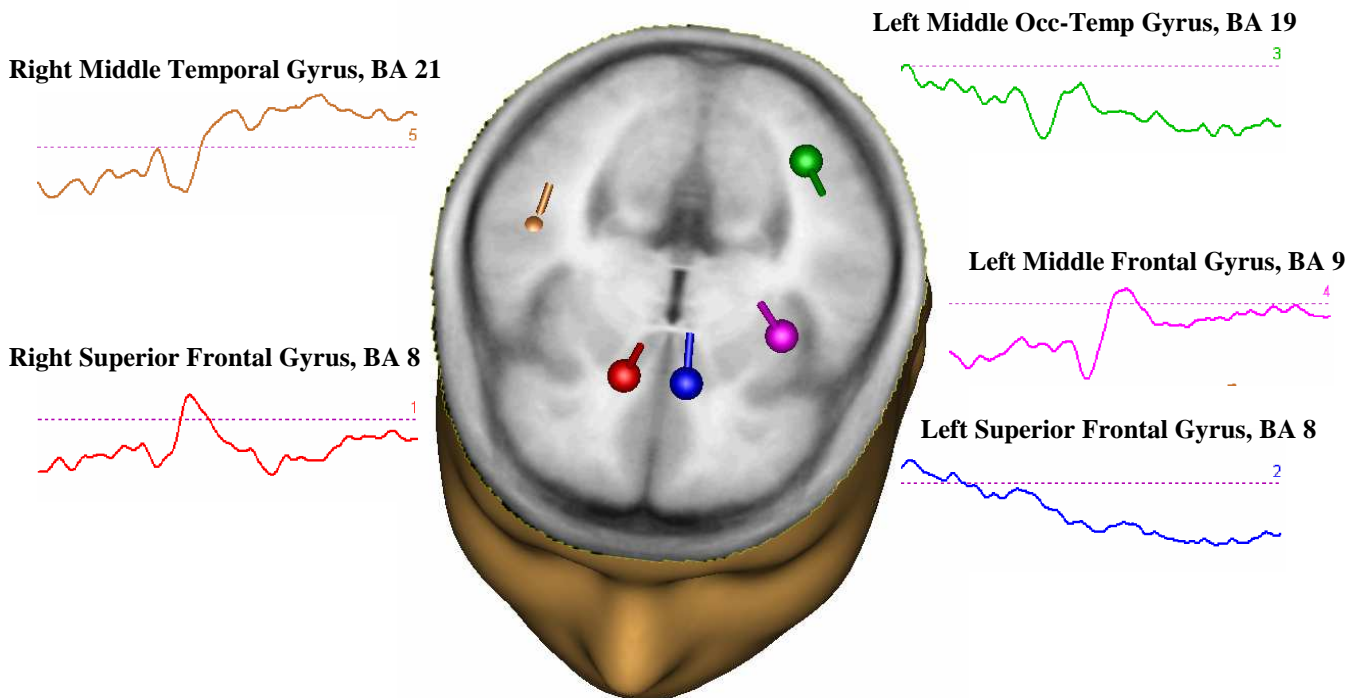
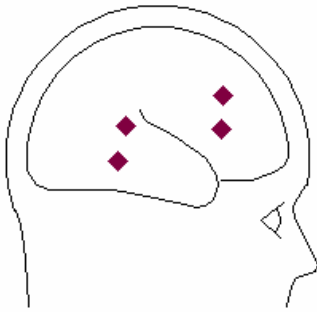


Figure 7.20 The Dipole models generated for pre-probe landmarks presented in generic MRI slices. Source waveforms show individual dipole activity across the 1000ms epoch.

TARGET PROBES

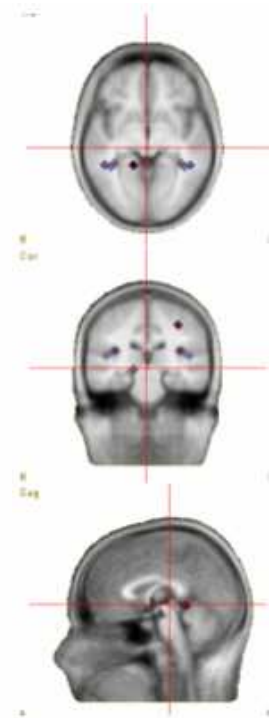
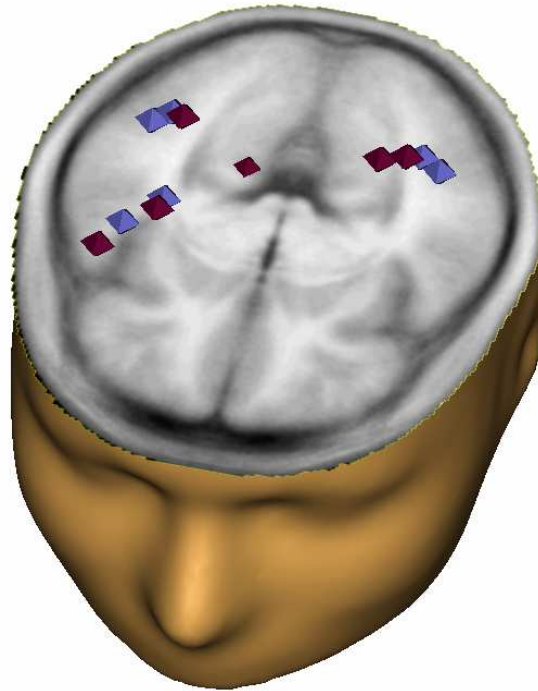
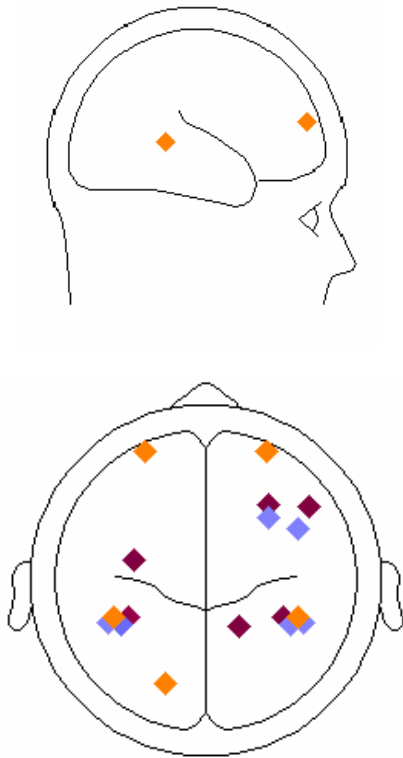
Locations



Objects



Pairs



TARGET PAIRS

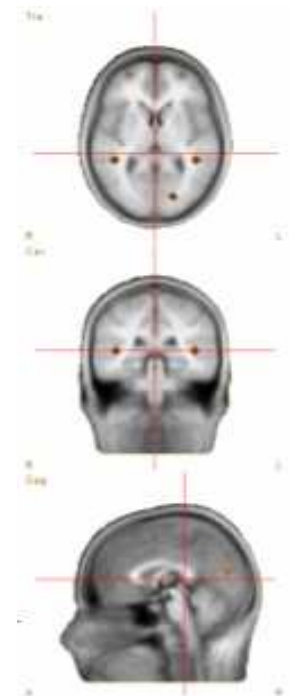
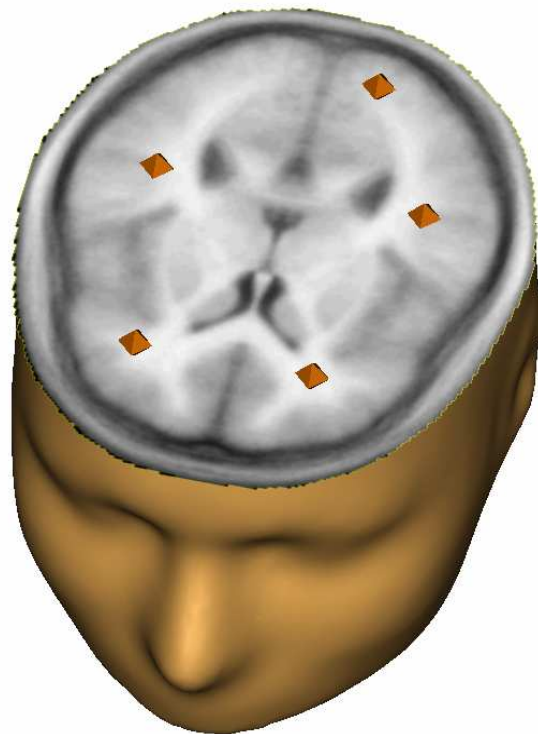


Figure 7.21 The Dipole models generated for both the probe stimuli (top head model) and the target pairs (bottom head model). The images along the left also display dipole locations with an overview allowing comparisons between probes and pairs.

Table 7.5 *Frequency of activation of brain structures involved in object-location processing according to their rate of occurrence in the generated dipole models*

| No. of Occurrences | (BA) | Structure | Mode Condition |
|---------------------------|-------------|---|-----------------------|
| 10 | 9 | Superior / Inferior / Middle / Medial Frontal Gyrus | 6-Object Trial |
| 7 | 22 | Superior Temporal Gyrus | 4-Object Trial |
| | 13 | Superior Temporal Gyrus / Insula | 4-Object Trial |
| 5 | 19 | Middle Occipito-temporal Gyrus | 4-Object Trial |
| | 8 | Superior / Middle / Medial Frontal Gyrus | 4-Object Trial |
| 4 | 41 | Superior Temporal Gyrus | 2-Pair Trial |
| | 31 | Precuneus / Cingulate | 3-Location Trial |
| 3 | 21 | Middle / Inferior Temporal Gyrus | 2-Location Trial |
| | 10 | Middle / Superior Frontal Gyrus | 2-Location Trial |
| | 6 | Middle / Superior Frontal / Precentral Gyrus | 2-Object Trial |
| 2 | 30 | Parahippocampal Gyrus | 2-Location Trial |
| | 37 | Parahippocampal Gyrus | 2-Location Trial |
| 1 | 40 | Inferior Parietal Lobule | 1-Object Trial |
| | 7 | Superior Parietal Lobule | 1-Object Trial |
| | 29 | Posterior Cingulate Gyrus | 1-Location Trial |
| | 18 | Middle Occipital Gyrus | 1-Pair Trial |
| | 45 | Inferior Frontal Gyrus | 1-Location Trial |

Summary of the modelled neural generators:

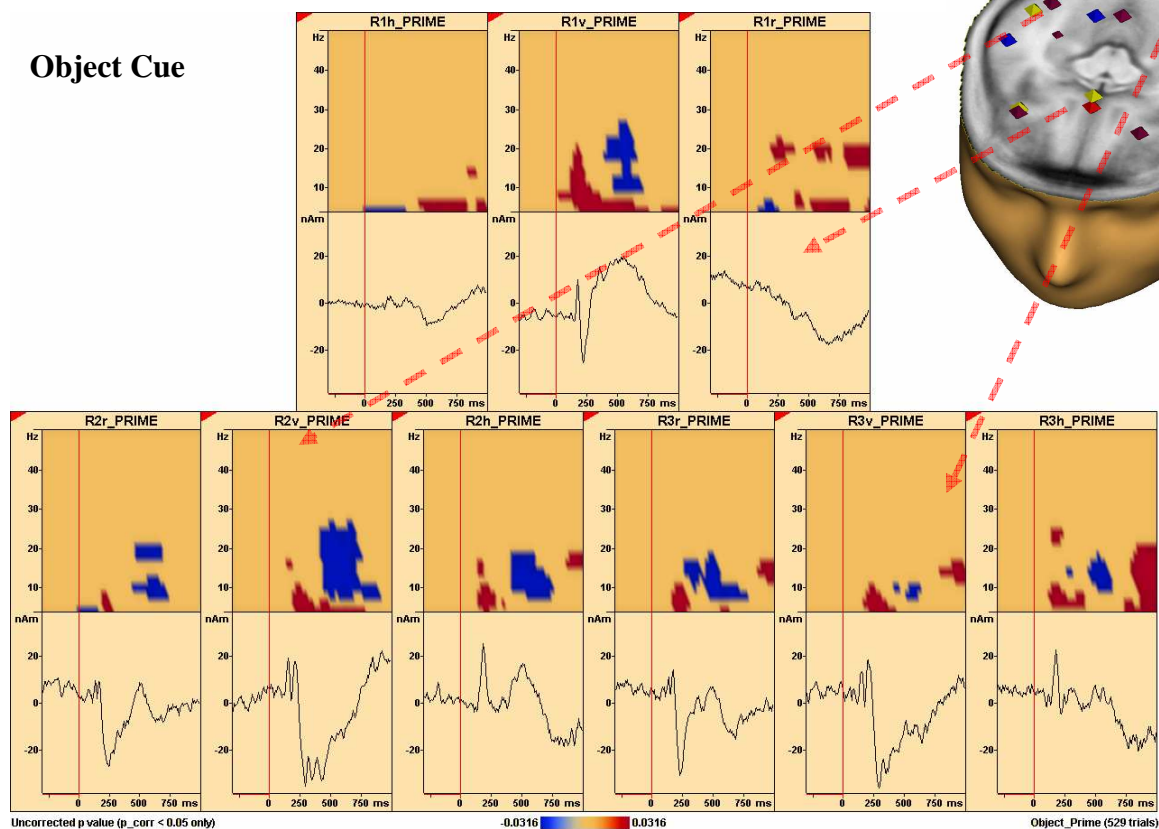
Looking at the Tables presented above, similar centres of activity appear to underlie the processing of locations and objects – most notably frontal and temporal cortices. These similarities can be seen when stimuli were presented as cues (see Figure 7.19 – red sources) and probes (Figure 7.21 – top head model) as well as between probes and pairs (Figure 7.21 – bottom left overview). However, differences can also be seen across trial types. For object cues, the more posterior bilateral dipoles appear to bundle in a line from medial temporal through superior temporal to parietal cortex (i.e. between Talairach coordinates 38 to 49 on the y-axis – Figure 7.19 top right-side view). A more distributed pattern of sources was observed for the location cues with a possible two-pronged

progression from the occipital cortex and temporal pole to more posterior superior temporal regions (Figure 7.19 bottom right-side view). For the probe stimuli, differences were seen in the localisations within the frontal cortex, with right-lateralised middle inferior frontal activity for both location and object probes compared to bilateral superior frontal activity for paired stimuli. Medial temporal (parahippocampal) activity was only found for probe locations and their object cues i.e. stimuli in the LOC trials.

7.4.4 Temporal Spectral Evolution (TSE)

Given the large number of ERP results and comparisons, and the large number of localisations undertaken, only a select number of conditions were put forward for time-frequency analysis. For the Cues, the three dipoles that both object and location models shared (i.e. medial frontal and bilateral temporoparietal) were converted to source montages and subjected to TSE analysis. A second TSE evaluated spectral changes for the Probe stimuli. Figures 7.22 and 7.23 show statistically significant increases and decreases (compared to baseline) in band power after 1799 bootstrapped samples were tested. For both cues, theta bursts were seen between 250-400ms extending in time for the medial frontal dipole. This increase was followed by a suppression of alpha/beta bands (~500ms). Increases and decreases were more widespread in the frequency domain for Location Cues. For Location Probes, large increases in oscillations of frequencies up to 20/25Hz were seen after participants made responses. Conversely, for Object Probes, a decrease in power was observed in the alpha and beta bands prior to responding. No coherence measures reached significance.

Object Cue

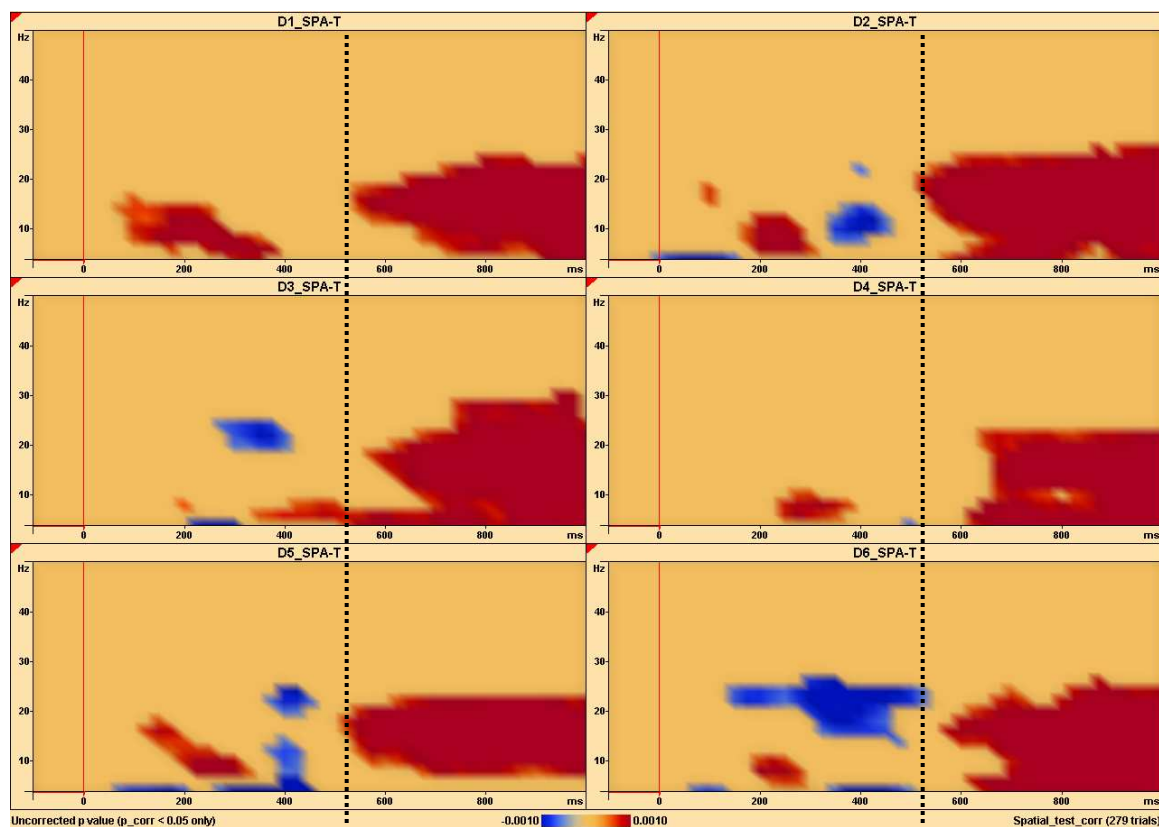


Location Probe

Right
Middle
Frontal
Gyrus

Middle
Frontal/
Precentral
Gyrus

Right
Superior
Temporal
Gyrus



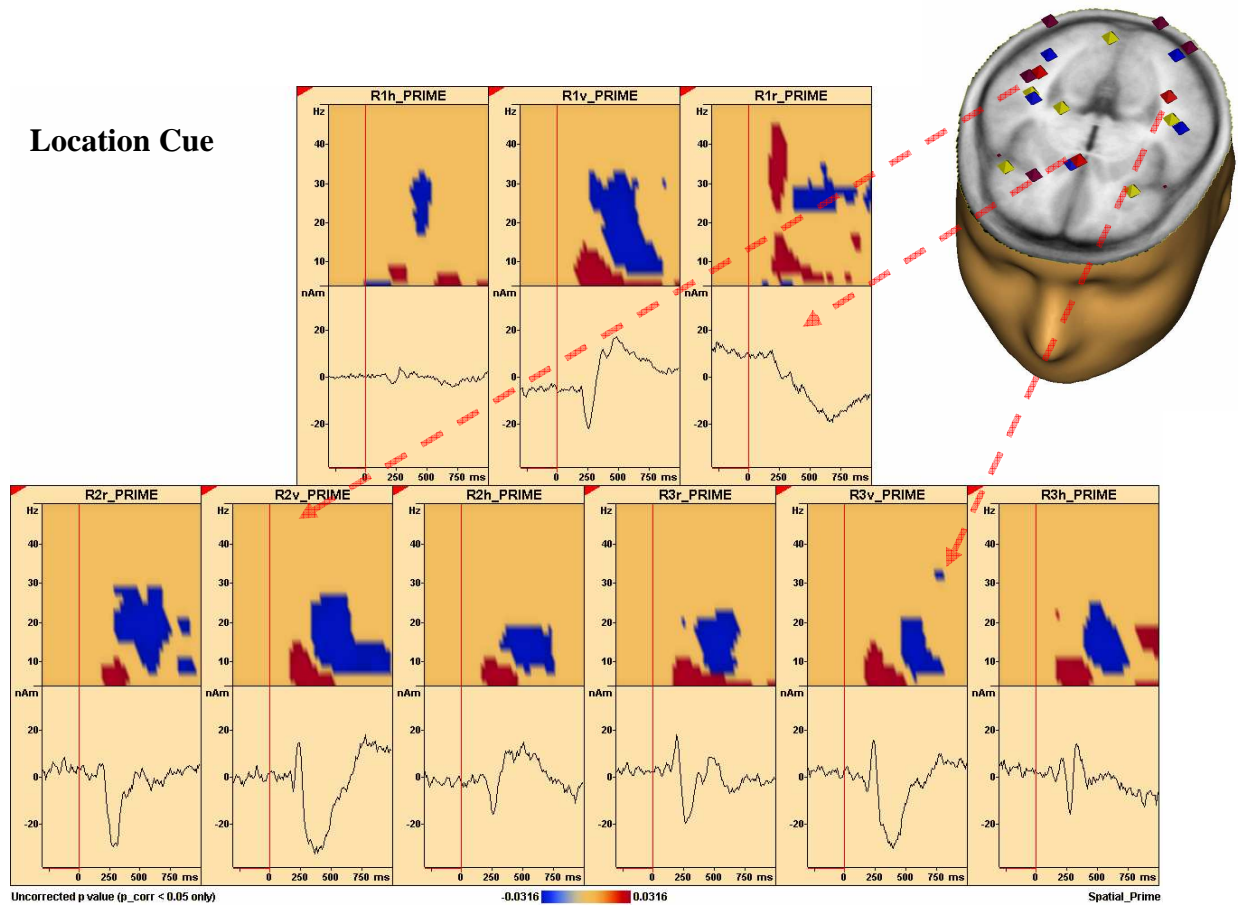
Right
Parahippocampal
Gyrus

Right
Inferior
Frontal
Gyrus

Left
Superior
Temporal
Gyrus

Figure 7.22 Plots generated after bootstrapping showing areas of significant power increases (red) and decreases (blue) in the time-frequency domain for each source for the LOC block. **a)** Object Cues 3-regional source model **b)** Location Probes 6-dipole model. Dotted lines show approximate mean RT

Location Cue



Object Probe

Right
Middle
Frontal
Gyrus

Left
Insula

Right
Superior
Temporal
Gyrus

Right Superior
Temporal Gyrus

Right
Inferior
Frontal
Gyrus

Left
Superior
Temporal
Gyrus

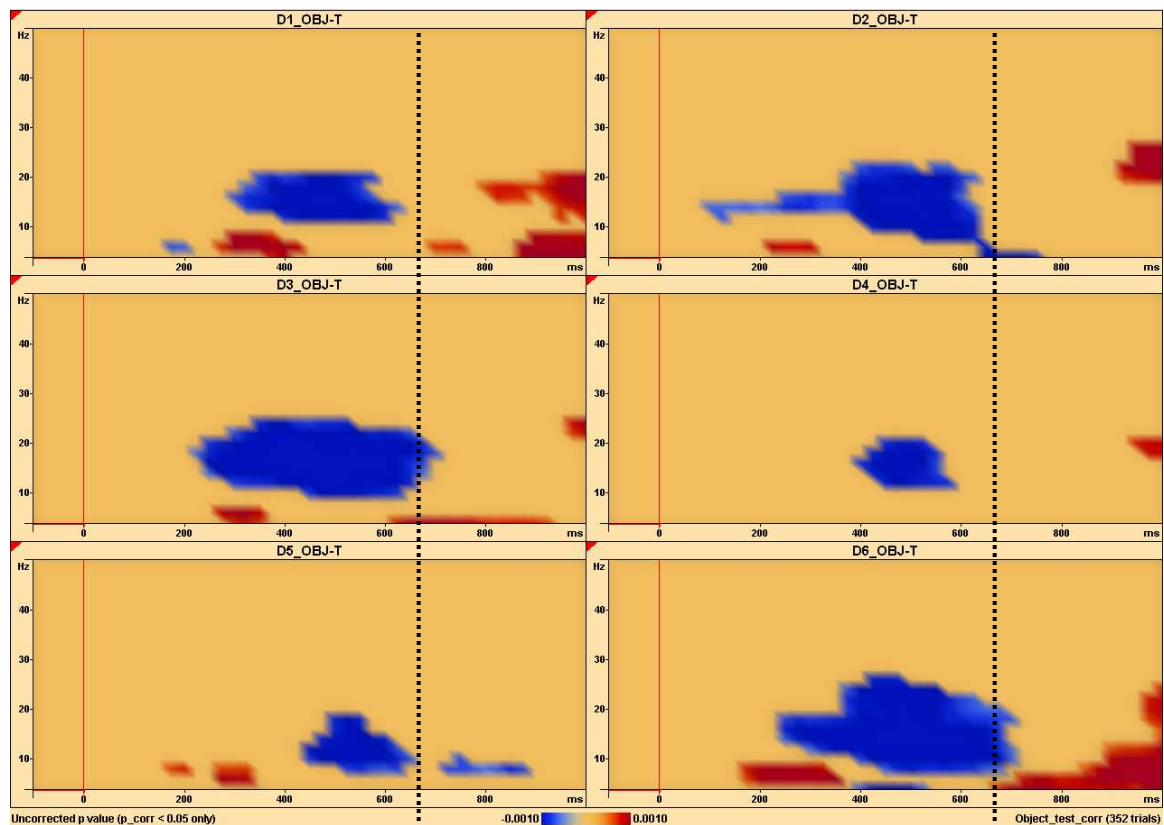


Figure 7.23 Plots generated after bootstrapping showing areas of significant power increases (red) and decreases (blue) in the time-frequency domain for each source for the OBJ block **a)** Location Cues 3-regional source model **b)** Object Probes 6-dipole model. Dotted lines show approximate mean RT.

7.5 Discussion

The behavioural data show that participants performed significantly faster for stimuli matching the cue than for mismatched stimuli, suggesting an expectation bias. They also had faster recognition times for location targets after seeing an object when compared to object recognition after seeing a location. However, this performance difference was eliminated for paired presentations. Overall, pairing the stimuli resulted in similar accuracy and response times for both object and object-location recognition. The type of pairing was found to have an effect on performance, with studied objects in their studied locations more easily recognised compared to odd pairings. Pairing inconsistencies resulted in longer response times and less accurate responses.

The lower accuracy overall in location recognition for the paired stimuli compared to the cued presentations may be explained by a speed/accuracy trade-off. Support for this comes from the data showing these less accurate responses were also faster. This trade-off may have been a confound in the design of the experiment as the response window was shorter for paired presentations (1000ms per question), possibly resulting in more rushed (i.e. faster and less accurate) responding. The faster response times for the paired stimuli may also be due to the fact that participants were responding to a subsequent question rather than stimulus onset. Nonetheless this possibility does not detract from the findings that show an object and its location are associated in the brain , as evidenced by the ability of one to influence recognition of the other – Figure 7.5a & 7.5b.

The data also suggest objects may cue location recognition more efficiently than locations cue object recognition. This difference may be due to basic differential processing times in visuo-spatial recognition. The difference was seen in the behaviour

chain [see object → respond vs. see location → respond]. However, the difference was absent for the paired stimuli where the behaviour chain was instead [see question → respond]. The difference may, on the other hand, be due to the pre-probe landmarks. Their presentation may have aided participants' speed of recognition for locations, as the landmarks were presented with the grid which may have allowed participants to focus their attention and expectations to a single square. Hence the behavioural results are difficult to interpret. However, the data from the cued trials alone seem to support the findings of Soto and Blanco (2004), as both spatial and object cueing effects were seen. Responses were faster when targets were cued correctly.

The electrophysiological findings may shed some light on the performance data as latency differences in waveforms were seen throughout the trials i.e. for the cues as well as the probe stimuli. This would suggest that processing which began prior to the pre-target landmarks affected performance. Indeed, the only significant electrophysiological measure that correlated significantly with reaction time was the latency of the frontal P2 related to the cues. This negative correlation suggests that a later peaking frontal component benefited participants across both cueing conditions, resulting in faster reaction times when they were presented with probe stimuli for evaluation. It is difficult, however, to reconcile this finding with the findings that overall, significantly faster-peaking frontal activity was recorded for the object cues (compared to the location cues) and subsequently faster reaction times were recorded for these trials. The latter finding (i.e. the significant difference in peak latencies for object and location cues) could be the result of a difference in the automatic processing of the cues, indicative of a qualitative externalised 'bottom-up' difference, whereas the correlation results may show a more individualised 'top-down' depth-of-processing difference. This view would suggest that

the activation of different areas localised over the first 300ms after cue onset (e.g. parahippocampal and cingulate processing for object cues and superior/inferior parietal and temporal processing for location cues) resulted in the differences seen in Figure 7.7, i.e. object cues eliciting earlier P2 components. Additionally, more extensive processing in these areas may have resulted in the individual differences in the frontal peaks.

Inspection of the dipole models generated for the cues reveals two distinct neural networks, as mentioned above, which may reflect differential task demands. Seeing an object and being asked to recall its location (object cue) recruited medial temporal areas suggesting an allocentric localising strategy. Here, participants were mentally recalling the associated location during the object cue. Seeing a location cue and being asked to recall the appropriate object recruited temporoparietal areas suggesting that a more egocentric strategy was employed for these trials (see also right-side hemispheres in Figure 7.19). The type of mental recall necessary during the cues is possibly very different from the recognition processing required once the probe stimulus appeared. This proposition received some support from anecdotal reports of participants after the experiment. Participants reported that the cues led them to mentally imagine the associated target stimulus and then respond to the probe based on whether it matched their mental image (expectation) or not.

The idea that participants are mentally recalling the targets very rapidly when they are presented with cues can be tested by examining what they are rehearsing during the pre-target landmarks. The ability to hold 'on-line' a representation of the features of an object or its spatial location following its initial perception is an active process dependent on sustained neural discharge, and is distinct from the passive representation knowledge in long-term memory (Baddeley, 1986; Goldman-Rakic, 1987). The scalp waveforms and

related dipole models generated for the pre-probe landmarks can illuminate what was being rehearsed. For example, dissociations in frontal activity for object and spatial working memory have previously been reported (Courtney *et al.*, 1998; Curtis & D'Esposito 2003; Logie & Marchetti, 1991; McCarthy *et al.*, 1994; Paller & Wagner, 2002; Petrides *et al.*, 1993; Ranganath *et al.*, 2004; Tresch, Sinnamon & Seamon, 1993). Negative scalp potentials are thought to reflect the allocation of attentional or processing resources towards a specific cortical region (Birbaumer, Elbert, Canavan & Rockstroh, 1990; LaBerge, 1997). An ERP study by Bosch, Mecklinger & Friederici (2001) examined the potentials related to the retention of object, spatial and verbal information in working memory. Applying their conclusions to the patterns of activity recorded during the pre-probe stimuli, the additional frontal negativity and posterior positivity seen for the pre-location landmarks could be an index of object memory processes or at least verbal rehearsal processes (that are more likely for object memory). It would be therefore unusual to see these activations if participants were mentally rehearsing locations – unless perhaps they were engaged in using verbal locatives (see Postma, Kessels and van Asselen, 2008). The presence of the grid and landmarks may have resulted in a more verbal, categorical rehearsal strategy. The left lateralised parietal dipole in the pre-location landmark model may be evidence of this. With this in mind, a comparison of the complete pre-probe dipole models for both conditions may help in separating out what participants were focusing on during this period.

Neural activity during location rehearsal and object rehearsal was previously investigated by Baker *et al.* (1996) using positron emission tomography. Bilateral DLPFC was activated in both tasks; activation was of higher significance on the right for rehearsing spatial locations and the left for rehearsing objects, and extended to anterior

frontal areas in the object condition. Active representation of spatial location was associated with co-activation of the medial and lateral parietal cortex and the extrastriate visual cortex. Similar dissociations were found in the current study.

Both pre-probe models contained bilateral frontal dipoles but the pre-object landmarks model also contained an additional left frontal source. In addition, the frontal activations for the pre-location landmarks were associated with (left) parietal and extrastriate activity. Analysis at the dipolar level would therefore suggest that participants were maintaining the targets in working memory after seeing the cues. However, another interpretation could follow that attention-based rehearsal (i.e. shifts of spatial selective attention to memorized locations), rather than spatial working memory, may have been responsible for the network of dipoles seen for pre-location landmarks. Several neuroimaging reports have provided data consistent with the idea that spatial attention and spatial working memory are linked in important ways, by demonstrating considerable overlap between brain areas active during directed attention tasks and those active during spatial working memory tasks (e.g., Chelazzi & Corbetta, 2000; Corbetta, Kincade & Shulman, 2002; LaBar, Gitelman & Parrish, 1999; Smith, *et al.*, 1998). These studies have reported overlaps, in particular within a network of posterior parietal and superior frontal areas. Recently, Postle *et al.* (2004) localised the effect of attention-based rehearsal to extrastriate regions and areas in the parietal lobe. This topography is also consistent with the dipoles in our model, suggesting that during this time, participants focused on the location within the grid prior to the target location presentation – a strategy that was not available for target object trials.

The electrophysiological data for the cued target presentations (i.e. the probes) reveal very similar topographies, with amplitude differences at frontal sites and latency

differences at right central scalp locations. The waveforms related to matched vs. mismatched targets show that correct location cues elicited an old/new effect for object recognition, with correctly located target objects eliciting greater frontal P2 and parietal P3 amplitudes. The effect of a mismatched object cue on the probe location ERPs was seen instead as a latency shift in the P3 component suggesting the earlier recruitment of areas localised after 300ms. The dipole models suggest the recruitment of a very similar network for both location and object probes after 300ms but prior to this similarity, the involvement of the right parahippocampal gyrus, *exclusively for location recognition*, is worthy of note.

The dipole model for the paired stimuli reveals a number of areas which were common to both object and location probes. These will be discussed in terms of object-location binding. As can be seen from the dipole models (and the summary in Table 7.5), activity across the trials was continually localised to similar areas (e.g. BA 8, 9, 13, 19, 22, 31 and 41) corresponding to frontal and temporal locations. These similarities in the models suggest areas of convergence in object-location memory. Two brain areas, the dorsolateral prefrontal cortex (DLPFC) and the superior temporal gyrus (STG), may therefore be necessary for object-location binding. In addition to their role in working memory, there is much evidence for the involvement of the frontal lobes in information binding (e.g. Baddeley, 2000; Browning *et al.*, 2005; Kesner & Ragozzino, 2003; Mitchell *et al.*, 2000; Piekema *et al.*, 2006; Prabhakaran *et al.*, 2000) with the DLPFC specifically implicated by Prabhakaran *et al.*, (2000). Interestingly, the frontal activity associated with the cues was left lateralised and medial whereas the frontal activity during target presentation was right lateralised. The involvement of the prefrontal cortex in more general episodic memory shows a hemispheric encoding/retrieval asymmetry

(HERA), such that the left side is preferentially involved in encoding, and the right in retrieval (Habib, Nyberg & Tulving, 2003; Nyberg *et al.*, 1996; Tulving, *et al.*, 1994). However, as memory retrieval was required for both cues and probes this asymmetry might apply to a lesser extent. Another possible reason for this hemispheric dissociation could be differing retrieval demands between cues and probes i.e. recall vs. recognition, respectively. Although studies have found lateralisation effects between cued recall and recognition (e.g. Rugg *et al.*, 1998), findings have been inconsistent (for review see Fletcher & Henson, 2001).

The STG, which was localised in many of the models, fits the classic idea that the posterior temporoparietal junction is critical in representing space. Marois, Chun and Gore (2000a) found that monitoring locations, objects and object-location conjunctions for ‘oddball’ occurrences recruited the lateral temporal cortex and the temporoparietal junction. Their findings support our view that a strict dorsal/ventral dual-stream model does not fully account for the perception of objects in space. The temporoparietal junction lies between the termination points of the dorsal and ventral streams (i.e. between the SPL and ITC) and consists of the inferior parietal lobe (IPL) and STG. This location would make the STG a cue candidate for binding object-location information, but most research has focused on this region’s involvement in auditory processing. Its function with regard to dorsal-ventral interactions is controversial (Shapiro, Hillstrom & Husain, 2002). Lesions here can lead to spatial neglect, a condition associated with abnormal visuospatial perception as well as impaired visually-guided movements, suggesting that the IPL/STG may have a largely ‘dorsal’ role (Mattingley *et al.*, 1998; Robertson & Marshall, 1993; Vallar, 2001). However, a number of studies have proposed that this area also has a non-spatial role incorporating the ventral stream (e.g. Coull &

Nobre, 1998; Wojciulik & Kanwisher, 1999; Marois, Chun & Gore, 2000b). Milner (1997) emphasised that inputs from the ventral system may be particularly critical and hypothesized that the IPL/STG might represent a nexus between dorsal and ventral streams. From their findings with lesion patients, Shapiro, Hillstrom and Husain (2002) also conclude that the IPL/STG has features of both the (spatial) dorsal and the (non-spatial) ventral streams. Located along the inferior edge of the STG and relatively invisible to ERP recording due to its tangential fields, the superior temporal sulcus (STS) has also been implicated in multimodal integration. Neuroimaging studies have highlighted a role for the posterior superior temporal sulcus (pSTS) in multimodal object representation. A multisensory study by Calvert *et al.* (2001) found crossmodal interactions within the superior temporal sulcus, intraparietal sulcus, insula and several foci in the frontal lobe, including the superior and ventromedial frontal gyri. The area around the temporoparietal junction (as well as more dorsal parietal areas) has connections with both the frontal and temporal lobes (see Figure 7.24).

The TSE analysis also revealed significant increases in theta power for these areas. A large body of evidence indicates that theta rhythm is likely involved in spatial learning and navigation (see Buzsáki, 2005). But the presence of theta also supports an information-binding role. Nishiyama and Yamaguchi (2001) found theta activity in the frontal and the temporoparietal regions in subjects navigating a virtual maze. They propose that this theta activity is indicative of the functional connections between the hippocampus, prefrontal cortex and parietal cortex.

The frequency differences seen between Probes are far more complex. The increase in spectral power after a response could be due to performance monitoring or

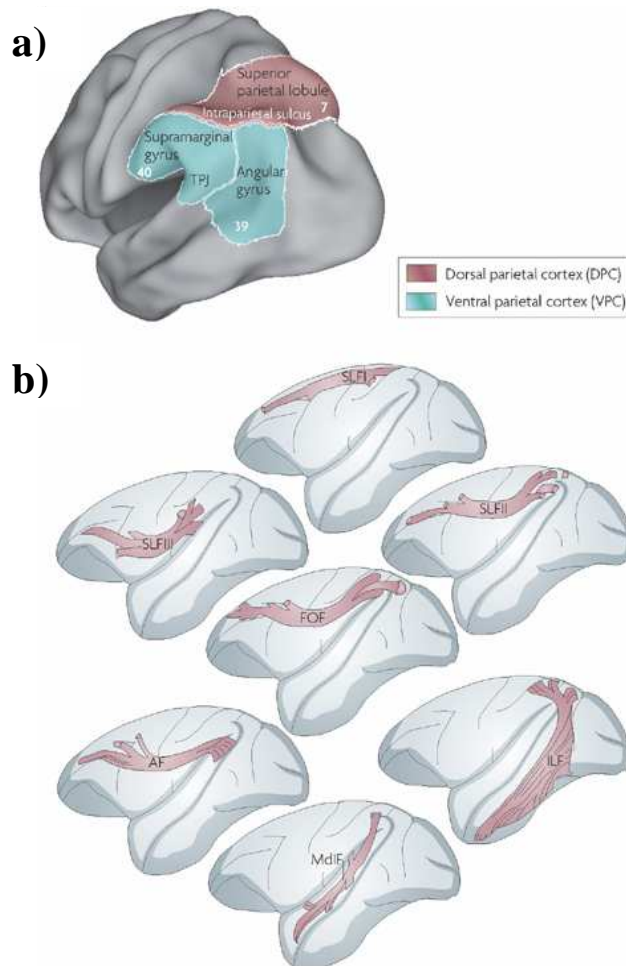


Figure 7.24 a) The posterior parietal cortex can be divided into the dorsal parietal cortex (DPC) and the ventral parietal cortex (VPC). The DPC comprises the lateral cortex including and superior to the intraparietal sulcus and the medial parietal cortex (the precuneus (not shown)) and largely corresponds to Brodmann area 7. The VPC includes the supramarginal gyrus and the angular gyrus and largely corresponds to Brodmann areas 39 and 40. **b)** The parietal cortex has direct anatomical connections with many brain regions. It is connected to the frontal lobes through the superior longitudinal fasciculi (SLFI, SLFII and SLFIII), the fronto-occipital fasciculus (FOF) and the arcuate fasciculus (AF). The parietal cortex is also connected to the temporal lobes through the middle longitudinal fasciculus (MdlF) and the inferior longitudinal fasciculus (ILF). TPJ, temporoparietal junction. Reproduced from Cabeza, Ciaramelli, Olson and Moscovitch (2008)

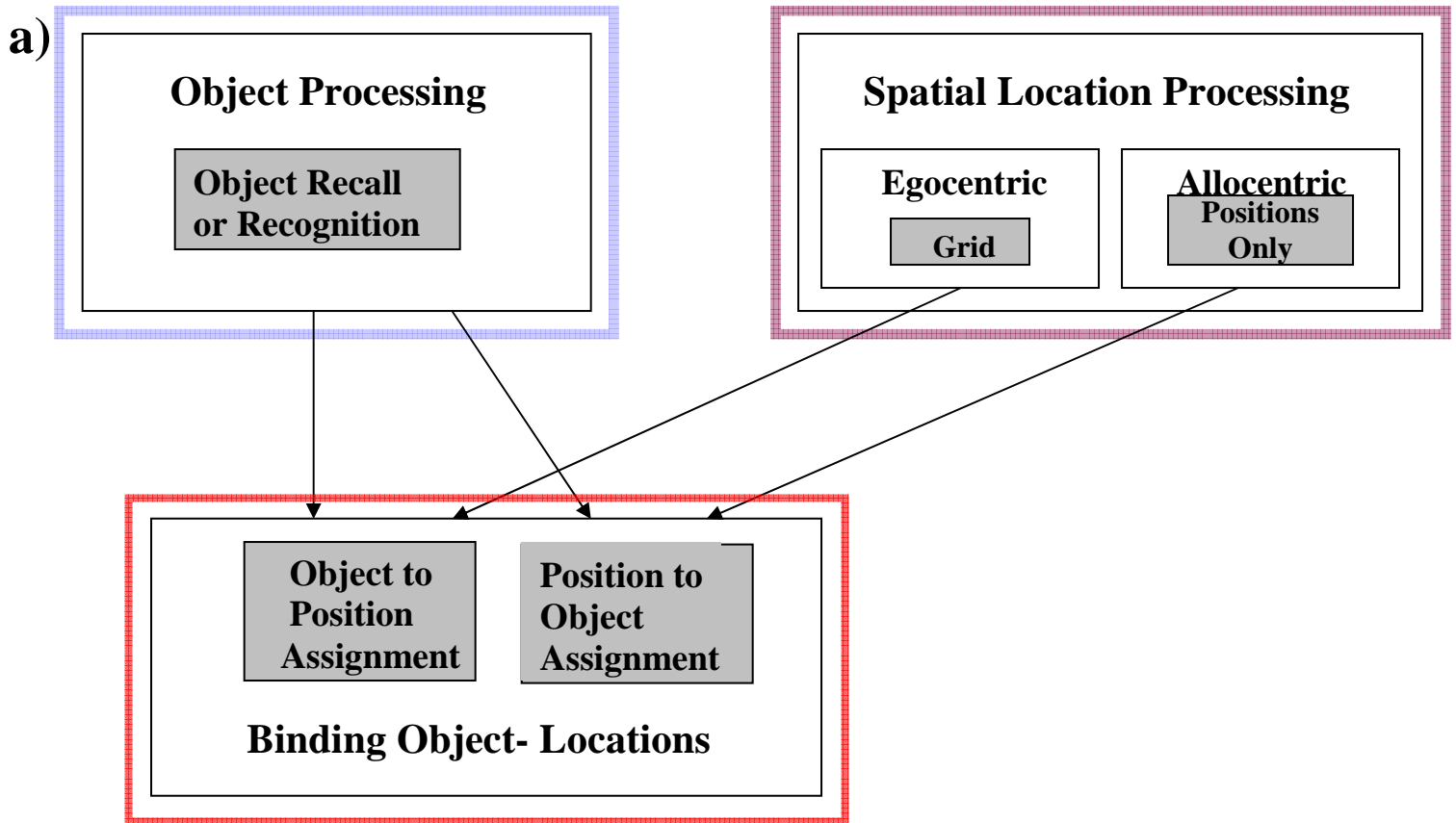
preparation for the next trial. Increases in theta have been reported in relation to error-related negativity (ERN – e.g. Trujillo & Alien, 2007) but such widespread increases are not seen in the literature. Furthermore, accuracy was high for these probes with no significant difference for Object Probes so such increases are unlikely to be linked to error checking. The suppression of rhythmic activity in the alpha and beta bands may be indicative of object processing and has previously been correlated with cortical activation during sensorimotor and language tasks using scalp electroencephalogram (Toro *et al.*,

1994) and subdural ECoG recordings (Crone *et al.*, 1994), as well as in basal temporal cortices during the picture naming tasks (Pfurtscheller & Aranibar, 1977; Pfurtscheller & Klimesch, 1991; Crone *et al.*, 1994; Hart *et al.*, 1998). Further investigation is necessary but this spectral difference provides stark evidence of processing differences between the tasks.

The aim of this study was to examine the neural substrates mediating object and location processing. Although early evidence suggested a functional segregation into two major, anatomically distinct pathways (Ungerleider & Mishkin, 1982; Haxby *et al.*, 1991, 1994; Kohler *et al.*, 1995; Clark *et al.*, 1996; Courtney *et al.*, 1996; Belger *et al.*, 1998), this study has found both dissociations and interactions between these streams. As predicted, the frontal cortex was identified as a possible site for object-location binding, and (along with the more unexpected involvement of the superior temporal/temporoparietal junction), it was found to be active for both location and object processing as well as paired stimulus processing.

There has been a notable absence of hippocampal involvement in this study and this must be addressed. As no changes in viewpoint occurred, participants may have retained object-location bindings in viewer-centered coordinates, a process that may be more dependent on prefrontal and posterior parietal cortices (Constantinidis & Wang, 2004; Curtis, 2006) than MTL structures (Hannula & Ranganath, 2008). The involvement of the PHG, however, suggests that a more allocentric localising process may have been used for the location recognition trials, as discussed earlier.

Taking the findings of this study, we can return to Figure 7.1 and adapt that model based on task demands. Figure 7.25 shows a new version of Postma, Kessels and van Asselen's (2004) model of interaction between the visual processing streams.



b)

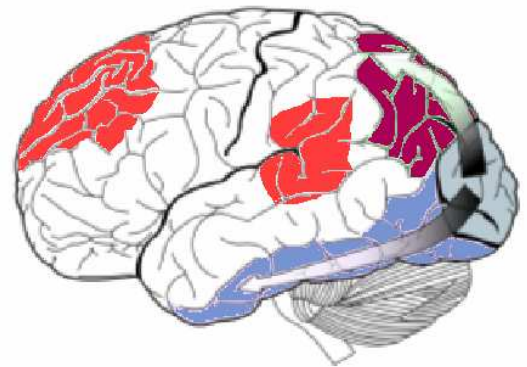


Figure 7.25 a) A revised functional analysis of object-location memory based on Postma, Kessels and van Asselen (2004). See Figure 7.1 for details. **b)** Propagation of the ventral (what) and dorsal (where) streams from primary visual cortex (shown in blue and purple respectively) along with proposed binding areas (shown in red)

The results of this study suggest that the tasks of ‘what goes here?’ (object memory) and ‘where does this go?’ (location memory) are dissociable both at the behavioural and electrophysiological levels. For the latter task, earlier recruitment of frontal areas aided by medial temporal structures and quicker access to (possibly

allocentric) mental representations seem to benefit decisions on location. However, attention-based rehearsal probably plays a role in aiding location recognition. As predicted, the presentation of correct cues benefited subsequent probe recognition as evidenced by the performance data and the ERP differences. The importance of consistency in the relationship between objects and their locations was also shown in the behavioural results for the paired stimuli, where performance was significantly better for congruent vs. incongruent pairs (i.e. CC and II pairs vs. CI and IC pairs – Figure 7.5). Correctly pairing the stimuli removed behavioural differences between object and location responding and resulted in a network of activation which was also identified as common across both of the cued stimuli, leading to the conclusion that the frontal lobes and DLPFC, along with the temporoparietal junction, play a part in binding viewer-centered objects and locations.

The complex binding elements involved in object-location memory directly connect it to episodic memory, i.e. memory for personal events (King *et al.*, 2004). With this in mind the general discussion will aim to seat the findings of this, and previous chapters into a more general memory context.

8

Chapter VIII General Discussion

8.1 Overview of findings

In this thesis I began by assessing the recruitment of and interaction between different spatial reference frames. To date, there have been very few studies which looked at translational processes in spatial representation, especially using EEG. This dearth of research has meant that very little is known about the temporal aspects of spatial representation, and to my knowledge, no electrophysiological markers differentiating representational formats have ever been reported. In the initial experimental chapter we aimed to address this, examining ego- and allocentric recruitment using ERPs as well as behavioural measures. We found that participants responded slower and less accurately when asked about object-locations from a rotated viewpoint compared to an egocentric viewpoint. As well as stark behavioural differences across viewpoints, it was shown that performance on the Spatial Grid Task was associated with amplitude differences in the P300, where exposure to rotated views resulted in increased parietal activity which was indexed to different cortical structures when compared to egocentric-related activity. Medial temporal involvement was found for rotated ‘allocentric’ viewpoints. It was suggested (in Chapter 3) that recruitment of a reference frame occurs quite early on (~200ms) and that ego-/allocentric translations occur prior to 400ms when differences in the waveforms begin to emerge. This time frame posits that translational processes begin well before categorisation processes. Additional to possible representational differences, oscillations in the P300 (driven by cingulate-generated theta) were also found for correct locations, and were discussed in relation to the old/new effect.

Following these behavioural and electrophysiological differences, an attempt was made to explain the qualitative and quantitative differences involved in spatial representations. In Chapter 4 we aimed to rule out the possibility of a detrimental effect

of not showing transitions between viewpoints on the ecological validity of the task. Issues such as the influence of possible intrinsic, environmental symmetry cues on performance were also assessed (Appendix 3). In Chapter 5 we attempted to rule out more contentious issues such as scene recognition confounds and training effects by manipulating the information available at encoding with different training regimes. Although this led to difficulties by blurring the lines between ego- and allocentric exposures, it did provide some evidence for the existence of viewpoint-independent representations. This chapter also provided evidence against the use of mental rotation on the task. These results were discussed in detail in the various chapters and they are collated below (see Section 8.2) in a dual-route ‘strategy-based’ model of spatial representation which includes some explanation of translational processes.

The latter Chapters (6 & 7) aimed to assess the interaction of spatial and object memory both implicitly and explicitly. In Chapter 6, location was found to significantly affect response times for object recognition, a finding that was mirrored in the related P300, suggesting that spatial evaluation can exhibit an early (and implicit) influence on object recognition. Interesting ERP differences were also found across sex, suggestive of implicit differences in the encoding of spatial information, where females may rely more on categorical and males on coordinate-type relations. The final experimental study (Chapter 7) was designed to examine the interaction of spatial and object memory in the brain, with the continuing aim of elucidating the temporal qualities of their relationship. Here we found faster response times to cued locations (compared to cued objects), again suggestive of the primacy of spatial processing. This was accompanied by earlier peaking frontal P2 components and centro-parietal P300s for the location evaluations. Dipole models relating to locations and objects were dissociable across the visual streams with

the relationship seemingly dependent on the directionality of the question. That is, the location-loaded question ‘where does this go?’ seemed to engage dorsal areas while the object-loaded question ‘what goes here?’ engaged the ventral stream. There were also areas of convergence across these tasks, in medial frontal and temporoparietal regions, two areas with growing support for a role in information-binding. Their involvement was found circa 300ms giving a temporal dimension to this complex process. Theta was also found to increase in these areas during this time. Additionally, large spectral increases and decreases were found to differentiate the brain activity related to locations and objects. The interaction of content and context in the brain will be discussed further in section 8.3 and 8.4 below.

8.2 Egocentric/allocentric dissociations and interactions

The idea of separate and fully dissociable systems of representation has, in recent years come under scrutiny (Burgess, 2006, Mou *et al.* 2004). A main objective of this thesis was to assess the validity of separate ego- and allocentric reference frames. To this end, spatial memory processes were investigated on a small computerised spatial array, without the influence of proprioception or vestibular signals. The Spatial Grid Task allowed for manipulations of viewpoint, which a number of previous (viewpoint-dependent) studies have shown is an effective way to test differences in egocentric/allocentric representations (e.g. Christou & Bulthoff, 1999; Feigenbaum, Polkey & Morris, 1996; King, Burgess, Hartley, Vargha-Khadem & O'Keefe, 2002; Johnsrude *et al.*, 1999; Milner, Johnsrude & Crane, 1997; Owen, Milner, Petrides & Evans, 1996).

In addition to behavioural differences, Chapter 3 found electrophysiological fluctuations (concentrated in a parietal P300) that were related to the manipulation of viewpoint. The differences existed between the 0° egocentric viewpoint and the rotated novel viewpoints. Furthermore, the differences were maintained after controlling for task difficulty. As the behavioural data from the rotated viewpoints suggested that mental rotation was not being used as a strategy, and in line with previous studies, we posited that an allocentric strategy was being implemented for the novel viewpoints. This would require translation to and from transient egocentric frames of reference (Burgess, 2006; Burgess *et al.*, 2001; Roche *et al.*, 2005). With three processes possibly underlying the summated parietal activity, an analysis of the modelled generators of the P300 was undertaken to differentiate spatial processing. Frontal, parietal and temporal sources were

seen for all viewpoints but a medial temporal (i.e. parahippocampal) contribution was found to be unique to the novel viewpoints.

However, some difficulties arose when interpreting the results of Chapter 3 and this led to the conducting of a number of control experiments which became Chapters 4 & 5 of the thesis. In Chapter 4 we tested whether the presentation method used in Chapter 3 (i.e. instantaneous transitions between viewpoints during the test block) had affected performance and reduced the ecological validity of our results. It was found that performance across the viewpoints was similar regardless of the presence of external cues or transitions. The effects of the orthogonal axes (and possible intrinsic axes) within the array were assessed with a Circular Grid Task. In this experiment (detailed in Appendix 3), the behavioural difference between studied vs. rotated viewpoints observed in Chapters 3 and 4 was maintained which suggested that the use of the square grid did not result in a beneficial orthogonality effect for rotated views. By removing the opportunity for scene recognition and altering the exposure to viewpoints at training, Chapter 5 provided evidence that the behavioural differences seen in the previous chapters were not the result of scene recognition. In addition to this, we demonstrated the construction of a viewpoint-independent representation which showed no ‘default view’ for a group of participants who received exposure to all viewpoints at training. Furthermore, a comparison of reaction times between this group and a group which was trained with a default view found that mental rotation back to a default viewpoint was an unlikely strategy for the Spatial Grid Task.

Below, we aim to incorporate the modelling and temporal evidence from the ERP data of Chapter 3 into a model of spatial memory that emphasises differential but interacting strategies. We use the model of Roche *et al.* (2005) as a template.

8.2.1 A Dual-Route Model of Spatial Memory

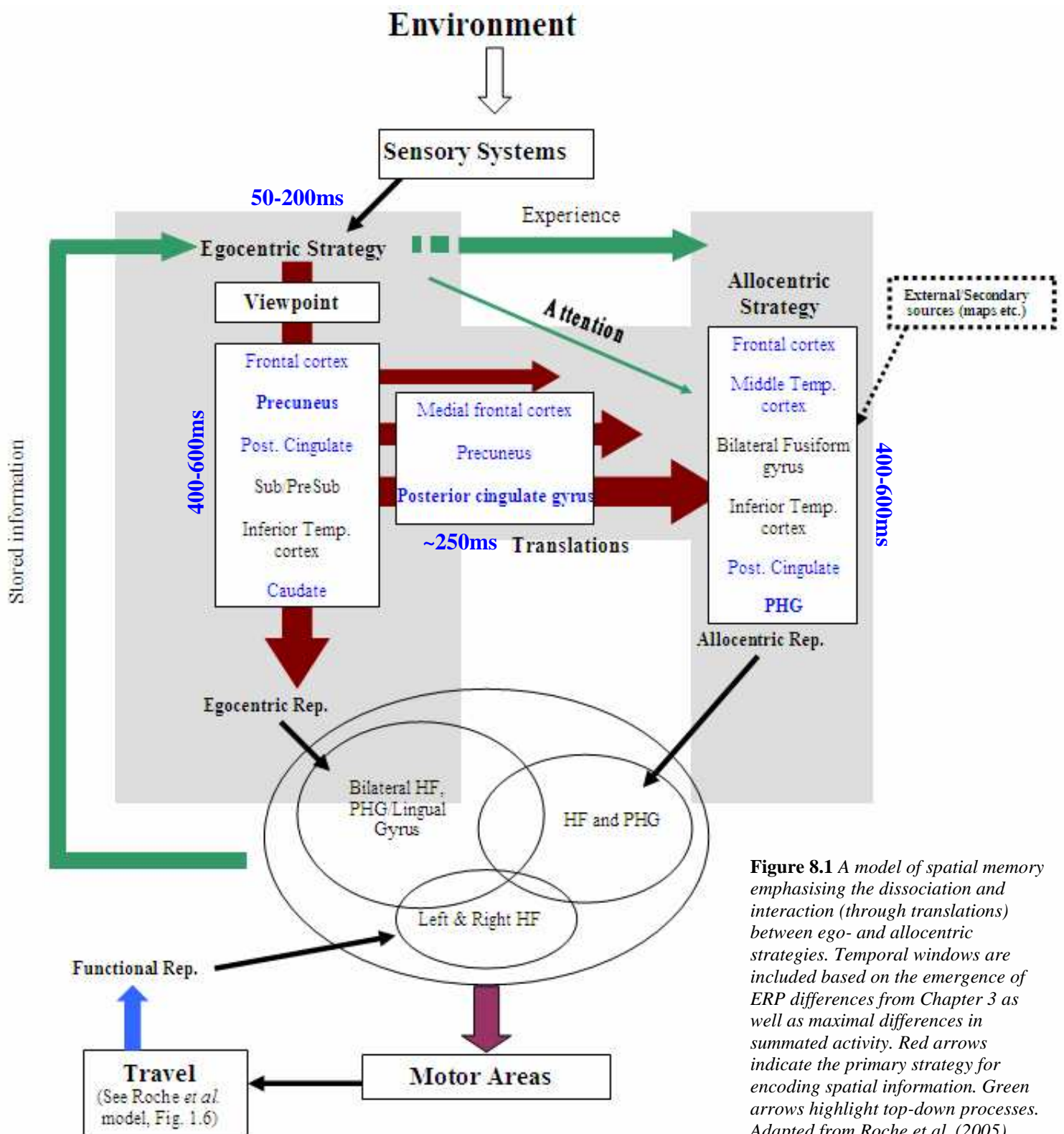


Figure 8.1 A model of spatial memory emphasising the dissociation and interaction (through translations) between ego- and allocentric strategies. Temporal windows are included based on the emergence of ERP differences from Chapter 3 as well as maximal differences in summated activity. Red arrows indicate the primary strategy for encoding spatial information. Green arrows highlight top-down processes. Adapted from Roche et al. (2005).

Based on the template of Roche *et al.* (2005), Figure 8.1 shows a model of ego- and allocentric interaction. However, where their model (see Figure 1.6) outlined the possible structures involved in spatial navigational processes during travel, the model below summarises the anatomical structures (suggested primarily by Chapter 3 of this thesis) possibly involved in the processing of spatial information from alternate (but stationary) viewpoints. In addition to findings from this thesis, parts of the model are suggested based on other relevant literature which is described below. Temporal windows have been applied to the model based on when ERP differences began to emerge and when they were maximal between viewpoints.

Sensory Systems

As can be seen, the model is egocentrically-driven⁵, with an egocentric strategy posited as the most direct encoding route between the environment and spatial memory (provided there are reliable proximal cues or ‘route-based information’). However, before strategy selection begins, sensory information must be integrated. Bottom-up information activates the visual streams which have been primed by top-down information (not shown), examples of which include head-direction information (from presubiculum; Taube, Muller & Ranck, 1990) and motor planning and movement (from frontal, sensory and motor cortices – Marois, 2002). The multiple egocentric inputs from our senses are likely integrated in parietal cortex using a top-down process⁶.

⁵ Everything is encoded egocentrically in a bottom-up manner (at the very initial stages) as perception is person-centred (Burgess, 2006), therefore input to and output from allocentric systems are mediated by transient egocentric representations due to the egocentric nature of perception and imagery.

⁶ Mechanisms for egocentric integration are suggested by “gain field” responses of neurons recorded in posterior parietal area 7a in primates (Andersen *et al.* 1987; Zipser & Andersen 1988; Pouget & Sejnowski 1997; Snyder *et al.* 1998; Deneve *et al.* 2001).

Egocentric Strategy

After the integration of information in parietal areas, processing is posited to continue in a person-centred manner. Rather than suggesting an innate grounding for egocentric processing, this ‘default strategy’ is likely a result of our use of the English language (Haun *et al.*, 2006) which mainly uses a relative, viewpoint-dependent frame of reference (with terms like front, back, left and right). Indeed it is likely that *allocentric encoding* is the native tendency in our species as there is a clear inherited bias for this spatial strategy in the great apes (Haun *et al.*, 2006a; 2006b; Gentner, 2007).

Transitional processes

Looking at the interaction between the ego- and allocentric strategies, the main transitional processes proposed in the model (three red horizontal arrows) are adopted from Roche *et al.* (2005), who state that ‘the successive gathering of route-based information leads to a sophisticated allocentric spatial construct being incrementally generated containing survey-based knowledge’ (p. 632). However in the current model, underlying structures possibly involved in this process are tentatively identified. These translations are posited to be mediated by superior parietal and posterior cingulate areas (Chapter 3). In addition to this, two top-down processes (green arrows) are suggested which may enhance translation or trigger the early adoption of an allocentric strategy, leading to a more allocentric representation. Hemifield effects, manifest as a lateralised P1 (Chapter 3) may be a part of the top-down ‘knowledge of orientation’ information that we use for selecting a strategy. Medial frontal and anterior cingulate involvement in strategy-switching seems more likely, being localised during landmark presentations, with the P1 likely associated with hemifield effects (Chapter 3). Studies of rats’ spatial

behaviour show that although they can be guided by ego- and allocentric strategies (White & Wise, 1999), the distinct neural systems underlying such strategies can also interact competitively or synergistically (Kim & Ragozzino, 2005) possibly similar to the interaction in human spatial systems (Burgess, 2006). Converging evidence suggests that regions of the frontal cortex are central in coordinating multiple memory systems (e.g. Ragozzino *et al.*, 1999; Rich & Shapiro, 2007; 2009).

Allocentric Strategy

As mentioned above, a number of extrinsic and intrinsic factors are posited to encourage the use of an allocentric strategy. For example, the degree of allocentric translation (posterior cingulate cortex) is posited to be dependent on attentional processes (frontal and parietal cortex) and prior experience of the environment (medial temporal cortex) as well as geocentric landmark information (parahippocampus).

Mental Representation

The anatomical correlates of actual mental representation (represented by the Venn diagram) have been left unchanged as there is overwhelming support for the involvement of these medial temporal structures in spatial memory (see Table 1.1; and Roche *et al.*, 2005). The question is also raised as to how useful (and valid) it is making distinctions at this level, when all representations seem to rely on the same medial temporal areas. Indeed, terming a representation as ‘allocentric’ or ‘egocentric’ only informs others as to the qualitative aspects of the spatial memory (qualities determined by the spatial strategies adopted at encoding, and ones which can only be tested via additional retrieval strategies).

Indeed, although much of the neurophysiological evidence that comes from animal studies is supportive of a separate egocentric representation (head direction cells; Taube, Muller & Ranck, 1990) and allocentric representation (place cells; O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978; and grid cells; Hafting *et al.*, 2005), the discovery of these specialised cells could more appropriately support separate strategies – these cells fire in novel as well as familiar environments based on visual cues and geocentric boundary properties – so it is likely they are involved in creating (and accessing) stored representations rather than being evidence of the representations themselves. Developmental evidence also supports the idea that the distinction be made between strategies, rather than representations. Various studies have revealed a clear transition between 18 and 24 months with regard to spatial ability and suggest the emergence of place learning occurs around age 2 (Sluzenski *et al.*, 2003). Although cue learning (Rieser, 1979) and dead reckoning (McKenzie, Day & Ihlen, 1984) are both available in the first 6 months of life, evidence suggests response learning dominates during this stage (Campos *et al.*, 2000; Clearfield, 2001; Newcombe & Huttenlocher, 2000; Newcombe & Sluzenski, 2004). As human hippocampal maturation continues until about this age (Kretschmann *et al.*, 1986; Seress, 1992), anatomical data would suggest that changes in the hippocampus occur in parallel with this behavioural shift. However a causal relationship cannot be established as increased mobility and exploratory behaviour at age 2 and above may lead to plasticity changes in the hippocampus rather than the other way around. Another factor, the development of language, may also mediate these plasticity changes and lead to the emergence of an allocentric spatial strategy. Then again, perhaps more excitingly, this relationship may possibly be reversed, where it is the

development of allocentric processing that predates language acquisition. A distinction between strategies allows more inference to be made in this regard.

Rather than thinking of the cognitive map as multiple integrated representations, it may be more useful to conceive of spatial memory as a distributed cortical representation with qualitative differences dependent on encoding and retrieval strategies (i.e. strategies which are determined by information available and task demands). Rather than a dichotomous relationship, the strategies are posited to be combinative and cooperative as suggested by previous work (Sholl & Nolin, 1997; Wang & Brockmole, 2003; Mou *et al.*, 2004; Waller & Hodgson, 2006; Cheng, 2005; Burgess, 2006; Byrne *et al.*, 2007; Burgess, 2008) and also by results in this thesis (Chapters 3 & 4).

8.2.2 *Testing the model*

There are a number of ways to test if our internal representation of space is encoded and accessed by differential strategies. A re-interpretation of former investigations of selective brain damage could form the basis of any such investigation. For example, the results of both the Teng and Squire (1999) study and the Maguire *et al.* (2006) study downgraded the importance of medial temporal areas in spatial memory. This could be evidence for a dual-route model where egocentric (or rerouted allocentric) strategies are compensating for the damage to medial temporal areas. It was posited that through repeated exposure to his house (over years) and his locomotion between the rooms, HM built an allocentric representation of his house enabling his topographic recall (Corkin *et al.*, 2002). If the hippocampus is the site of topographical information storage then this would seem impossible. Instead, the MTL regions may be specialised at extracting object-to-object relations (and other complex associations) used in an allocentric strategy.

Allocentric encoding would then be very difficult, but not impossible, without hippocampal involvement. These studies (discussed in section 1.3.2) also suggest a more distributed storage of remote spatial memory.

Another novel way of mediating participants' spatial representations was introduced in Chapter 5. In that chapter differential training regimes were administered to show a dissociation in spatial representation. One could also interpret this as a difference in representational quality due to a dissociation in strategy. As it has been posited that an allocentric representation emerges from successive exposure to an environment from a variety of egocentric viewpoints (Burgess *et al.*, 2001; Roche *et al.*, 2005), it stands to reason that experience is both quantitatively (e.g. level of exposure) as well as qualitatively (e.g. person-centred vs. object-centred) different for ego- and allocentric representations. The qualitative difference has readily been assessed in experiments which manipulate information-type (route vs. survey) during training (see section 1.2.1). The influence of quantitative experience has however proven to be a difficult variable to manipulate. Giving a participant additional exposure to a spatial array obviously introduces training effects, but keeping the level of exposure the same across ego- and allocentric training regimes (as was the case in Chapter 5) introduces problems with memory load (where an allocentric training condition involves multiple perspectives over the same number of trials) and can only show a qualitative difference. Therefore, the confounding exposure effects may be the essence of the ecological difference between representations. A re-analysis of the behavioural data from Chapter 3, which compared how performance changed over the test block (see Appendix 5), revealed that as participants completed more trials they became faster and more accurate. Again, concluding that this is an allocentric-type 'experience effect' is difficult as an exposure

effect (i.e. exposure to all viewpoints increased over the course of the test) may be fundamentally responsible.

Yet another way of testing representational differences involves manipulating attention. The role of attention in the model is assumed to encourage the adoption of an allocentric strategy. This assumption is based on the possibility that instructions to attend to particular features of an environment may be categorised as an external source of information which makes object-to-object relations more salient, similar to survey-type information (e.g. maps). But how does attention differ between spatial strategies? Goal-directed attentional processes are likely connected with an egocentric strategy (due to the egocentric nature of endogenous ‘person-centred’ attention). It has been suggested that the dorsal parietal cortex contributes top-down attentional processes guided by retrieval goals (Cabeza, 2008; Cabeza *et al.*, 2008). Conversely, bottom-up attentional processes may encourage the construction of an allocentric viewpoint-independent representation. Reflexive ‘object-centred’ attention elicits MTL activity which is tracked in ventral regions of the parietal cortex (Cabeza, 2008; Cabeza *et al.*, 2008). Manipulating attention to spatial information (with task-irrelevant stimuli) may be a good way to assess the automaticity of spatial coding, and whether this coding is person-centred or object-centred. The above model would predict that encoding and retrieval are egocentric unless the task or environment demands otherwise.

To test if people maintain a default egocentric strategy (with some degree of automatic translations), while reserving the ability to engage in attentional allocentric processing, two potential experiments will be described.

Experiment 1 - The House Party Experiment

In this computerized experiment two groups of participants are shown the activity at a house party from three different vantage points (A, B and C – Figure 8.2). Group 1 is told to listen to the *conversations* between party guests (1-6) from each of the vantage points. Group 2 is told to pay attention to the *locations* of party guests (1-6) and the layout of the house from the same vantage points (while the party guests engage in the same conversations attended to by Group 1). Note, neither group will have access to the house schematic as presented in Figure 8.2. Hence, both groups receive the same visual and auditory information but are given instructions to direct their attention to one (the visual environment) or the other (the auditory conversations) type of information. The test phase consists of several visual snapshots of the house either consistent or inconsistent with the house's actual layout. Snapshots would be presented from the participants' perspective but also from the guests' perspectives. The participants are required to identify 'correct' scenes i.e. scenes in which the geometric relations between walls and doors is consistent with the study phase. In addition to this they are asked questions about more detailed spatial information relating to intra-environment objects and spatial relations.

I would predict, based on my suggestion of dual-routes in spatial memory, that both groups would be accurate and fast when responding to correct and distorted layouts from first-person perspectives. This would rely on the default egocentric processing suggested above. Additionally, Group 1 should show increases in response times when judging views from alternative perspectives (Chapter 3/5), whereas the change in viewpoint would not affect Group 2 to the same extent (Chapter 5). Accuracy is predicted to remain high for both groups on all perspectives, supporting the idea that automatic translations occur (Chapter 6) during encoding that underlie contextual coding in episodic

memory. It is hypothesised that major differences in the encoding strategies will emerge on the questions relating to intra-environment details e.g. ‘Which room contained a fire extinguisher’? or ‘What was on the coffee table’? Group 2, who engaged in an attention-driven allocentric strategy during encoding, is predicted to be superior at this task.

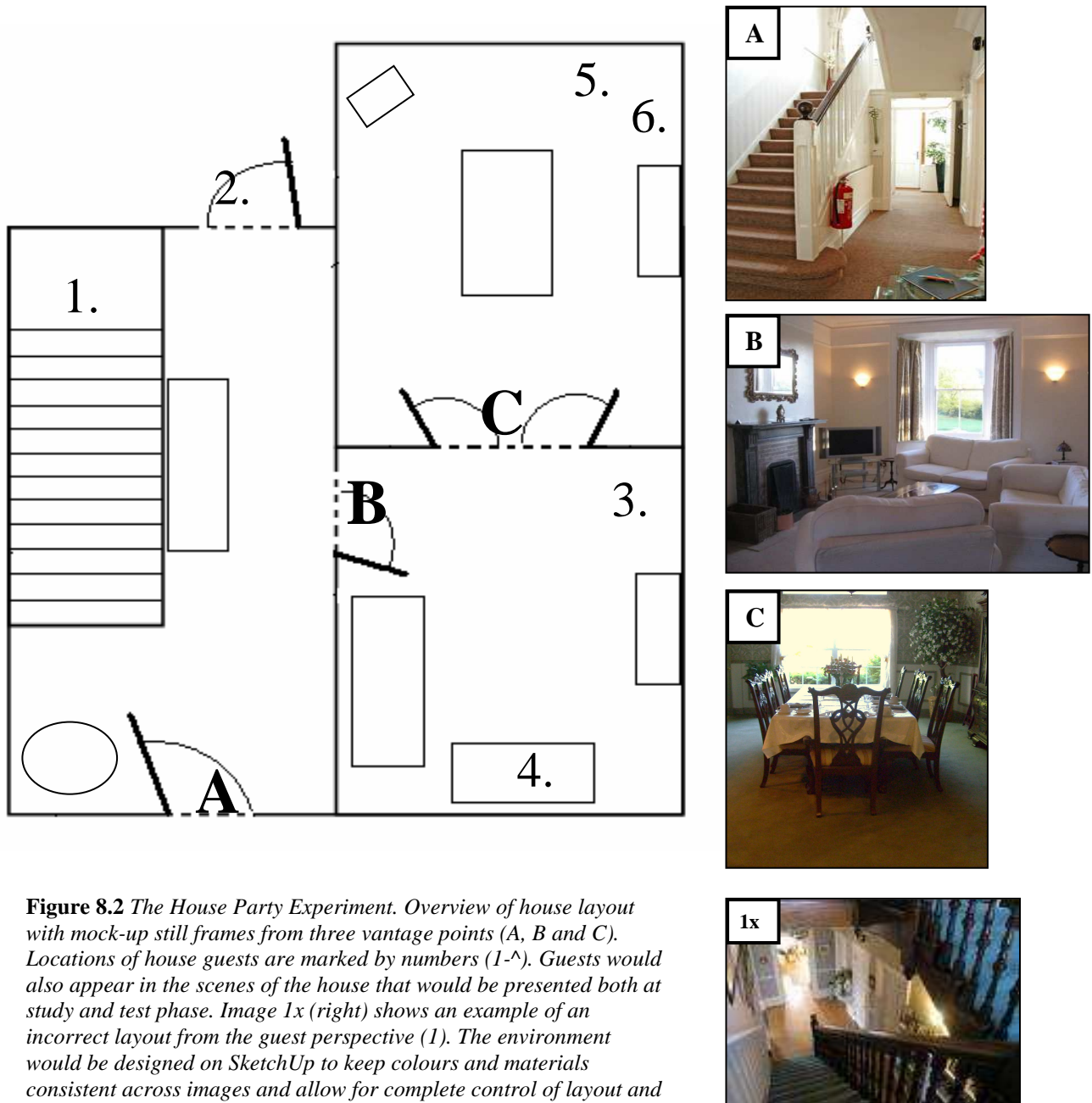


Figure 8.2 *The House Party Experiment. Overview of house layout with mock-up still frames from three vantage points (A, B and C). Locations of house guests are marked by numbers (1-6). Guests would also appear in the scenes of the house that would be presented both at study and test phase. Image 1x (right) shows an example of an incorrect layout from the guest perspective (1). The environment would be designed on SketchUp to keep colours and materials consistent across images and allow for complete control of layout and spatial relations.*

Experiment 2 - Escape the Maze

This experiment may be useful for exploring the influence of goal-directed (top-down) and reflexive (bottom-up) attention on spatial memory. Similar to the experiment above, two groups of participants would be required. Each participant begins at the start of a maze (Figure 8.3) and is required to navigate their way out. Note, that the maze contains no wrong turns or dead ends. Also, neither group will have access to the maze schematic as presented in Figure 8.3. After they have exited the maze they would be asked to recall or map their route of escape. The proposition here is that the goal-directed behaviour of escaping the maze would only require an egocentric strategy. However, during their escape one group would receive salient but task irrelevant cues at turns and junctions (Figure 8.3b) which may recruit reflexive attentional processes that encourage a more allocentric representation of their escape route. It is posited that the group receiving these cues during their time in the maze would subsequently be more accurate at remembering their route of escape (i.e. the layout of the maze). The influence of these cues could also be assessed using free recall to probe object memory.

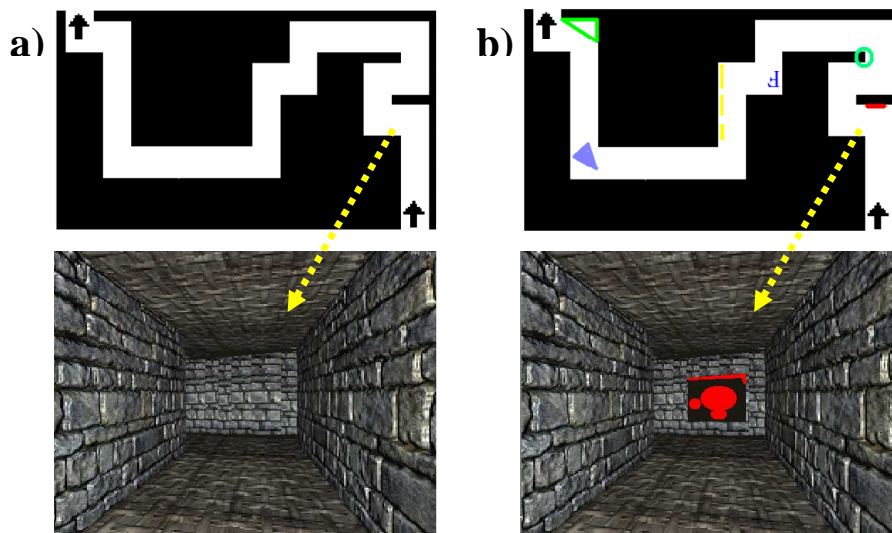


Figure 8.3 Route schematics and still-frames from the *Escape the Maze* experiment. **a)** shows an uncued route through the maze and **b)** shows a cued route which is posited to result in a more allocentric and accurate spatial memory due to bottom-up attentional processes.

To summarise, I am proposing that human spatial cognition is pluralistic: we can typically encode the same external scene in many ways. Humans (and animals) can adopt different frames of reference according to the task and context. Medial frontal and anterior cingulate structures possibly play a role in a rapid strategy-selection process at encoding, dependent on the information available, where egocentric encoding is the dominant and automatised strategy. Translations occurring in posterior cingulate areas (a.k.a. the retrosplenial cortex) operate on superior parietal information to give rise to object-to-object based qualities in the stored representation. Similar dissociations can be seen upon retrieval, again based on the context of the situation.

8.3 Object-location memory

Chapters 6 & 7 both make claims about object-location memory. The main aim of these latter chapters was to gain an understanding of how spatial and object information interacts in the brain, electrophysiologically. This question is based on an earlier hypothesis developed by Ungerleider and Mishkin (1982), who suggested that visual information is processed along parallel ventral and dorsal streams, which are concerned, respectively, with what objects (form, shape etc.) are present and where the objects are located. But the validity of these streams, how they interact and the temporal properties of such an interaction are all still relatively unknown.

With the object recognition test in Chapter 6 we demonstrated that implicitly, spatial information helps to inform categorisation decisions. One suggestion that can be made from this chapter is that spatial processing precedes object processing, evidenced by the reaction time differences, the latency difference in the P300 and the possible presence of a spatially-related P1 (earlier peaking component) for non-conflicting (correctly located) vs. conflicting (incorrectly located) objects. But this does not necessarily suggest a serial process, only that spatial processing may begin prior to object evaluation. Work in visual perception has also revealed that visual processing can be accelerated by spatial attentional processes, with studies showing superior letter detection (Hoffman & Subramaniam, 1995) and more accurate letter identification (Kowler, Anderson, Doshier, & Blaser 1995) at the location of a saccade target shortly before the saccade. Another study suggests that spatial localisation even precedes temporal determination in visual perception (Park, Schlag-Rey & Schlag, 2003).

The findings that locational information removed individual differences in recognition performances (Chapter 6) also seem to suggest that spatial processing is more

instinctive and less variable than object processing. There is some evidence that efficiency in the spatial domain develops earlier in children. Schumann-Hengsteler (1992) used a picture reconstruction task with children aged 5, 8 and 10 years and found age-related differences for object-location memory (matched correct objects to their locations). However, when looking at the number of locations remembered correctly whether or not the correct objects were matched with them, the age effect disappeared. A similar distinction has also been found in adults by Postma and De Haan (1996). A recent study (Leijenhorst *et al.*, 2007) examined developmental trends in object and spatial working memory (WM). Assessing 4 age groups (6–7, 9–10, 11–12, 18–26), the authors concluded that spatial WM task performance reached adult levels before object WM task performance, supporting previous claims (e.g. Hamilton *et al.*, 2003; Logie & Pearson, 1997; Pickering *et al.*, 2001). There is also evidence that this efficiency difference results from an evolutionary bias. It has been shown that infants initially track by location rather than by object features (Newcombe & Huttenlocher, 2000), and we share this initial location bias with apes (Haun *et al.*, 2006).

The results from Chapter 7 also suggest a temporal difference in processing across the dorsal and ventral streams. This chapter reported an experiment that investigated how the ‘where’ and the ‘what’ pathways interact. By evaluating and comparing the relative efficiency of retrieval in two directions [‘what goes here?’ and ‘where does this go?’] this experiment gives an indication of processing times in the visual streams. Locations were recognised significantly faster than objects. Moreover, as well as amplitude differences, a latency difference was also seen in the ERP components where the P300 related to location probes peaked earlier than that for objects. Previous results predicted that the two directions were either equally efficient (e.g., Nissen, 1985;

Johnson *et al.*, 2002) or that from-where-to-what retrieval is faster than from-what-to-where retrieval (e.g., O'Reilly & Munakata, 2000). Quite surprisingly, our results contradicted both predictions.

In a recent study investigating processing speeds along the ventral and dorsal streams, retrieval from-what-to-where was found to be faster than the retrieval from-where-to-what (Wang, Johnson & Bao, 2005) supporting the behavioural findings from Chapter 7. Wang and colleagues concluded that such a finding suggests 'that the link strength from object identity (or other visual features) to its location is stronger than the link strength from object location to its identity'. It seems that an object's location, as an important feature of the object, is readily represented and strongly bound with the object representation. Therefore, given an object, its location can be quite quickly retrieved, as was found in Chapter 7. On the other hand, there may not exist a readily retrievable location representation that links to the object that occupied that location. Such information may have to be computed online when needed, therefore taking longer time (e.g., Hunt & Waller, 1999). The ERP results from this chapter not only index this difference electrophysiologically but also begin to answer more difficult questions relating to object-location integration, identifying possible binding sites for object-location memory. Rather than restate the findings of Chapter 7, where object-location was given an ample discussion, a more general discussion of content and context will follow.

8.4 Content and context in memory

When people think of memory or knowledge, they usually envision something of substance; a series of images depicting content, a store of descriptive information probed by interrogative determiners, most commonly ‘what’. Indeed, it was this content-driven view of memory that led to many of the ‘memory-store’ theories being developed in an attempt to locate this content. Episodic and semantic memories have had close ties in memory research, falling under the umbrella of declarative memory. But our sensory systems can each be sub-divided into at least two parts, one for perceiving content and the other for perceiving contextual information.

Vision typically dominates spatial processing because visual spatial acuity is more accurate than auditory spatial acuity (King, 2009). When it comes to content and context dissociations in the visual system, we turn to the visual pathways. The existence of a separate dorsal ‘where’ pathway is probably the biggest indication of the importance we place on spatial and motion processing but the ability to localise stimuli has been found with our other senses (e.g. audition - Jeffreys, 1948; touch - Dassonville, 1995; smell - Porter & Sobel, 2005; Porter *et al.*, 2007; taste - Lim & Green, 2008). In reviewing our means of sensory perception, we see the brain as being specialised in coding spatial contextual information that is separate from content. The question again returns to interactional and combinative processes; specifically, how is spatial information combined in experience to create cohesive memories and why is it processed separately in the brain to begin with? Could it be possible that a specialised spatial system, or more likely, a *spatiotemporal* system, has developed to exploit the 4-dimensions of the physical world in order to bind objects and events and create a stable percept for self-consciousness?

The idea of a spatiotemporal ‘glue’ in memory is merely an extension of previous theories of hippocampal involvement in episodic memory (Redish, 1999; Burgess *et al.*, 2001a; Burgess, 2002; Burgess & O’Keefe, 2002; Hartley & Burgess, 2002). Here it is suggested that areas additional to the hippocampus may be involved in such context-to-content binding.

Figure 8.4 is based on the results from Chapter 7 and summarises the partially distinct pathways engaged during location-to-object and object-to-location processing, with areas specifically involved in the binding process shown as common across both tasks. These are the areas that also overlap with the processing of the paired stimuli. These findings agree with findings on episodic memory (e.g. Burgess, *et al.*, 2001b; Cabeza, 2008; Cabeza & Nyberg, 2000; Svoboda *et al.*, 2006). Although most research now assesses the role of medial temporal structures in episodic memory, the literature linking the frontal cortex to episodic memory is extensive (see Stevens & Grady, 2006 for review) and there are suggestions that episodic memory engages both frontal and temporal areas (Cabeza & Nyberg, 2000). More recent evidence from a study by Söderlund *et al.* (2007) showed both cued recall and recognition were significantly impaired in patients with frontotemporal degeneration. Lateral parietal activation in autobiographical memory tends to be centred around the temporoparietal junction (reviewed in Svoboda *et al.*, 2006). Wheeler and Buckner (2004) found greater activity in this region and in ventral parietal areas for items that participants classified as recollected than for items classified as familiar. Every episodic memory has a spatial element, providing the location and surrounds into which the events we experience sit. The frontal and temporal areas identified in Chapter 7 may perhaps play a greater role in the binding of content to context in episodic memory than had previously been supposed.

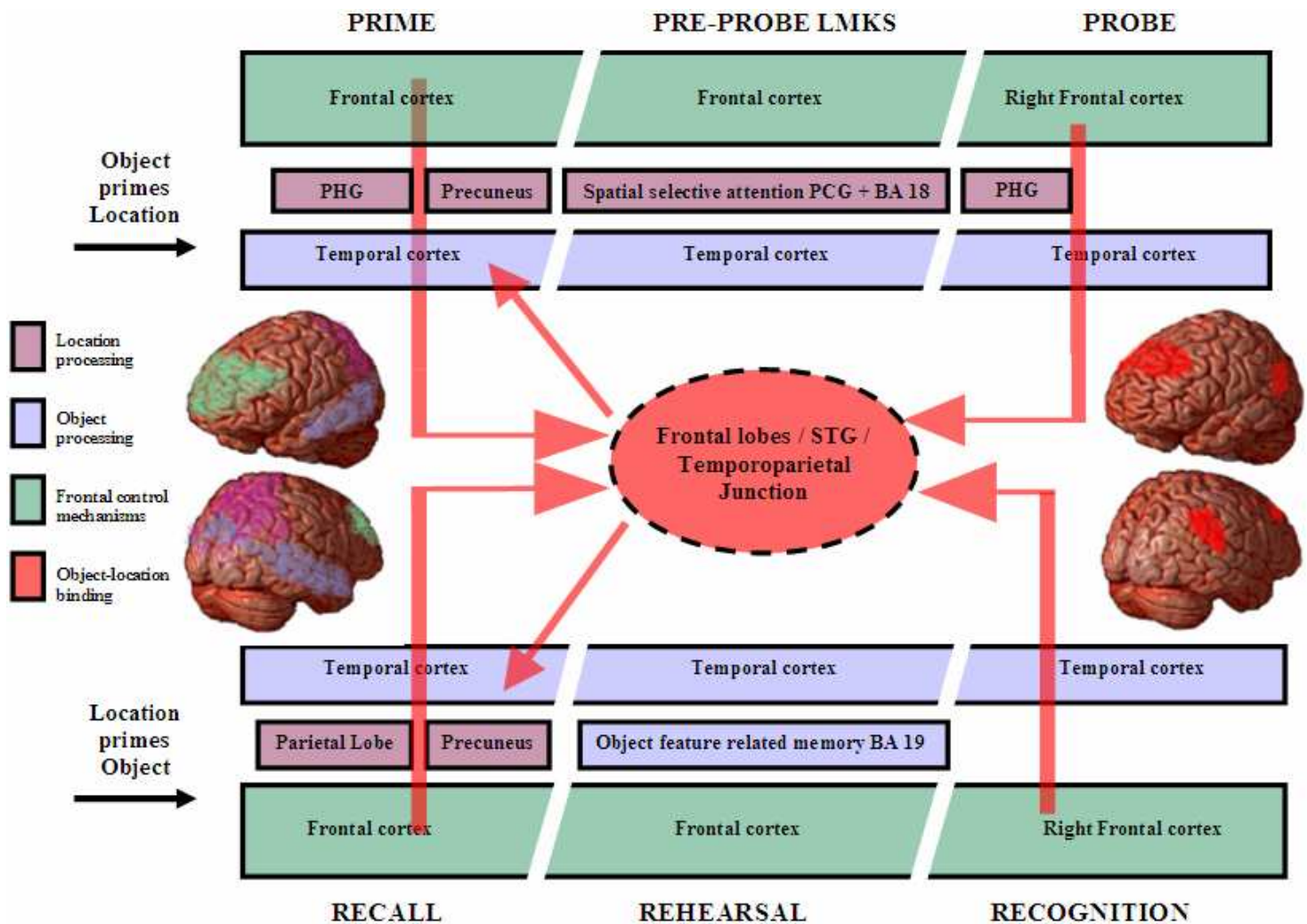


Figure 8.4 A box-and-arrow flow diagram detailing the distinct and common brain areas involved in spatial and object memory. Time moves from left to right with the stimulus type shown at the top of the diagram and the related task demands posited to be involved shown at the bottom. The processes posited to be involved are colour coded with a legend to the left of the diagram. The top set of boxes show the areas involved in spatial memory i.e. deciding ‘where does this go?’ The bottom set of boxes list the brain areas involved in object memory i.e. deciding ‘what goes here?’ The brain areas common to both tasks are shown in the middle and are posited to be crucial for binding processes.

Indeed, a greater role for these areas has been espoused by proponents of another network. The Default Network is a recently proposed brain system (Raichle *et al.*, 2001; Gusnard & Raichle, 2001; Gusnard *et al.*, 2001), engaged when individuals are left to think to themselves undisturbed (Shulman *et al.*, 1997; Mazoyer *et al.*, 2001; Raichle *et al.*, 2001) but also activated by diverse forms of tasks that require mental simulation of alternative perspectives or imagined scenes (see Figure 8.5). The relevance of the default network to spatial processing and memory can be seen firstly through anatomical

similarities and secondly through its suggested role in information-binding (Hassabis & Maguire, 2007; Hassabis *et al.* 2007). The default network contains a set of interacting brain areas that are tightly functionally connected and which overlap heavily with areas identified in this thesis including: the dorsal and ventromedial prefrontal cortex, the posterior cingulate/retrosplenial cortex, the inferior parietal lobule, the lateral temporal cortex and the hippocampal formation.

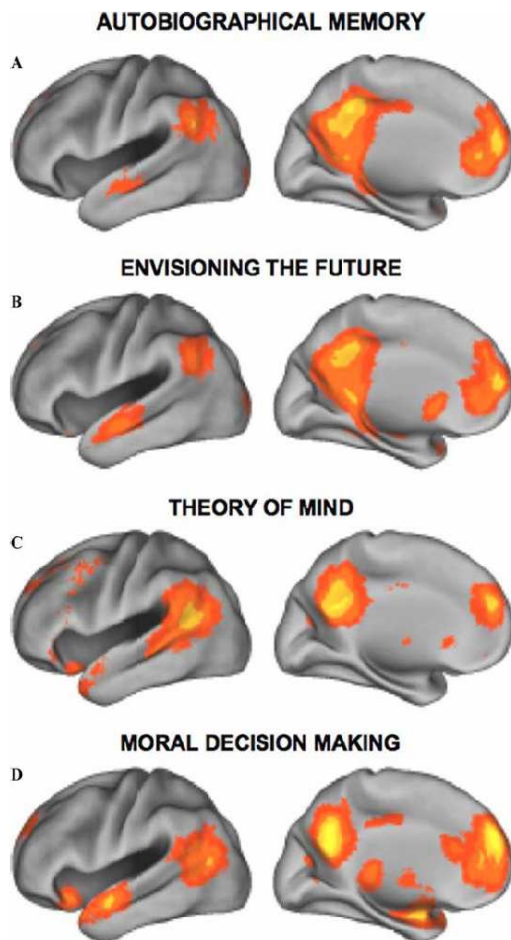
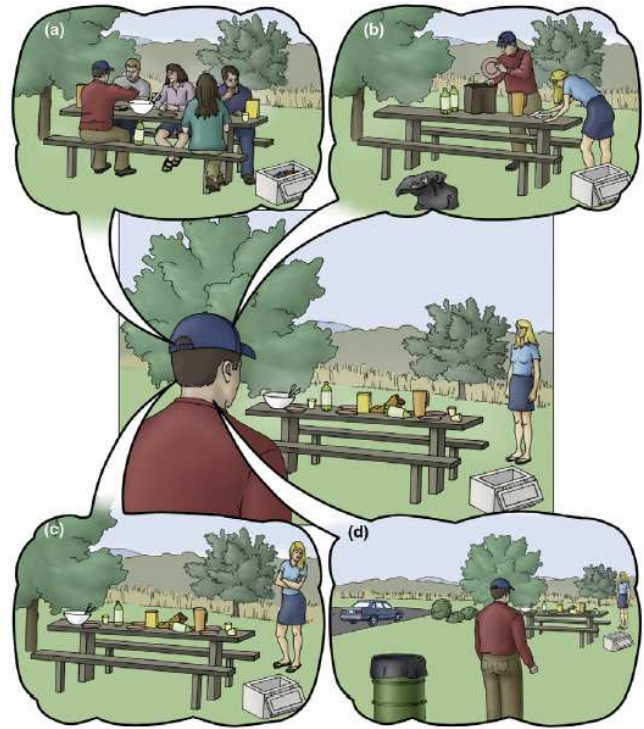


Figure 8.5 (A) Autobiographical memory: subjects recount a specific, past event from memory. (B) Envisioning the future: cued with an item (e.g., dress), subjects imagine a specific future event involving that item. (C) Theory of mind: subjects answer questions that require them to conceive of the perspective (belief) of another person. (D) Moral decision making: subjects decide upon a personal moral dilemma. Reproduced from Buckner, Andrews-Hanna and Schacter (2008). Data in A and B are from Addis *et al.* (2007). Data in C uses the paradigm of Saxe and Kanwisher (2003). Data in D is from Greene *et al.* (2001). Note that all the studies activate strongly PCC/Rsp and dMPFC. Active regions also include those close to IPL and LTC, although further research will be required to determine the exact degree of anatomic overlap. It seems likely that these maps represent multiple, interacting subsystems.

The fact that this network has been reported to be involved in perspective taking, both in terms of temporal perspectives (retrospective and prospective memory) and in social settings (theory of mind) makes it a good candidate network for underlying spatial

perspective taking. In fact, Buckner and Carroll (2007) included spatial perspective taking as a possible form of self-projection (Figure 8.6).

Figure 8.6 *Forms of self-projection. Four forms of self-projection are illustrated to highlight their common reliance on a personal, mental simulation of another time, place or perspective. The scene being experienced is shown in the center and each alternative form of conceived perspective is in a thought bubble. Simulated perspectives include first-person and third-person views. (a) Remembering involves simulating the past, such as the picnic earlier. (b) Prospection involves simulating a possible future event, such as cleaning up the mess. (c) Theory of mind involves conceiving another person's perspective – in this instance, the mental state of the person about to be recruited to help clean. (d) Navigation – or topographic orientation – involves simulating another view or mapping the environment, such as a mental map of the world that surrounds the picnic area, including the location of the nearest trash bin. All these abilities depend on a shift from the present perspective to a simulated model of an alternative world. Reproduced from Buckner and Carroll (2007)*



In a recent study which assessed system overlap, Spreng, Mar and Kim (2009) conducted four separate quantitative meta-analyses of neuroimaging studies on: (a) autobiographical memory, (b) navigation, (c) theory of mind, and (d) default mode. The results demonstrated a high degree of correspondence which was maintained in a separate analysis that included (e) prospection studies. Across all domains, correspondence was found within the MTL, precuneus, posterior cingulate/retrosplenial cortex, and the temporoparietal junction. The first three of these structures have been identified in this thesis as important for allocentric strategies (MTL), egocentric strategies (precuneus) and translational processes (PCG). I have also suggested the temporoparietal junction, being ideally located between the ‘what’ and ‘where’ streams, is involved in object-location binding. It could be argued then, that it is spatiotemporal processing that facilitates the

retrieval and integration of relevant informational components through the activation of a common network. Perhaps then the default network uses this contextual information during internal mentation to engage in the self-projection tasks described above? Tasks such as remembering, considering hypothetical social interactions, and thinking about one's own future all seem to evince the importance of context. To this end, the interpretation of context by the brain (possibly through a specialised spatial system) emerges as a possible candidate for information-binding and episodic memory formation.

A similar suggestion has been made previously, in an attempt to link spatial context to more general episodic memory. A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events was identified by Burgess, Maguire, Spiers and O'Keefe (2001b). Their network consisted of a continuous temporoparietal strip of activation from parahippocampal cortex to precuneus (similar to Figure 7.19 – top panel), in conjunction with posterior parietal, hippocampal and prefrontal activations. Rather than distinguish between object vs. spatial activations within this network, the authors instead related differential activity to ego- and allocentric contributions (as well as translational processes). Their suggestion that medial temporal activity contributed to the allocentric processing of spatial context while parietal contributions were indicative of egocentric processing is very similar to the conclusions made in Chapter 7, i.e. matching an object to a location involved an egocentric spatial strategy, while matching locations to objects involved a more allocentric strategy (see Figure 7.25).

8.5 Further applications of the Spatial Grid Task

Although alternative experiments are suggested above, the Spatial Grid Task has been shown to be a versatile method of investigating small-scale spatial memory. Both its computerised administration and its flexibility (i.e. the ease in which alterations to the task can be made) permit possible applications beyond spatial memory research. Due to the task's ability to discriminate between behaviours across viewpoints (Chapters 3, 4 and 5) and object placements (Chapters 6 and 7) as well as its ability to identify individual differences by distinguishing between level of performance (e.g. Chapters 3 and 6) and between gender (Chapter 6), it can usefully be applied to a variety of other research and clinical questions. For example, the Spatial Grid Task could be used to assess cognitive domains which are related to or rely on spatial memory capabilities or indeed other mental abilities which may recruit similar frontal, parietal and medial temporal brain systems (e.g. cognitive abilities associated with the Default Network). To this end it could possibly be used to assess brain damage and dysfunction. Without dwelling on possible future applications, I will discuss some areas which may require immediate attention before describing some studies that could further assess spatial memory using the Spatial Grid Task.

8.5.1 *Additional validation studies*

Spatial Intelligence

The Spatial Grid Task remains to be fully validated as a sensitive test of spatial memory by means of correlational analyses with the currently accepted paper-and-pencil tests of spatial ability. This type of concurrent validity is necessary if the task is to be used more

widely in spatial memory research. Standardised tests of spatial ability to which it could be compared to include both recognition tasks such as copying, embedded figure, visual memory, form completion and form rotation tasks, as well as tasks involving manipulation such as block counting, block rotation, paper folding, surface development and perspectives tasks. Correlational analyses may then reveal similarities between performances on the shifted-viewpoint conditions in the Spatial Grid Task and the standardised tasks that require more allocentric processing. Similarly, high performance on the studied viewpoint would be posited to be associated with high scores on tasks requiring egocentric processing. This type of analysis may also help to define the different spatial processes underlying performance on more traditional tests. In addition, a finding of low to no correlation between performance on the Spatial Grid Task and more simple mental rotation tasks would provide further evidence against the suggestion that mental rotation could explain the response time differences across viewpoints in the Spatial Grid Task.

Allocentric representation

Administering the Spatial Grid Task on a patient population with varying neurological damage to assess how performance differs across viewpoints dependent on said damage would be another means of validating the task's ability to differentiate between ego- and allocentric processes. These clinical populations are hard to find in Ireland. Patients with very specific damage to medial temporal (e.g. HM; Corkin *et al.*, 2002) and parietal cortices (e.g. MU; Wilson *et al.*, 2005) and/or localised hippocampal damage like Jon (King *et al.*, 2002; Hartley *et al.*, 2007) or TT (Maguire *et al.*, 2006) are in high demand

and their involvement in a Spatial Grid study would greatly enhance our ability to localise the relevant structures that underlie small-scale spatial memory.

Alternatively, TMS or rTMS could be used on healthy participants to produce cortico-cortical disruptions in superficial cell assemblies and mimic neurological lesions. Effects on spatial processing have been reported over parietal cortex (Formisano *et al.*, 2002; Harris & Miniussi, 2003; Knauff, Kassubek, Mulack & Greenlee, 2000; Sack *et al.*, 2002). Stimulating deeper brain regions requires a high intensity that cannot be achieved by standard transcranial magnetic stimulators. Moreover, even special stimulators, such as the figure-8 coil, with greater power outputs do not allow safe stimulation of much deeper brain sites, as the intensity required could lead to undesirable side-effects induced in more superficial regions (Nadeem *et al.*, 2003). These problems simulating deep brain dysfunction may soon be overcome however. Deep TMS using a newer ‘H-coil’ is purported to produce safe and measurable deep brain effects (Roth *et al.*, 2002). It has been found, at least in one study, to positively affect spatial memory through stimulation of deep portions of the prefrontal cortex (Levkovitz *et al.*, 2007). There are exciting advances being made in TMS technology and possible applications with the Spatial Grid Task are very appealing.

8.5.2 *Variations on a theme*

Pure topographical memory

The studies conducted for this thesis used a Spatial Grid Task which included variances among locations but also amongst the objects presented. Therefore all locational recognition tasks would have required some degree of object segregation, identification and placement, some combination of location and object. The final experimental chapter

attempted to tease apart this relationship and isolate both the locational and object processing demands involved in spatial memory. Again, the ecological utility of locational memory lies in the location's properties, for example, what the location contains. Although this chapter (and indeed the previous chapters) recreated ecologically valid object-location tasks, an investigation into locational memory without object discrimination would be an interesting endeavour. This could easily be studied with some simple alterations to the Spatial Grid Task. A single study object presented in a number of study locations would remove the need for object discrimination. With a larger spatial grid (e.g. 36 squares), these locations could be manipulated in terms of distance and direction from landmarks to further explore relational memory and tap into important contextual parameters necessary for accurate spatial memory (Figure 8.7a & b). Highlighting locations during the test phase rather than presenting the study object (Figure 8.7c & d) would again reduce object processing and provide a discrepancy between study and test which would also discourage scene recognition.

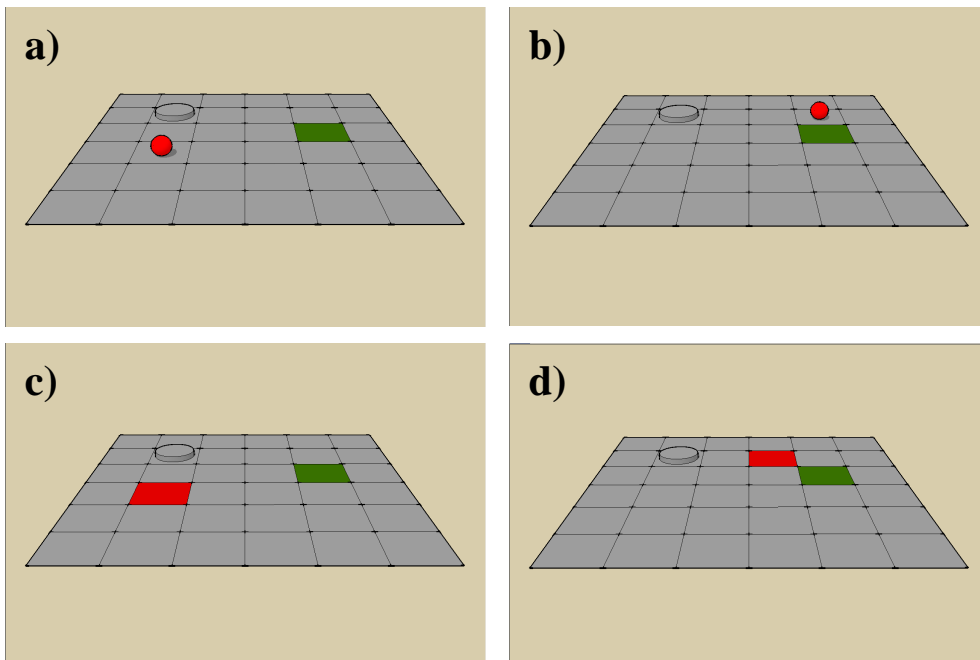


Figure 8.7 A larger 36-square Spatial Grid Task which could assess memory for locations without the object component **a)** A study presentation with a 'ball' object at location x **b)** A study presentation with the same object at location y **c)** A test presentation of correct location x **d)** Presentation of an incorrect test location

Extra-environment and conflicting cues

For the purpose of this thesis the Spatial Grid Task has been presented with intra-environment cues in the absence of an outside environment (i.e. engaging surroundings) in order to restrict cue usage to proximal landmarks. Setting the grid within a more complex environment (Figure 8.8) would allow the use of distal cues and provide an opportunity to compare the benefits of proximal and distal landmarks on small-scale spatial memory. This would also permit investigations into the effects of conflicting intra- and extra-environment cues (e.g. where the grid and intra-environment landmarks are rotated within stationary surroundings). The influence of non-physical cues such as light source position and shadowing could also be assessed in such a scenario. With simple alterations the Spatial Grid Task could be used for a plethora of spatial studies. As such, I believe it has more than met the objective of being a simple and versatile test.

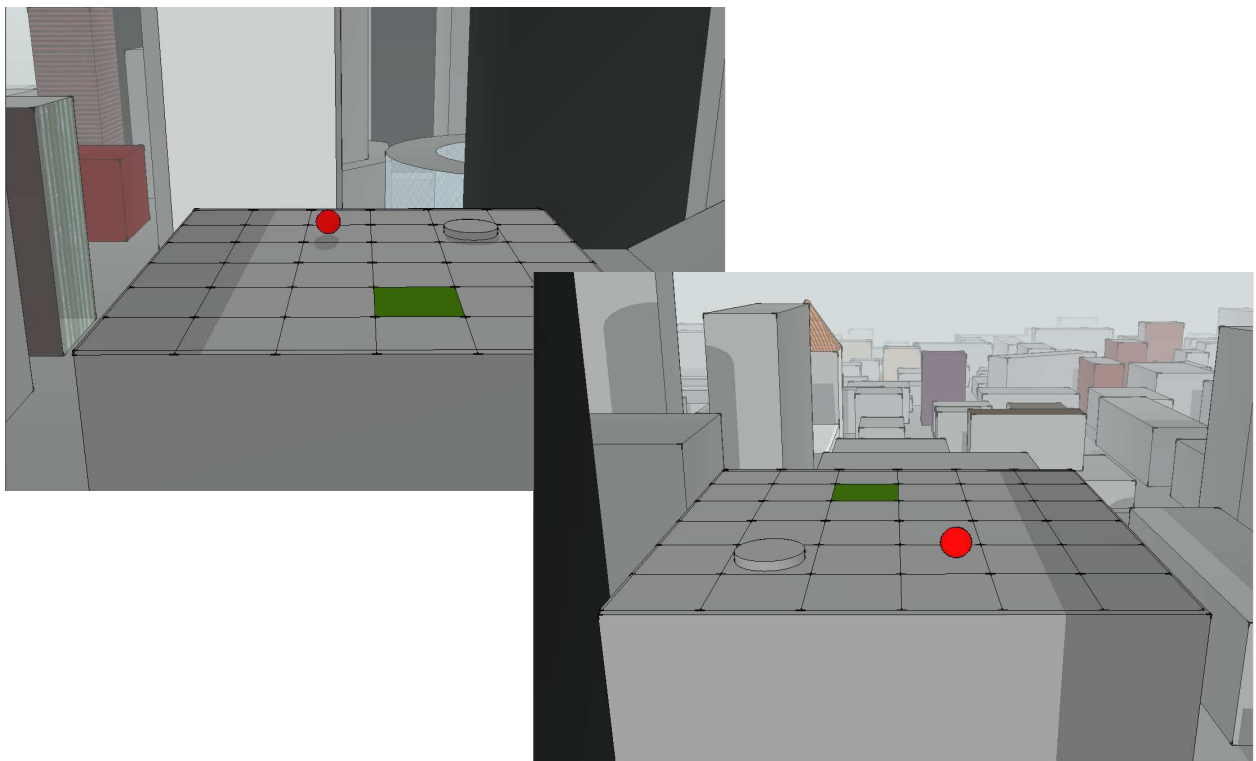


Figure 8.8 A spatial grid within a cityscape from two opposite viewpoints.

8.6 Concluding Remarks

This general discussion began by assessing how dissociable egocentric and allocentric processes really are, drawing on evidence from the experiments described in this thesis (Chapters 3, 4 & 5) as well as other recent studies. With some speculation, a model of spatial memory was constructed which included interactive and cooperative spatial strategies, and in turn some of the putative anatomical and temporal elements of this model were added to the model of Roche *et al.* (2005) in an attempt to highlight translational processing. How such spatial strategies might combine with object information in the brain was then discussed, drawing on the findings from Chapters 6 and 7. This was followed by a discussion of more general memory processes and the possible role of context for information-binding in episodic memory. Finally, further studies were suggested which could take advantage of the versatile nature of the Spatial Grid Task to probe spatial cognition in healthy (and brain damaged) patients. I believe this thesis has provided important electrophysiological markers of these processes, and by tentatively relating them to neural generators, I have identified possible areas of translation between spatial representations and constructed a model of object-location memory which can be explored by experimenters and clinicians alike.

9

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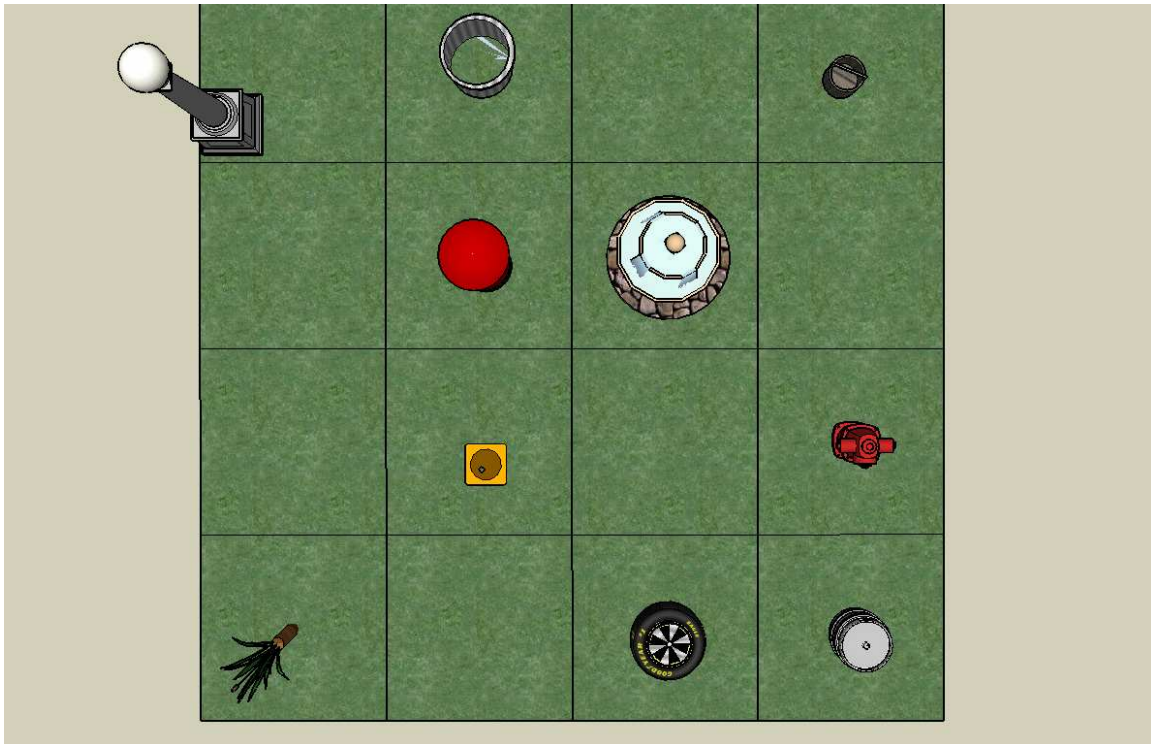
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Appendices

Appendix I

Stimuli of the Spatial Grid Task

Overhead



See attached DVD

1. 0° objects
2. 90° Left objects
3. 90° Right objects
4. 180° objects
5. Circular Grid stimuli
6. Cueing stimuli
7. Transition slides
8. Distractors
9. Cues
10. Probes

Appendix II

Consent Forms

C. 3 – used for Chapter 3

C.4a/b – used for Chapter 4

C. 5 – used for Chapter 5

C. 6a / C. 6b – used for Chapter 6

C. 7 – used for Chapter 7

Subject Consent Form

Project Title:

INVESTIGATING THE NEURAL CORRELATES OF SPATIAL REPRESENTATION & MEMORY

Researcher: Jonathan S. Murphy

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Ireland

The total time for your participation will be *approximately 120 minutes*.

The purpose of this study is to examine behavioural differences in memory for objects' locations in a small environment and map these differences to neural activity through the use of electroencephalography, to show a functional distinction between different spatial representations. Electroencephalography is a non-invasive recording technique involving electrodes connected to an elasticated cap that reads the electric potentials from the scalp and brain.

The results of each individual's participation will be strictly confidential. The results of your participation will be documented by subject number only. No names or individual identifying information will be recorded. With the exception of the researcher(s) involved in running this study, nobody will be allowed to see or discuss any of the individual responses. Your responses will be combined with many others and reported in group form.

I have read the above and understand the nature of this study and agree to participate. I also understand that I have the **right to refuse to participate** and that **my right to withdraw from participation at any time during the study** will be respected with no coercion or prejudice.

Participant signature

Date

This research project has been approved by the University Ethics Committee.

If during your participation in this study, you feel that the information and guidelines that you were given have been neglected or discarded in any way, or if you are unhappy about the process, please contact the Secretary of the National University of Ireland, Maynooth Ethics Committee at pegdean@nuim.ie or 01 7036018. Please be assured that concerns will be dealt with in a sensitive manner.

C. 4a/b

Subject Consent Form

Project Title:

INVESTIGATING THE NEURAL CORRELATES OF SPATIAL REPRESENTATION & MEMORY

Researcher: Jonathan S. Murphy
Department of Psychology...
National University of Ireland, Maynooth
Maynooth, Co. Kildare, ...
Ireland

Supervisors: Dr. Richard Roche
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Department of Psychology...
National University of Ireland,
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Dr. Sean Commins
Lecturer
Department of Psychology...
National University of Ireland,
Maynooth
Maynooth, Co. Kildare, ...
Ireland

The total time for your participation will be *approximately 20 minutes*.

The purpose of this study is to examine behavioural differences in memory for objects' locations in a small environment

The results of each individual's participation will be strictly confidential. The results of your participation will be documented by subject number only. No names or individual identifying information will be recorded. With the exception of the researcher(s) involved in running this study, nobody will be allowed to see or discuss any of the individual responses. Your responses will be combined with many others and reported in group form.

I have read the above and understand the nature of this study and agree to participate. I also understand that I have the **right to refuse to participate** and that my **right to withdraw from participation at any time during the study** will be respected with no coercion or prejudice.

Participant signature

Date

This research project has been approved by the University Ethics Committee.

If during your participation in this study, you feel that the information and guidelines that you were given have been neglected or discarded in any way, or if you are unhappy about the process, please contact the Secretary of the National University of Ireland, Maynooth Ethics Committee at pegsean@nuim.ie or 01 7086018. Please be assured that concerns will be dealt with in a sensitive manner.

Subject Consent Form

Project Title:
MEMORY FOR OBJECT-LOCATIONS

Researcher: Jonathan S. Murphy
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Dr. Sean Commins
Lecturer
Department of Psychology...
National University of Ireland,
Maynooth
Maynooth, Co. Kildare, ..
Ireland

The total time for your participation will be *approximately 6 minutes*.

The purpose of this study is to examine behavioural differences in memory for object locations in a small environment.

The results of each individual's participation will be strictly confidential. The results of your participation will be documented by subject number only. No names or individual identifying information will be recorded for publication. With the exception of the researcher(s) involved in running this study, nobody will be allowed to see or discuss any of the individual responses. Your responses will be combined with many others and reported in group form.

I have read the above and understand the nature of this study and agree to participate. I also understand that I have the right to refuse to participate and that my right to withdraw from participation at any time during the study will be respected with no coercion or prejudice.

Participant signature

Date

Researcher

Date

This research project has been approved by the University Ethics Committee.

If during your participation in this study, you feel that the information and guidelines that you were given have been neglected or discarded in any way, or if you are unhappy about the process, please contact the Secretary of the National University of Ireland, Maynooth Ethics Committee at pegdean@nuim.ie or 01 7086018. Please be assured that concerns will be dealt with in a sensitive manner.

Subject Consent Form

C. 6a

Project Title:

ELECTROPHYSIOLOGICAL CORRELATES OF OBJECT RECOGNITION MEMORY

Researcher:

Jonathan S. Murphy

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Dr. Sean Commings

Lecturer
Department of Psychology...
National University of Ireland,
Maynooth
Maynooth, Co. Kildare, ...
Ireland

The total time for your participation will be *approximately 100 minutes*.

The purpose of this study is to examine behavioural differences in memory for objects in a small environment and map these differences to neural activity through the use of electroencephalography. Electroencephalography is a non-invasive recording technique involving electrodes connected to an elasticated cap that reads the electric potentials from the scalp and brain.

The results of each individual's participation will be strictly confidential. The results of your participation will be documented by subject number only. No names or individual identifying information will be recorded. With the exception of the researcher(s) involved in running this study, nobody will be allowed to see or discuss any of the individual responses. Your responses will be combined with many others and reported in group form.

I have read the above and understand the nature of this study and agree to participate. I also understand that I have the **right to refuse to participate** and that my **right to withdraw from participation at any time during the study** will be respected with no coercion or prejudice.

Participant signature

Date

Researcher

Date

This research project has been approved by the University Ethics Committee.

If during your participation in this study, you feel that the information and guidelines that you were given have been neglected or discarded in any way, or if you are unhappy about the process, please contact the Secretary of the National University of Ireland, Maynooth Ethics Committee at pegdean@nuim.ie or 01 7086018. Please be assured that concerns will be dealt with in a sensitive manner.

Subject Consent Form

Project Title:
MEMORY FOR OBJECTS

Researcher: Jonathan S. Murphy
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National University of Ireland, Maynooth
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Dr. Sean Commings
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Maynooth, Co. Kildare, ...
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The total time for your participation will be *approximately 10 minutes*.

The purpose of this study is to examine behavioural differences in memory for objects in a small environment.

The results of each individual's participation will be strictly confidential. The results of your participation will be documented by subject number only. No names or individual identifying information will be recorded for publication. With the exception of the researcher(s) involved in running this study, nobody will be allowed to see or discuss any of the individual responses. Your responses will be combined with many others and reported in group form.

I have read the above and understand the nature of this study and agree to participate. I also understand that I have the **right to refuse to participate** and that **my right to withdraw from participation at any time during the study will be respected with no coercion or prejudice**.

Participant signature

Date

Researcher

Date

This research project has been approved by the University Ethics Committee.

If during your participation in this study, you feel that the information and guidelines that you were given have been neglected or discarded in any way, or if you are unhappy about the process, please contact the Secretary of the National University of Ireland, Maynooth Ethics Committee at pegdean@nuim.ie or 01 7086018. Please be assured that concerns will be dealt with in a sensitive manner.

Project Title:
ELECTROPHYSIOLOGICAL CORRELATES OF OBJECT-LOCATION RECOGNITION
MEMORY

Researcher: Jonathan S. Murphy
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Supervisors: Dr. Richard Roche
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Dr. Sean Commins
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Maynooth
Maynooth, Co. Kildare, ...
Ireland

The total time for your participation will be *approximately 100 minutes*.

The purpose of this study is to examine behavioural differences in memory for objects in a small environment and map these differences to neural activity through the use of electroencephalography. Electroencephalography is a non-invasive recording technique involving electrodes connected to an elasticated cap that reads the electric potentials from the scalp and brain.

The results of each individual's participation will be strictly confidential. The results of your participation will be documented by subject number only. No names or individual identifying information will be recorded. With the exception of the researcher(s) involved in running this study, nobody will be allowed to see or discuss any of the individual responses. Your responses will be combined with many others and reported in group form.

I have read the above and understand the nature of this study and agree to participate. I also understand that I have the **right to refuse to participate** and that my **right to withdraw from participation at any time during the study** will be respected with no coercion or prejudice.

Participant signature

Date

Researcher

Date

This research project has been approved by the University Ethics Committee.

If during your participation in this study, you feel that the information and guidelines that you were given have been neglected or discarded in any way, or if you are unhappy about the process, please contact the Secretary of the National University of Ireland, Maynooth Ethics Committee at pegdavis@nuim.ie or 01 7086018. Please be assured that concerns will be dealt with in a sensitive manner.

Appendix III

Orthogonal Viewpoints and Intrinsic Axes in the computerised Spatial Grid Task

A3.1 Introduction

In Chapter 3 we used a Spatial Grid Task to test participants' spatial memory across four viewpoints (i.e. 0° , 90° left, 90° right and 180°). A possible criticism of this task and the methodology we used suggests that participants' could perform better at spatial tasks when these tasks are aligned with an intrinsic reference frame (e.g. front-back and left-right axes). Support for this claim comes from experiments by Mou and McNamara (2002) which investigated the frames of reference used to represent the spatial structure of the environment in memory. They noted that accuracy on a pointing task within a spatial array was higher from front, back and side views, concluding that participants were able to represent the layout along two intrinsic axes, 0° – 180° and 90° – 270° . These are the exact orthogonal axes upon which our square grid task was based and along which rotated viewpoints were aligned. Therefore there is a possibility that the results of our original study (i.e. differences between 0° and rotated viewpoints but *no differences between rotated viewpoints*) may have been due to the compensatory effect of orthogonal axes on performance. It could be argued for example, that we did not find a linear gradient in reaction times as viewpoints moved further away from 0° (the mental rotation effect) due to this compensatory effect. It is therefore necessary to test performance on these orthogonal viewpoints against performance on non-orthogonal viewpoints to ascertain whether the orthogonal viewpoints only affect performance due to an

underlying alignment along intrinsic axes (related to array layout and object and environmental symmetry).

In the current experiment we implement a Circular Spatial Grid Task which includes the novel, non-orthogonal viewpoints of 45° and 135° for both clockwise and anti-clockwise rotations. The influence of all of these non-egocentric reference frames on performance could be now tested and we assess the claim that the orthogonal viewpoints are aligned along intrinsic axes which benefits performance. If a saw tooth pattern of accuracy and reaction time was seen across viewpoints (replicating the findings of Mou and McNamara, 2002; i.e. good, poor, good, poor, good performance for 0° , 45° , 90° , 135° and 180°), then the results of the original Spatial Grid Task experiment could be left open to this criticism. If, on the other hand, the behavioural differences only exist between the 0° study viewpoint and all other novel viewpoints, mirroring the results of the original study (Chapter 3), then both the task and our hypothesis of an egocentric-allocentric separation would be further strengthened.

We predicted that participants would be more accurate and respond quicker for the 0° trials and show a separate performance pattern for all novel viewpoints with no differences in performance between these viewpoints. We hypothesise that data matching these predictions would be due to participants switching between spatial representational formats; egocentric for the 0° studied viewpoint and allocentric for the novel viewpoints.

A3.3 Methods

A3.3.1 Participants

Twenty volunteers, recruited *ad hoc* from the student population of the National University of Ireland (NUI Maynooth), participated in this experiment. Participants were aged between 19 and 28 (mean 23.5 years). Thirteen were female and nineteen were right-handed. All were in good health and had normal or corrected-to-normal vision. The experiment was conducted in accordance with the Code of Ethics of the World Medical Association and the ethical standards of the APA and approved by the NUI Maynooth University Ethics Board.

A3.3.2 Stimuli

The Circular Spatial Grid Task was used for this experiment – see General Methods section 2.2.2. All stimuli were presented using E-Prime on an Intel Pentium 4 Processor (3.00GHz CPU) and displayed on an LCD monitor. They consisted of 8 different objects including a bin, a bucket, a post-box, a road-cone, a fire hydrant, a tree, a tyre and a keg.

A3.3.3 Procedure

Participants were seated in a cubicle (150cm x 180cm) half a metre from the computer monitor and had access to a mouse for responses. A study block preceded a test block. Instructions were presented on screen. These have been described in greater detail in the General Methods section 2.3.

STUDY BLOCK

During the study block participants were required to memorize the locations of each object within the dartboard grid. The study block consisted of 48 trials (each of the 8 objects presented 6 times). The temporal sequence of a trial is displayed in Figure A3.1a. The presentations were pseudo-random (objects were presented randomly in a run of 8 and this was repeated 8 times) so that numerous presentations of the same object did not coincide. More instructions followed the study block, explaining how to respond in the test block.

TEST BLOCK

Participants were instructed to respond to objects in their *correct* location by clicking the left mouse button with their index finger and by clicking the right mouse button with their middle finger when objects were presented in *incorrect* locations. For the Test block, the sequence of a single trial followed the same pattern as above (Figure A3.1a). The participants were instructed to respond as speedily as possible within a 2 second time limit while also attempting to respond accurately. A response terminated the current trial. The test block began with 8 trials presented from the same viewpoint as in the study block. This allowed participants to adapt to the response criteria before the rotated trials were presented. The objects were presented either in their correct location or in an incorrect location (Figure A3.1b). There were four possible incorrect locations pseudo-randomly chosen from the 13 remaining spaces (16 spaces minus 2 landmarks minus the correct location). Presentations were randomised in the construction of the task on E-Prime and this random order was the same for all participants. After the initial 8 trials, participants were again required to recognise the location of a particular stimulus that

they had previously seen in the study block. However they were instructed that the environment would be rotated on a proportion of trials. Following these instructions the test continued through 256 trials with a self-timed rest break after the 128th trial. The environment (including the landmarks) was rotated by either 0°, 45° left, 90° left, 135° left, 45° right, 90° right, 135° right, or 180° (see Figure A3.1c) on each trial. Therefore, excluding the initial eight 0° trials, participants were tested on 128 trials with correct location objects (8 objects x 8 rotations x 2 presentations) and 128 trials where objects were out of position (8 objects x 8 rotations x 2 random incorrect locations). Trials were presented in the same random order to all participants.

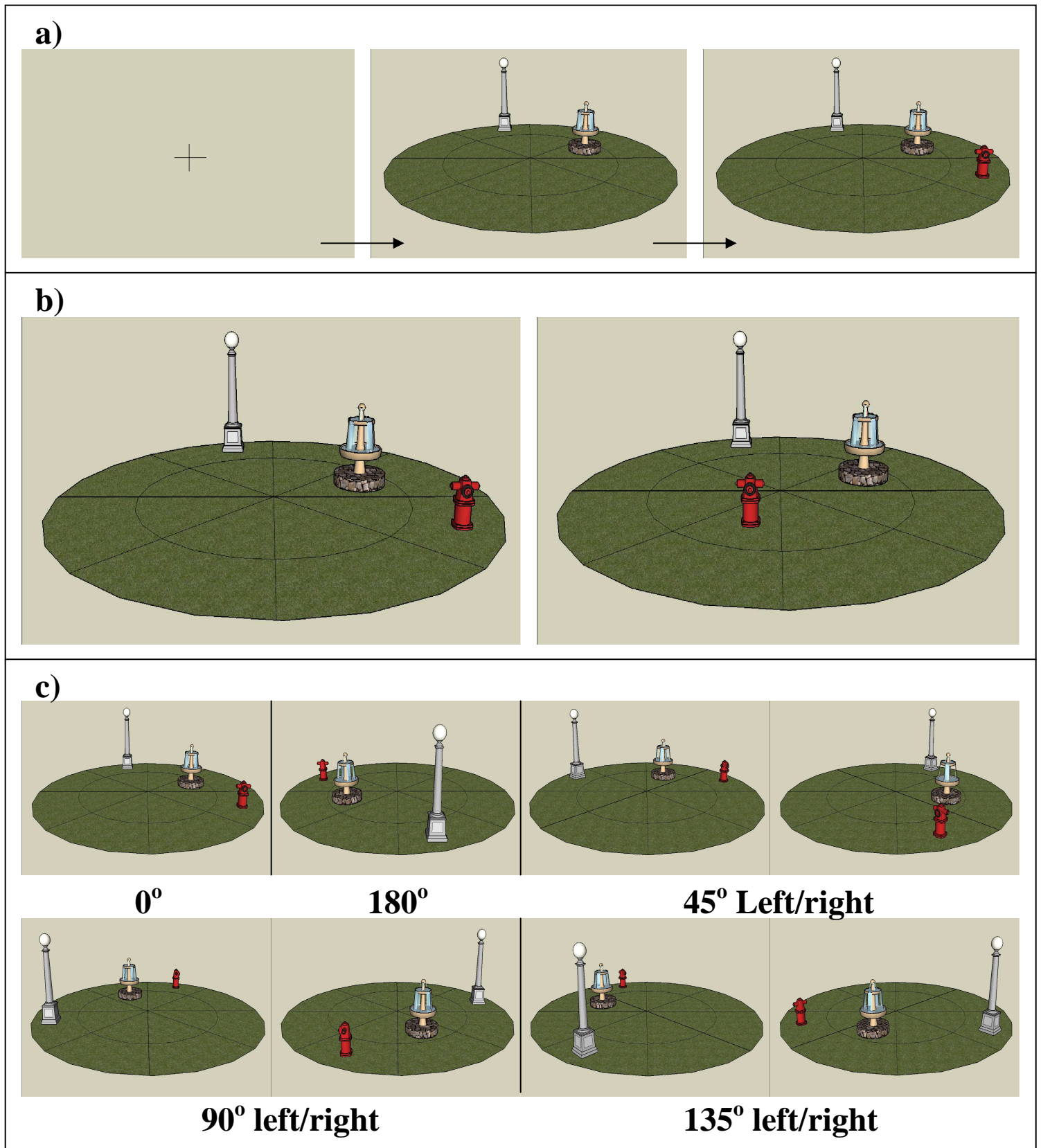


Figure A3.1 The Circular Grid Task **a)** Sequence of a single trial showing fixation, landmarks and object presentation. **b)** Demonstration of different object locations with 'correct location' in left panel and 'incorrect location' in right panel. **c)** Example of the viewpoints presented to participants during the test phase grouped by their angle of rotation from the study viewpoint (correct location shown).

A3.4 Results

Individual mean accuracy scores for each of the eight viewpoints were collected and collated into 5 totals based on degree of rotation (0° , 45° , 90° , 135° and 180°) for both correct and incorrect object locations. Participants were significantly more accurate at recognising displacement, with overall higher scores when objects were presented out of place (82.1% versus 69.5% recognition of correctly placed objects). Across viewpoints, regardless of object location, percentage scores were highest for the 0° condition. These observations were confirmed with a two-way repeated-measures ANOVA. The within-subjects comparisons revealed a main effect of location [$F(1, 19)=17.823$, $p<0.001$] and viewpoint [$F(4, 76)=4.934$, $p<0.001$] and a significant interaction effect was found for location*viewpoint [$F(4, 76)=2.808$, $p<0.05$]. Figure A3.2a shows the main effect of viewpoint with the significance levels of Bonferroni corrected paired-samples t-tests marked above the bars. Significant differences were found between 0° and 45° [$t(19)=3.348$, $p<0.05$], 0° and 90° [$t(19)=3.687$, $p<0.05$] and 0° and 135° [$t(19)=3.847$, $p<0.01$]. The Bonferroni correction removed the significant p-value for the 0° vs. 180° comparison [$t(19)=2.676$, $p>0.05$]. Analysing the novel viewpoint trials separately with an ANOVA we found no significant difference in accuracy overall [$F(3, 57)=2.49$, $p=0.862$] and a comparison of the average accuracy from the novel viewpoints to that from the 0° trials with a paired-samples t-test (Figure A3.2b) revealed a significant difference [$t(19)=4.115$, $p=0.001$].

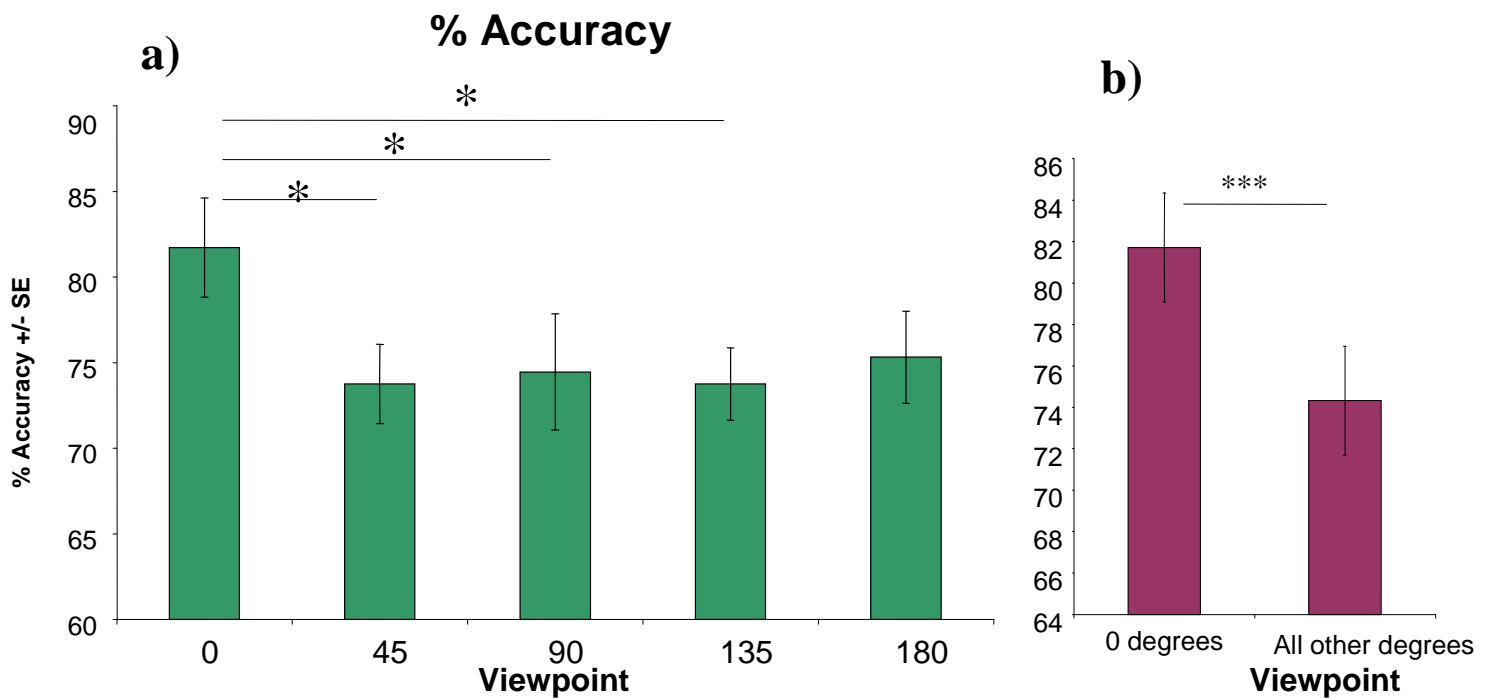


Figure A3.2 a) Bar Graph showing the average accuracy of participants across viewpoints for correct and incorrect object locations combined. **b)** Mean accuracy for 0 degree trials versus combined mean accuracy for novel viewpoints Significance bars are displayed with *p*-values *=*p*<0.05, ***=*p*<0.001

Reaction times (from accurate trials) were found to be quicker on average for 0° presentations ($916.29 \pm 20.56\text{ms}$) compared to rotated viewpoints ($961.71 \pm 24.76\text{ms}$) but results from an ANOVA showed no significant effect of viewpoint [$F(2.6, 49.6)=2.722$, $p>0.05$] (Greenhouse-Geisser corrected). A significant effect of location was found [$F(1, 19)= 6.270$, $p<0.05$] and the interaction effect between location*viewpoint also yielded significance [$F(2.7, 53.08)=4.214$, $p<0.05$]. Bonferroni corrected *t*-tests comparing reaction times in trials from the study view with those from the novel viewpoints revealed a significant difference between 0° and 90° presentations [$t(19)=-3.265$, $p<0.05$], as seen in Figure A3.3a. Analysing the novel viewpoint trials separately with an ANOVA we found no significant difference in reaction time overall [$F(1.76, 33.37)=0.465$, $p=0.607$] and a comparison of the average reaction time from the novel viewpoints to that from the 0° trials with a paired-samples *t*-test (Figure A3.3b) revealed a significant difference [$t(19)=-2.895$, $p=0.009$].

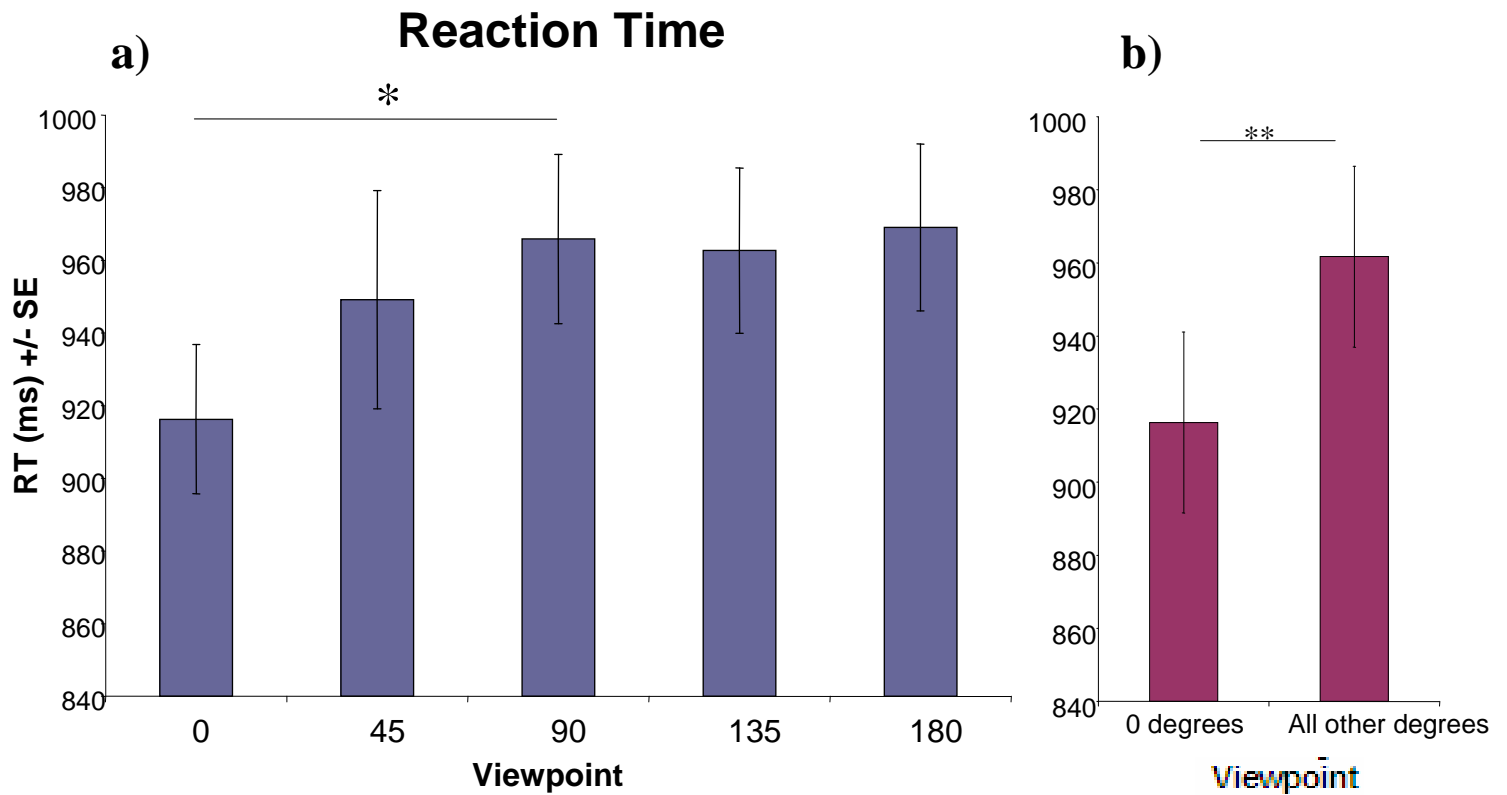


Figure A3.3 a) Histogram showing the average reaction time of participants across viewpoints for correct and incorrect object locations combined. **b)** Mean reaction time for 0 degree trials versus combined mean reaction time for novel viewpoints. Significance bars are displayed with p -values $*=p<0.05$ $**=p<0.01$

A3.5 Discussion

In this study we demonstrated that performance on viewpoints aligned with orthogonal axes was not superior to performances on non-orthogonal axes and that the only significant differences in our task existed between 0° and all other viewpoints. This would suggest that there perhaps exists an egocentric-allocentric separation, with object-location on egocentric viewpoints easier to identify. This proposition is supported by a neural dissociation (see Chapter 3). Our findings contrast those of Mou and McNamara (2002) who found superior performance on intrinsic and orthogonal viewpoints in an experiment conducted in a circular room. Although both methodologies may have led to a similar ‘environmental’ perspective, differences in encoding strategy may have occurred. Taylor and Tversky (1996) describe gaze, route and survey descriptions. In describing rooms that can be seen from one viewpoint, people prefer gaze descriptions (Ehrich & Koster 1983; Levelt, 1989). A gaze description (Ehrich & Koster, 1983; Levelt, 1989; Ullmer-Ehrich, 1982) has a stationary viewpoint outside the environment, from which the entire scene can be viewed. Objects are described with respect to each other from the external viewpoint in terms of *left*, *right*, *front* and *back*. It is possible differential strategies may have been employed in the Mou and McNamara study compared to ours. In their study the array of objects may also have been encoded in a more categorical than co-ordinate manner. Categorical spatial relations are easily described by verbal locatives (e.g. one object is on the left/right or above/below with respect to another), whereas co-ordinate spatial relations represent precise, quantitative aspects of the spatial relationships (Kosslyn, 1987). Again, in the Mou and McNamara study all objects were presented together and therefore could be more likely encoded and remembered as a scene where certain manipulations of this scene (coinciding with intrinsic axes) are more easily

accomplished than others. We would suggest that our presentation of one object at a time along with landmarks may have resulted in a more relational and co-ordinate based spatial representation. In addition there is a strong likelihood that our array does not contain an intrinsic axis. There is no immediately apparent symmetry in our object array and with the single presentation of objects for evaluation it would have been very difficult for participants to perceive any particular viewpoint as coinciding with an intrinsic axis. Even if the orthogonal viewpoints were aligned along intrinsic ‘environmental’ axes (due to the environmental geometry) participants showed no significant differences between orthogonal and non-orthogonal novel viewpoints suggesting that the use of orthogonal viewpoints in previous experiments (see Chapters 3 & 4) did not confound the results. The results of this task support the findings of the Spatial Grid Task (Chapter 3), with data pointing towards two distinct response patterns and two possible neural generators.

In support of this idea, Burgess (2006) reviewed evidence that both egocentric and allocentric representations exist in parallel, and these representations combine to support behaviour depending on the demands of the task. One type of interaction between the representations occurs with angular movements of viewpoint between presentation and retrieval, with increasing dependence on allocentric representations as this variable gets larger (Burgess, 2006). We posit that both egocentric and allocentric representations underpin the observed response topography in our data and, as Burgess (2006) suggests, it is not a clear-cut recruitment of one or the other but an interaction of the two representations with allocentric reliance increasing as a function of degree of rotation from zero.

The results of this experiment provide additional evidence that mental rotation is insufficient to explain the performance of participants on novel viewpoints of a spatial array. Participants had the capability to perform well above chance levels on the novel viewpoints without the additional time needed for mentally rotating the array (Shepard & Metzler's (1971) mental rotation effect). We suggest that an allocentric representation is necessary for an adaptive and flexible spatial memory system and maintain that the Spatial Grid Task is a valid method of testing differences in mental representations. Consequently, we can also conclude that viewpoints along orthogonal axes, aligned with environmental geometry, only aid spatial memory for object location when the object relations have intrinsic structure and when the orthogonal and intrinsic axes overlap.

Appendix IV

Possible sex differences in object-location memory

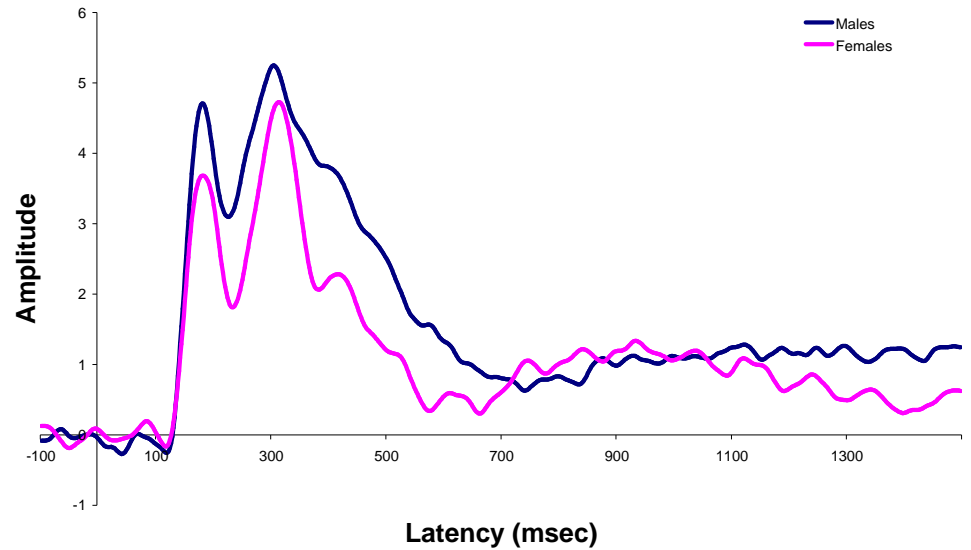
A re-analysis of the data from Chapter 6 was conducted to investigate the electrophysiological underpinnings of the sex differences reported in the literature (e.g., Eals & Silverman, 1994; James & Kimura, 1997; McBurney *et al.*, 1997; Silverman & Eals, 1992). With regard to this sexual dimorphism we predict superior performance in females and a possible hemispheric asymmetry over parietal areas. This hemispheric difference should highlight the categorical and coordinate spatial strategies used by females and males respectively (Kosslyn *et al.*, 1992).

Male vs. Female comparisons: For male/female comparisons ERPs were re-averaged so that even numbers of males (7) and females (7) were being compared. The selection of male subject data to be included was decided at random. Both groups included 6 right-handed participants. Amplitude differences between male and females were found across a number of midline and left parietal electrode sites. An example of this difference can be seen in Figure A4.3 where conditional ERP waveforms from electrode P3 show the additional positivity recorded from female participants. A mixed-factorial ANOVA compared hemispheric mean amplitudes for males and females and found significant effects for stimulus type [$F(3, 120)=16.094$, $p<0.001$]. The effect of hemisphere just fell short of significance [$F(1, 40)=4.053$, $p=0.051$] but there was a significant interaction effect of sex*hemisphere [$F(1, 40)=22.346$, $p<0.001$] and the between-subjects effect (sex) was also significant [$F(1, 40)=5.212$, $p<0.05$]. We conducted separate analyses on

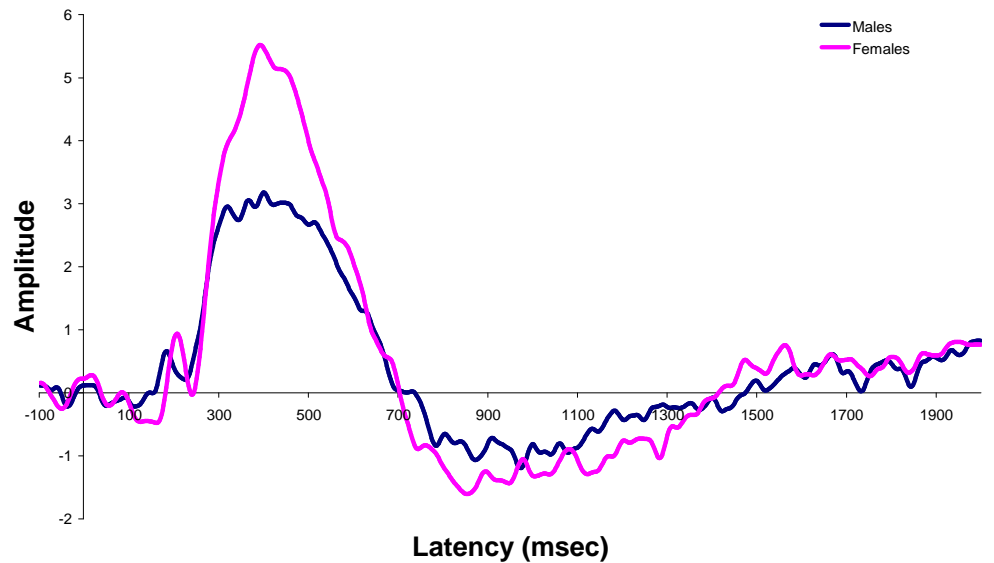
stimulus and landmark presentations. Using independent-samples t-test to compare male and female ERPs elicited by stimulus presentations, we found a significant difference in mean amplitudes over the left parietal cortex (P1, P3, E118) in the time interval 300-550ms for the Study Stimuli [$t(40)=-3.550$, $p<0.001$] ($M=2.40\mu V$ for males and $4.27\mu V$ for females), Correct Location stimuli [$t(40)=-2.489$, $p<0.05$] ($M=3.31\mu V$ for males and $4.83\mu V$ for females), Incorrect Location stimuli [$t(40)=-3.506$, $p<0.001$] ($M=2.48\mu V$ for males and $4.43\mu V$ for females) and Distractors [$t(40)=4.669$, $p<0.001$] ($M=2.23\mu V$ for males and $4.65\mu V$ for females). None of the comparisons between males and females for the right cluster (i.e. P2, P4, E121) reached significance ($p>0.05$) nor did the t-test comparing mean amplitude responses to landmark presentations [$t(24)=1.950$, $p<0.05$].

A further comparison of the electrophysiological data was undertaken for the time period identified (410-480ms). Figure A4.2 shows the hemispheric sex differences in high threshold time-series CSD (Current Source Density) maps. Current densities below $1.0\mu V/cm^2$ cortex for females and $0.80\mu V/cm^2$ cortex for males are filtered out, displaying only areas of highest density through the cortex across the time series demonstrating greater activity in the left hemisphere for females and the right hemisphere for males.

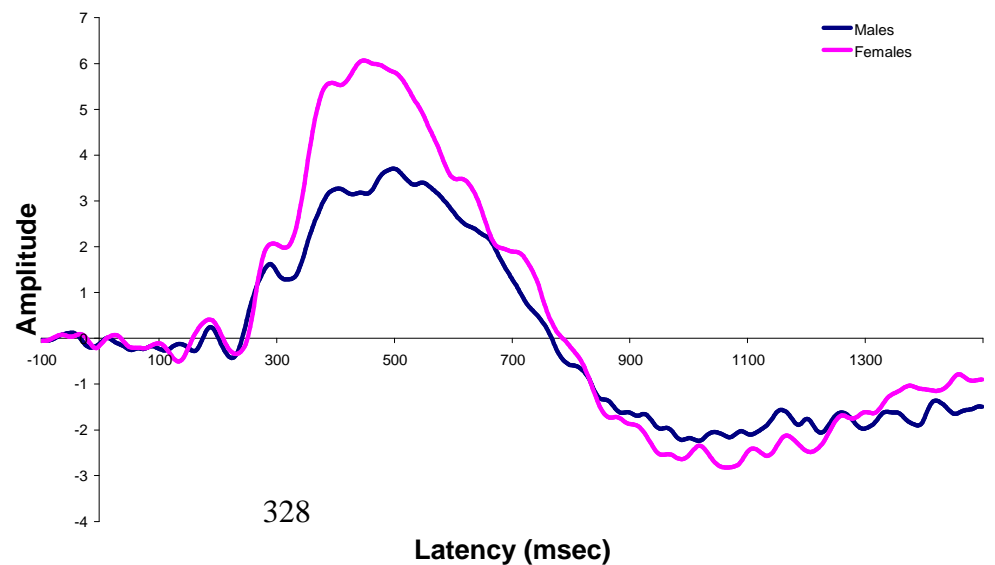
LANDMARKS



STUDY STIMULI



TEST STIMULI



ELECTRODE SITE P3

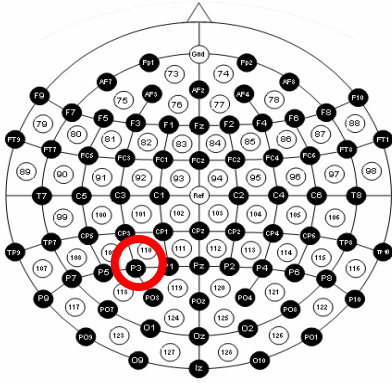


Figure A4.1 Averaged ERP waveforms for male and female participants for each of the landmark and stimulus presentations. Significantly larger amplitudes can be seen for females during the stimulus presentations. These differences were visible across the parietal cortex and left lateralised.

FEMALE

MALE

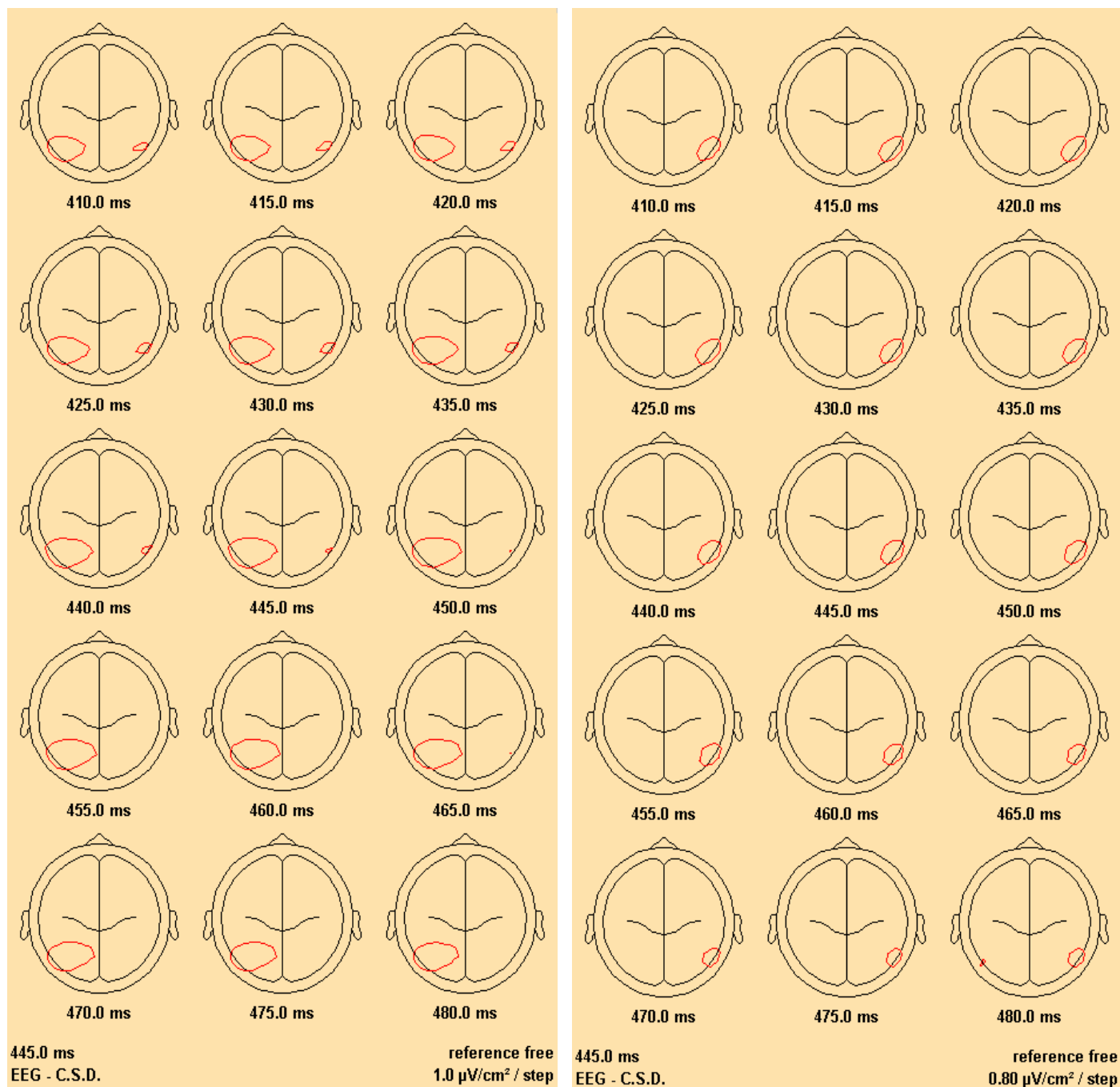


Figure A4.2 Time-series current source density maps shown for males and females with density thresholds applied. A hemispheric difference can be seen with regard to areas of cortex with maximum current densities.

Sex Differences: The amplitude differences recorded between males and females indicate a possible sex difference, perhaps related to differential strategy implementation, which shows additional left hemispheric cortical activation for females over males. Data from Alexander *et al.* (2002) suggest that the processing of object features and object identification in the left cerebral hemisphere may include processing of spatial information that may contribute to superior object-location memory in females relative to males. The female superiority for object-location memory was first explored by Silverman and Eals (1992) who developed a task intended to measure object-location memory; they reported that females outperformed males on their paper and pencil version of this task. This has been confirmed by other research (James & Kimura, 1997). Our data extend previous claims for sex differences in object-location memory by demonstrating possible electrophysiological sex differences consistent with an evolutionary model (Eals & Silverman, 1994; Silverman, Choi & Peters, 2007). However the results of this analysis are merely suggestive and at best provide an area for further more focused study. A thorough investigation of sex differences would require significant controls for menstrual cycle, testosterone levels, stress etc.

Appendix V

Re-analysis of Chapter 3 behavioural data by Test Block

ACCURACY

Tests of Within-Subjects Effects

Measure: MEASURE_1

| Source | | Type III Sum of Squares | df | Mean Square | F | Sig. |
|--------------|--------------------|-------------------------|--------|-------------|--------|------|
| block | Sphericity Assumed | 1259.914 | 3 | 419.971 | 11.289 | .000 |
| | Greenhouse-Geisser | 1259.914 | 1.885 | 668.427 | 11.289 | .000 |
| | Huynh-Feldt | 1259.914 | 1.983 | 635.424 | 11.289 | .000 |
| | Lower-bound | 1259.914 | 1.000 | 1259.914 | 11.289 | .002 |
| Error(block) | Sphericity Assumed | 4129.336 | 111 | 37.201 | | |
| | Greenhouse-Geisser | 4129.336 | 69.741 | 59.210 | | |
| | Huynh-Feldt | 4129.336 | 73.363 | 56.286 | | |
| | Lower-bound | 4129.336 | 37.000 | 111.604 | | |

Pairwise Comparisons

Measure: MEASURE_1

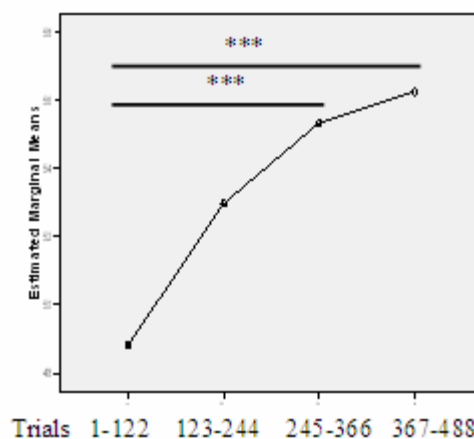
| (I) block | (J) block | Mean Difference (I-J) | Std. Error | Sig. ^a | 95% Confidence Interval for Difference ^a | |
|-----------|-----------|-----------------------|------------|-------------------|---|-------------|
| | | | | | Lower Bound | Upper Bound |
| 1 | 2 | -4.158 | 1.729 | .128 | -8.978 | .662 |
| | 3 | -6.526* | 1.097 | .000 | -9.586 | -3.467 |
| | 4 | -7.447* | 1.213 | .000 | -10.829 | -4.065 |
| 2 | 1 | 4.158 | 1.729 | .128 | -.662 | 8.978 |
| | 3 | -2.368 | 1.350 | .526 | -6.132 | 1.395 |
| | 4 | -3.289 | 1.894 | .544 | -8.569 | 1.990 |
| 3 | 1 | 6.526* | 1.097 | .000 | 3.467 | 9.586 |
| | 2 | 2.368 | 1.350 | .526 | -1.395 | 6.132 |
| | 4 | -.921 | .820 | 1.000 | -3.206 | 1.364 |
| 4 | 1 | 7.447* | 1.213 | .000 | 4.065 | 10.829 |
| | 2 | 3.289 | 1.894 | .544 | -1.990 | 8.569 |
| | 3 | .921 | .820 | 1.000 | -1.364 | 3.206 |

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

ACCURACY



REACTION TIME

Tests of Within-Subjects Effects

Measure: MEASURE_1

| Source | | Type III Sum of Squares | df | Mean Square | F | Sig. |
|--------------|--------------------|-------------------------|--------|-------------|--------|------|
| block | Sphericity Assumed | 870704.351 | 3 | 290234.784 | 59.615 | .000 |
| | Greenhouse-Geisser | 870704.351 | 2.132 | 408348.592 | 59.615 | .000 |
| | Huynh-Feldt | 870704.351 | 2.266 | 384172.014 | 59.615 | .000 |
| | Lower-bound | 870704.351 | 1.000 | 870704.351 | 59.615 | .000 |
| Error(block) | Sphericity Assumed | 540404.521 | 111 | 4868.509 | | |
| | Greenhouse-Geisser | 540404.521 | 78.894 | 6849.795 | | |
| | Huynh-Feldt | 540404.521 | 83.858 | 6444.248 | | |
| | Lower-bound | 540404.521 | 37.000 | 14605.528 | | |

Pairwise Comparisons

Measure: MEASURE_1

| (I) block | (J) block | Mean Difference (I-J) | Std. Error | Sig. ^a | 95% Confidence Interval for Difference ^a | |
|-----------|-----------|-----------------------|------------|-------------------|---|-------------|
| | | | | | Lower Bound | Upper Bound |
| 1 | 2 | 104.752* | 16.077 | .000 | 59.937 | 149.567 |
| | 3 | 164.487* | 20.737 | .000 | 106.682 | 222.293 |
| | 4 | 199.579* | 18.664 | .000 | 147.552 | 251.607 |
| 2 | 1 | -104.752* | 16.077 | .000 | -149.567 | -59.937 |
| | 3 | 59.735* | 14.991 | .002 | 17.945 | 101.526 |
| | 4 | 94.827* | 12.227 | .000 | 60.745 | 128.910 |
| 3 | 1 | -164.487* | 20.737 | .000 | -222.293 | -106.682 |
| | 2 | -59.735* | 14.991 | .002 | -101.526 | -17.945 |
| | 4 | 35.092* | 11.242 | .021 | 3.753 | 66.431 |
| 4 | 1 | -199.579* | 18.664 | .000 | -251.607 | -147.552 |
| | 2 | -94.827* | 12.227 | .000 | -128.910 | -60.745 |
| | 3 | -35.092* | 11.242 | .021 | -66.431 | -3.753 |

Based on estimated marginal means

*. The mean difference is significant at the .05 level.

a. Adjustment for multiple comparisons: Bonferroni.

REACTION TIME

