Investigations of Attentional Processing in Parietal and Occipital Human Cortical Regions With Magnetoencephalography

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Synopsis

Attention defines our mental ability to select and respond to stimuli, internal or external, on the basis of behavioural goals in the presence of competing, behaviourally irrelevant, stimuli. The frontal and parietal cortices are generally agreed to be involved with attentional processing, in what is termed the 'fronto-parietal' network. The left parietal cortex has been seen as the site for temporal attentional processing, whereas the right parietal cortex has been seen as the site for spatial attentional processing. There is much debate about when the modulation of the primary visual cortex occurs, whether it is modulated in the feedforward sweep of processing or modulated by feedback projections from extrastriate and higher cortical areas.

MEG and psychophysical measurements were used to look at spatially selective covert attention. Dual-task and cue-based paradigms were used. It was found that the posterior parietal cortex (PPC), in particular the SPL and IPL, was the main site of activation during these experiments, and that the left parietal lobe was activated more strongly than the right parietal lobe throughout. The levels of activation in both parietal and occipital areas were modulated in accordance with attentional demands.

It is likely that spatially selective covert attention is dominated by the left parietal lobe, and that this takes the form of the proposed sensory-perceptual lateralization within the parietal lobes. Another form of lateralization is proposed, termed the motor-processing lateralization, the side of dominance being determined by handedness, being reversed in left- relative to right-handers. In terms of the modulation of the primary visual cortex, it was found that it is unlikely that V1 is modulated initially; rather the modulation takes the form of feedback from higher extrastriate and parietal areas. This fits with the idea of preattentive visual processing, a commonly accepted idea which, in itself, prevents the concept of initial modulation of V1.

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Chapter 1: Attention - An Overview.

Attention has been defined many different ways over the course of its history as an independent subject of study. To my mind, the following seems the most logical of definitions, while being one of the oldest. Attention is the selection of one object, sound, or thought, in the presence of competing others, for further processing. It requires the withdrawal processing capabilities from some objects in order to deal more effectively with others (James, 1950). In other words attention defines our mental ability to select and respond to stimuli, internal or external, on the basis of behavioural goals in the presence of competing, behaviourally irrelevant, stimuli.

Attention was first introduced as an independent topic, within the discipline of psychology, by Wolff in 1738 (Hatfield, 1998). Wolff defined attention as bringing about the perception of one part of the external world with greater clarity than others. He referred to the limited capacity of attention, saying that it was easier for us to attend to one image than several. What he also did was to define four aspects of attentional processing: the harder attention is to distract the stronger the effect, attention can last for long or short periods of time, it may be possible to attend to several objects simultaneously, and it is subject to voluntary control (Hatfield, 1998). So, although William James is often attributed as the first to pioneer attention as a separate subject within psychology, it was Wolff that first made this distinction.

1.1.Covert Attention

Covert attention is automatically drawn to sudden onsets or offsets of perceptual stimuli in the visual field, tied to sudden changes or novel stimuli in the visual field (Egeth & Yantis, 1997; Watson & Humphreys, 1995), these can be either related or not to behavioural goals. The automatic process of covert attention occurs without any disruption to other mental processes, and does not necessarily produce awareness (McCormick, 1997), conversely overt, controlled attentional processing requires both awareness and intention (McCormick, 1997)(see later). Covert attention can be seen as transient, having rapid engagement and dissipating quickly, being fully activated in about 50ms and dissipating in about 250ms (Posner & Cohen, 1984). It is linked with early, bottom-up, visual processing

(Steinman & Steinman, 1998; Watson & Humphreys, 1995). The covert attentional system can be equated with a visual 'alerting' system. We cannot attend to something that does not change without conscious effort, a vital property of attention is signalling change. Sudden onsets or offsets in the visual field may signal something of danger in the external world, regardless of eye position, which ought to be attended to if the individual is to remain safe. The presence of unchanging stimuli is not alarming, whereas the sudden onset of new stimuli may signal danger and must be attended to for survival. Unchanging objects are perceptually 'invisible' until attention is once more drawn to them. Posner et al refer to this requirement of attention (Posner & Gilbert, 1999), stating that attention must be signalled or cued in some manner for it to be drawn to a stimulus, otherwise attention is not drawn at all and the stimulus goes unnoticed.

Shifts of covert attention may facilitate analysis of visual stimuli in two ways: processing is completed more rapidly at the attended location, time is needed to reorient after a cue proves false (see the following section); and such shifts may directly influence visual processing by enhancing sensitivity at attended locations (Corbetta, 1998)

1.2. Cues

Without some form of cue attention is not summoned and there is no awareness of the target (DeSchepper & Treisman, 1996). Obviously there is a behavioural advantage to knowing when a stimulus is going to occur (Coull & Nobre, 1998), the heightened awareness being evident in improved response times. Two types of cue are used in attentional experiments, many of which are based on Posner's 'Cost-Benefit Paradigm', to be detailed later (Posner, 1980): endogenous and exogenous cues. A cue that is interpreted and used to voluntarily change the locus of attention, such as an arrow (Posner et al, 1978), is said to be an endogenous cue. This literally translates into 'from within' (Reber, 1995), hence meaning is derived from the cue which is not obvious without prior knowledge. This type of cue is not entirely necessary in itself, as similar results have been found without a cue, where participants are asked to direct attention to a particular location (Lee, et al., 1999). A cue that depends on sensory information is said to be exogenous, for example a light flash, and this appears at the target location. This translates into 'from without' (Reber, 1995), there is no information to predict the target location other than the location of the cue itself, the information from the cue is apparent on surface appraisal, there is no internal meaning. Exogenous cues facilitate stimulus detection when sensory information is used as advance information about target position (Jonides, 1981). It is also possible that exogenous cues facilitate attention quicker than do endogenous cues, (Muller et al, 1998), as there is no processing to be done with regard to determining the meaning of the cue (for a discussion about types of cue see: Wright, 1998). Endogenous cues provide only location-based information about the target; there is no object for attention to specifically orient itself to, yet with exogenous cues there can be an object and a location predicted, giving both types of information to the observer (Egly et al, 1994). It is for this reason that I consider exogenous cues to be most useful in the study of attentional processing, they provide no bias of predictive information and also do not rely on learned associations as do endogenous cues.

The use of spatial cues enhances stimulus processing in the absence of eye movements, through the mechanisms of covert attention, reflecting the activation of mechanisms to shift attention to the stimulus location before its appearance (Corbetta, 1998). There are two ways in which cues can facilitate stimulus analysis. Firstly, the visual analysis proceeds more rapidly at the attended location as time is needed for attention to move to other locations in the visual field (Corbetta, 1998; Posner, 1980); and secondly attention may directly influence visual processes by enhancing sensitivity to the attended location, this could be an explanation for improved sensory thresholds found in attended locations (Corbetta, 1998).

Peripheral cues are generally used when one wishes to manipulate covert attention as they draw attention automatically, unlike central cues, which require a deliberate shift in attention and are more suited to overt attentional manipulations. Central cues draw attention only when they are informative, in other words endogenous cues, while peripheral cues draw attention whether they are informative or not, they are exogenous cues (Jonides, 1981). Peripheral cues are characterised by eliciting a fast, transient response, producing a rapid rise, and fall, in attention (Egeth & Yantis, 1997).

One of the most well known experiments in the attention literature that uses endogenous cues is that of Posner et al (Posner et al., 1978). They had participants fixate on a central line and presented a stimulus (an 'X') either to the right or to the left of this. The participants were told to respond as fast as possible by pressing the appropriate key for the target (for example the left key for the left stimulus). The target was preceded by a cue, in the same location as the fixation line, at varying time intervals, from 0-1000 milliseconds (ms). The cue was neutral, a cross, on 50% of trials. On the remaining 50% of trials, 80% were valid (an arrow pointing in the correct direction to the forthcoming target) and 20% were invalid (an arrow pointing in the opposite direction to the target). They found that there were highly significant advantages and disadvantages to the valid and invalid trials respectively, even when the cue only preceded the target by 50ms. The effect increased up to 150ms following the cue and then declined. Invalid trials up to 150ms post cue onset showed performance at near chance levels.

They found that there was a behavioural advantage conferred to the 'valid' trials when the cue indicated the correct location of the target, and a behavioural disadvantage in the 'invalid' trials, when the cue predicted the opposite location to the target. This led Posner (1980) to formulate the 'Cost-Benefit' paradigm, where a valid cue provides a 'benefit' to the behavioural response, facilitating the reaction to the stimulus, and the invalid cue provides a 'cost' to the behavioural response, inhibiting the reaction to the stimulus.

However, there are instances when attention only favours a new cue if the target is at a new location. In these instances, if the cue is at the same location as the target, attention actually inhibits processing of the target, known as an inhibitory period (Posner & Cohen, 1984). This inhibitory period is thought to begin around 300ms after the original cue, and last for up to 1-2 seconds afterwards (Posner & Cohen, 1984; Steinman & Steinman, 1998). This inhibition is accompanied by an equivalent amount of excitation in the rest of the visual field, allowing attention to be moved more easily to new locations (Steinman & Steinman, 1998).

Posner and Cohen (Posner & Cohen, 1984) demonstrated that the inhibitory effect of directing attention away from the target location, using peripheral cues, arises from the sensory information contained within the endogenous cue. A feedback mechanism prevents attention being continuously drawn to a repeating stimulus. However this only occurs in peripheral vision, foveal cues are always attended to (Posner & Cohen, 1984).

1.3. Overt Attention

Overt attention involves a conscious effort to remain focused on a particular stimulus in the visual field (Mackeben & Nakayama, 1993), which is unchanging and thus would not draw the automatic attentional capacity of covert attention. This can also be described as 'concentration' or 'paying attention'. Voluntary attention can only be sustained for a few seconds at a time, so that what is seen as sustained attention is actually a series of repeated efforts where attention is diverted, the pull of covert attention being an automatic response that takes precedence over the conscious, overt, response. The sudden onset of novel stimuli overrides overt attention in favour of the transient response. The process of overt attention facilitates sustained attention, which uses cognitive, active decisions to keep attention focused on the required portion of the visual field. It is tied to late, top-down, visual processing mechanisms of attention (Steinman & Steinman, 1998).

1.4. Eye Movements and Attention

Attention is independent of gaze, although attention can influence gaze and vice versa (Posner, 1980). A good analogy for this relationship comes from Posner (1980). He states that the relationship between the eye and attention is somewhat like the relationship between the eye and the hand, with the two systems being different physiologically, but nevertheless being linked functionally.

Attention guides saccadic eye movements, so if the eye moves to a new location, attention must be directed there first in order for the eye to then follow. We cannot make saccadic eye movements without first moving visual attention (Sereno et al., 1995). Saccadic eye movements are associated with overt attentional processing (Corbetta, 1998).

All visual information is processed faster when attention is directed to the necessary location or object prior to the eyes being moved. Shifts in attention are used to choose the position of the next eye fixation (Hoffman & Subramaniam, 1995). Hoffman (1995) made two predictions of saccades and attention: that preparation for a saccade produces attentional enhancement; and that attending to a location results in faster saccades. This does not mean that saccades are necessary for attention, but rather attention is required for a saccade to be produced at all. However, according to some (Corbetta, 1998; Nobre et al, 2000) there are similar underlying neural systems for saccadic eye movements and attention. Nobre et al (2000) found that there were common posterior parietal regions, the inferior parietal sulcus (IPS) and inferior parietal lobe (IPL), for the covert attentional and the overt oculomotor tasks, supporting a relationship between saccadic eye movements and visual spatial orienting. Corbetta et al (1998) support this data. We can shift attention covertly, and independently of saccadic eye movements, in response to peripheral stimulation (Posner & Dehaene, 1994).

1.5. Theories of Attentional Processing

There are two broad classes of theories to try and explain how we selectively process information: location-based theories, where attention is said to operate at the level of the spatial relationships, where the object is a secondary consideration; and object-based theories, where attention is said to operate at the level of the individual objects, where locations are spatially invariant.

A summary of the two schools of thought is provided: location-based and object-based accounts for attentional selectivity, this is followed by a comparison of the two types of theories.

1.5.1. Location-based Accounts of Attentional Selectivity

Location-based, or space-based, theories place a limit on the spatial areas information can be drawn from (Duncan, 1984). The most common analogy for how attention works within the location-based theories of attention is the spotlight model (Eriksen & St James, 1986; Posner & Cohen, 1984). This states that attention only highlights relatively small regions of interest, in a small portion of the visual field. The spotlight enhances processing within the spotlight, so that responses are facilitated, making it easier for objects in the 'beam' to be identified and differentiated (Posner & Cohen, 1984; Nakayama, 1990). As stimuli get closer to the edges of the attentional beam, the less a portion of the processing capacity they receive. Outside the spotlight the opposite is seen, detection rates are slower and processing is inhibited and less accurate (Brefczynski & DeYoe, 1999). Many researchers have tried to determine the exact properties of the spotlight: size, shape, speed to movement between locations, whether it is possible to split the 'attentional beam' (Kim

& Cave, 2001). These studies have produced modifications to the original idea of a 'spotlight', the 'Zoom lens' model, where the spotlight has different levels of resolutions and focus (Eriksen & Yeh, 1985; Vecera, 2000), and the 'Gradient' model, where spatial attention is said to be a fixed resource spread across the visual field, providing a gradient of resolution (Vecera, 2000). These modified models still share the basic assumption that selection of visual information is based on location, not objects.

Studies where cues have been used (Brefczynski & DeYoe, 1999; Carver & Brown, 1997; Posner et al., 1978) have traditionally been interpreted in support of location-based theories; where spatial cues influence the perception of a likely location for the forthcoming target. Responses tend to be faster when the cues are valid, in the same location as the forthcoming target, and slower when the cues are invalid, in a different location to the forthcoming target. These studies have shown that, even though there is no explicit requirement for selection by location, the task generally having no bearing on the presence or absence of the cue, this is how attention is operating and any objects in this cued location are likely to benefit (Kim & Cave, 2001).

1.5.2. Object-based Accounts of Attentional Selectivity

Object-based accounts of visual attention place a limit on the number of separate objects that can be perceived at any one time (Duncan, 1984). In object-based accounts, the focus of attentional selection of visual properties is based on objects rather than locations. This idea is in line with the concept that the response to attended objects is enhanced while those objects not attended to show inhibited, or suppressed, responses.

Neisser (Neisser, 1967) was an early advocate of the object-based models. According to him, perceptual analysis takes place in two successive stages: firstly a preattentive stage where the field is segmented into separate objects on the basis of Gestalt properties, for example spatial proximity and continuity. Secondly there is a focal attention stage where each object, perceptually formed in the preattentive stage, is analysed in more detail. Preattentive processing is parallel while focal attention is processed serially; hence there is a limit on how many items we are able to see at any one time (Duncan, 1984).

Duncan (1980 – in: Kim & Cave, 2001) is a good example of these types of theories. He proposed that spatially invariant object representations are constructed in parallel before selection occurs; visual attention then selects the required information from these representations. Selection thus operates at the level of abstract, location-independent object representations rather than feature-based or spatially organised visual input. Duncan (Duncan, 1984) demonstrated this by using two overlapping objects, a line and a rectangle, and requiring the identification of one or more properties of the objects, this could be on one or both the objects. He found that, when discriminations involved the same objects, fewer errors were made, but when the discriminations involved different objects, more errors were made. According to Duncan (1984) the location-specific accounts could not explain the results, as the two objects were overlapping in the same location; there was a difficulty in attending to two objects, which is difficult to account for in purely location-based terminology, as the two objects were at the same location (Egly et al., 1994). An explanation was only possible within the framework of an object-based hypothesis.

However, experiments interpreted within an object-based framework are not necessarily fully conclusive, more than one form of selection is required to explain the combination of grouping and location effects that are typically seem (see: Kim & Cave, 2001). Kramer and Jacobson (1991 – in: Kim & Cave, 2001) showed that distance, as well as object selection, was occurring. Increasing spatial separation between targets and distracters decreased any interference from the distracter, even when the target and distracter were part of the same object. Spatial distance is important in selection, but any interference in this experiment cannot be concluded to be either spatial selection of location based on the distracter, or spatial distance directly influencing the strength of object representations within the spatially invariant representations (Kim & Cave, 2001). Kim and Cave (2001) concluded from their experiment that interference from distracters could be attributed to spatial selection at those locations, providing evidence for selection independently of location. They state that object-based selection may be mediated by selection of the locations of target objects. Their data cannot be explained solely in terms of object-based selectivity, some elements of location selectivity must be considered. Kim and Cave (2001) state that there may be feedback connections from the initial processing of object representations, which then causes the location to be selected, and from that further objects within the visual field.

1.5.3. Location- and Object-based Accounts Compared

Attentional models have to be able to account for both object organisation within a scene, and how it can direct attention to specific locations, and vice versa, how spatial location can influence the selection of objects within a visual scene.

The main problem with these type of theories for attentional processing, is that they have been seen as mutually exclusive; theorists tend to use one or other of the ideas, but less commonly both (for example see: Vecera & Farah, 1994). It is illogical to think that the source of attentional selectivity is based on either objects or locations when our behaviour in the external world clearly calls for both options to be available to us. There is no reason that both cannot be used, and even in the same situation, complementing each other and being activated under particular circumstances, when there is an advantage conferred by our behavioural goal to use one or the other. The way forward for this debate is to accept that both location-based and object-based processes are available to us, what we now have to decide is how separate the two systems are, or rather how integrated. There is no doubt that the two processes can work in tandem, the question now is whether they are synchronised and interlinked.

However, some researchers, (Lavie & Driver, 1996; Vecera & Farah, 1994), traditionally supporting the 'object-based' theories, are now supporting the idea that there are two interlinked processes, one which selects on the basis of location in spatially organised representations, and one which selects location-independent object representations (Kim & Cave, 2001). Egly et al (Egly et al., 1994) used a variation of the spatial cueing paradigm to measure costs of shifting attention between points in the same object and also between objects. They found evidence for both location-based and object-based effects. The invalid cues produced a cost when attention was shifted within objects, indicating location-based components to attentional processing. However, there was a larger cost of the invalid cues when attention was shifted between objects, indicating a significant object-based component to attentional processing. Using fMRI, Egly et al (1994) concluded that the left hemisphere was specialised for location-based effects, whereas the right hemisphere was specialised for object-based effects.

The experiments in Chapters 6 and 7 provide some evidence that the two processes are in fact interlinked, working in harmony to accomplish the same behavioural goal.

In Kim and Cave (2001) there is the admission that the two sets of theorised attentional selection processes can work in parallel, although in this case, the object-representations are concluded to be processed first, the location following as a consequence of the object being perceived. Of course, theorists favouring the location-based theories would say it is the other way around, that the location is selected before the object. The location-based selection is seen as an early selection mechanism and the object-based selection is seen as a late selection mechanism (Vecera & Farah, 1994) (for a discussion of early and late selection mechanisms see Chapter 2). This is a bit like the 'chicken and egg' debate. Further research may clarify things a little further. The research reported in Chapter 7 concludes the latter processing pattern, that locations are processed before objects at the locations. In my mind this makes the most sense, as all objects have to be in a location, it is not possible to have an object without a location, yet it is possible to have a location without an object. In evolutionary terms too, this is a logical viewpoint. In terms of warning signals, we need to know where a target is before what it is. The target could be a danger to us and therefore we would need to know where it was so we could orient, determine what is it, and then launch the 'fight or flight' response. However, the object-based response is not too much slower, otherwise it would not prevent us fleeing safe and/or inanimate objects.

1.6. Inhibition of Return (IOR)

Attention serves a purpose. Surely attention serves the purpose of enabling us to survive in our environment. It has been thought that this is achieved by the facilitation of perceptual processing, to integrate these processes so information can be analysed by the various neural structures (Tipper & Weaver, 1998). But is this really what attention is for? The properties of our world are perceived and selected in order to guide action and behaviour. Tipper and colleagues (Tipper & Weaver, 1998) state that attention is the mechanism by which we select internal representations from the environment to guide action; it is a highly flexible process that is not rigidly constrained like the location-based Spotlight model.

Tipper and colleagues (Tipper & Weaver, 1998) believe attention to be object-based, that the purpose of attention is to achieve behavioural goals within an action-based framework. Attention manipulates object-based representations as our actions are generally directed towards objects, whether animate or inanimate. This does not however, preclude location-based attentional mechanisms, rather that in the circumstances described in their experiments, the object-based mechanisms were dominant. Action-based behavioural goals require object-based mechanisms, not location-based mechanisms, as the participants were typically reaching for an object in space, or attending to objects in a confined space.

Inhibition is the process that enables attention to function as efficiently as it does. This can be dynamic, moving with objects through space, or static, remaining with a particular location. The most important interactions in our environment tend to be animate, so we will have developed effective mechanisms for dealing with these complex perceptual-motor interactions (Tipper & Weaver, 1998). Attention must be able to search a scene to find the object required by the behavioural goal, returning attention to a previously searched area is inefficient, thus we have developed what has been termed 'Inhibition of Return' (IOR) to prevent this (Tipper & Weaver, 1998). Posner & Cohen (Posner & Cohen, 1984) argue that once attention has been directed to a location, inhibition prevents it from returning. However, this is defined as a location in space rather than a location on the retina, which would obviously cause an even less efficient search process (Tipper & Weaver, 1998). Many objects in our environment have a propensity to move, locations do not. It is therefore likely that we have evolved an IOR mechanism to deal with this feature of search. It makes sense for the effects of IOR to be longer lasting to locations than to objects within our environment; spatial locations are stable, particularly if there are no animate objects in that location, animate objects though, are capable of changing suddenly, and any long-term inhibition would impair performance with regard to that object (Tipper & Weaver, 1998). It is possible for object-based IOR and location-based IOR to exist simultaneously and individually, depending on the task.

1.7. The Limited Capacity of Attention

There is a danger in psychological research to overlook the most basic qualities in the hunt for intricate knowledge of a process. After a while this oversight is accepted and, as a result, there are some theories contrary to a basic quality that are formulated. This has happened to some degree in attentional research. James (1950) refers to attention as having a limited capacity, the idea that we cannot attend to more than a few items at a time. While this idea holds for much of the research field (for example: Carver & Brown, 1997; Lee et al., 1999; Ward & Duncan, 1996), the reverse idea has been held by some, (for example see Deutsch & Deutsch, 1963 - in Neisser, 1967).

Attention has to have a limited capacity; it is not possible to attend to all things at once, so there must be some form of filter to get rid of information that is not relevant. We are constantly bombarded with millions of pieces of sensory information, along with internal thought processes, it is impossible for us to process this vast amount of information; the brain would not be able to cope with the processing load. It is possible that processing of some items may lead to an impairment of processing for others.

Donald Broadbent suggested that attention acted like a filter, preventing an overload of information by allowing some inputs through and not others. His 'Filter Model' (see Figure 1.1), shows how information is let through to further processing on the basis of a 'first come first served' method of selection. It is also known as the 'Bottleneck Theory' and the 'Early Selection Theory' (Broadbent, 1977). A discussion of 'early selection' and 'late selection' ideas is to be found in Chapter 2. In this model, inputs compete for the output channel and must pass through the sensory store if they are to be processed further. However, while the inputs wait in the sensory store they decay, becoming less clear the longer the wait for processing capacity. The only way the competing input gets through is when the attentional filter swings in a favourable direction

The shift in attention takes time, so that, when recall is systematic, relying on the predesignated order of recall where order of presentation denotes order of recall, a greater amount of time is needed for the filter to swing back and forth, thus decay is more evident. Broadbent suggested that attention operates at the level of the filter and that everything that was filtered out was lost (Broadbent, 1977).

1.8. The Biased Competition Model

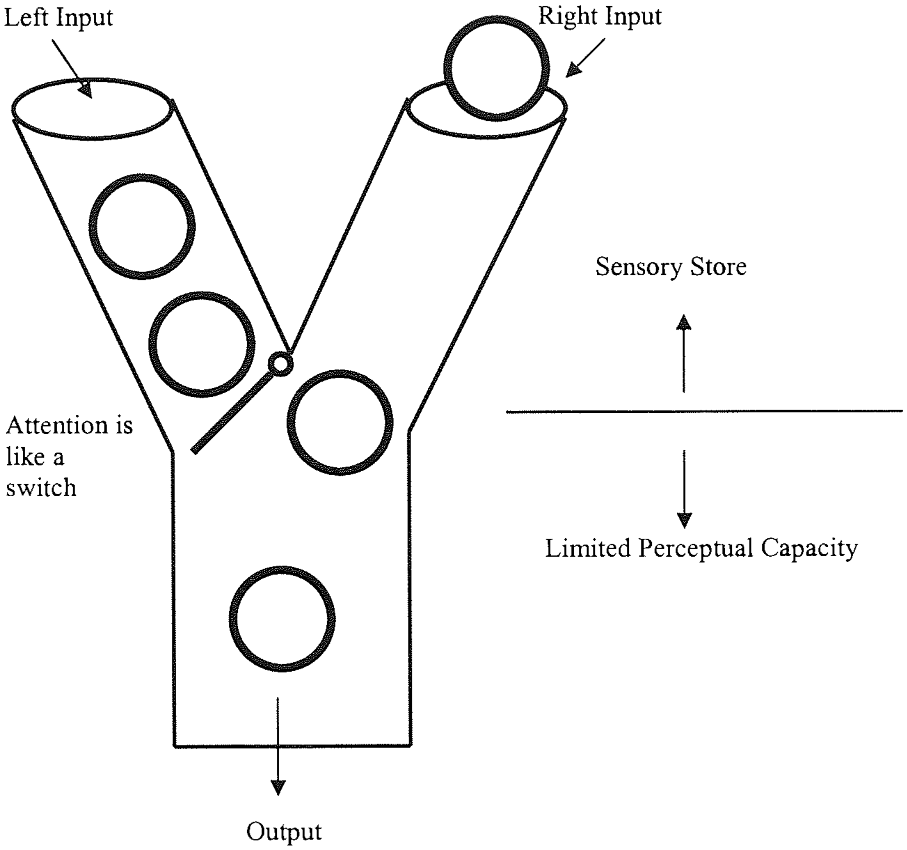
An alternative to Broadbent's Filter model, within the area of a limited capacity of attention, is the 'enhancement' theory of attention that comes in the form of the 'Biased

Competition Model' (Desimone, 1998; Desimone & Duncan, 1995). This model states that the enhancing effect of attention is best understood in terms of competition between all stimuli in the visual field for control of behaviour, information in the visual field does not wait to be processed, rather there is a cognitive bias on which information is processed first. A full visual analysis of a scene is inconsistent with the idea of attention having a limited capacity so there is a competition between objects in the visual scene for analysis. There is a computational bias towards the processing of behaviourally relevant stimuli. After the initial parallel activation of the cortical representations for all stimuli, behaviourally irrelevant stimuli information is suppressed, or inhibited, in favour of behaviourally relevant stimuli (Desimone, 1998). This model supports the view that attention is an emergent property of numerous neural mechanisms working together to resolve competition in visual processing and behavioural control (Desimone & Duncan, 1995).

There are five main parts to the Biased Competition Model relative to cortical visual processing: objects in the visual field compete for limited processing resources; the competitive interactions are stronger the more stimuli are competing for the same processing resources in the same area of cortex; the competitive interactions can be biased in favour of a single stimulus by a variety of mechanisms, rather than one overall attentional mechanism; the feedback as a result of the ensuing processing is not purely spatial; and finally, that the source of feedback is involved with working memory (Desimone, 1998).

Through mutually suppressive interactions, objects in the visual field compete for the responses of cells in the visual cortex, the strongest responses being where cells are competing in the same area of cortex. There is no single 'attentional control' mechanism', rather different mechanisms within the attentional system dictate which stimuli will be processed. This model sees attention as a slow, emergent process, resulting from competitive interactions working in parallel across the visual field, rather than a rapid spotlight mechanism (Duncan, 1984).

Figure 1.1: Broadbent's Filter Model of Attention



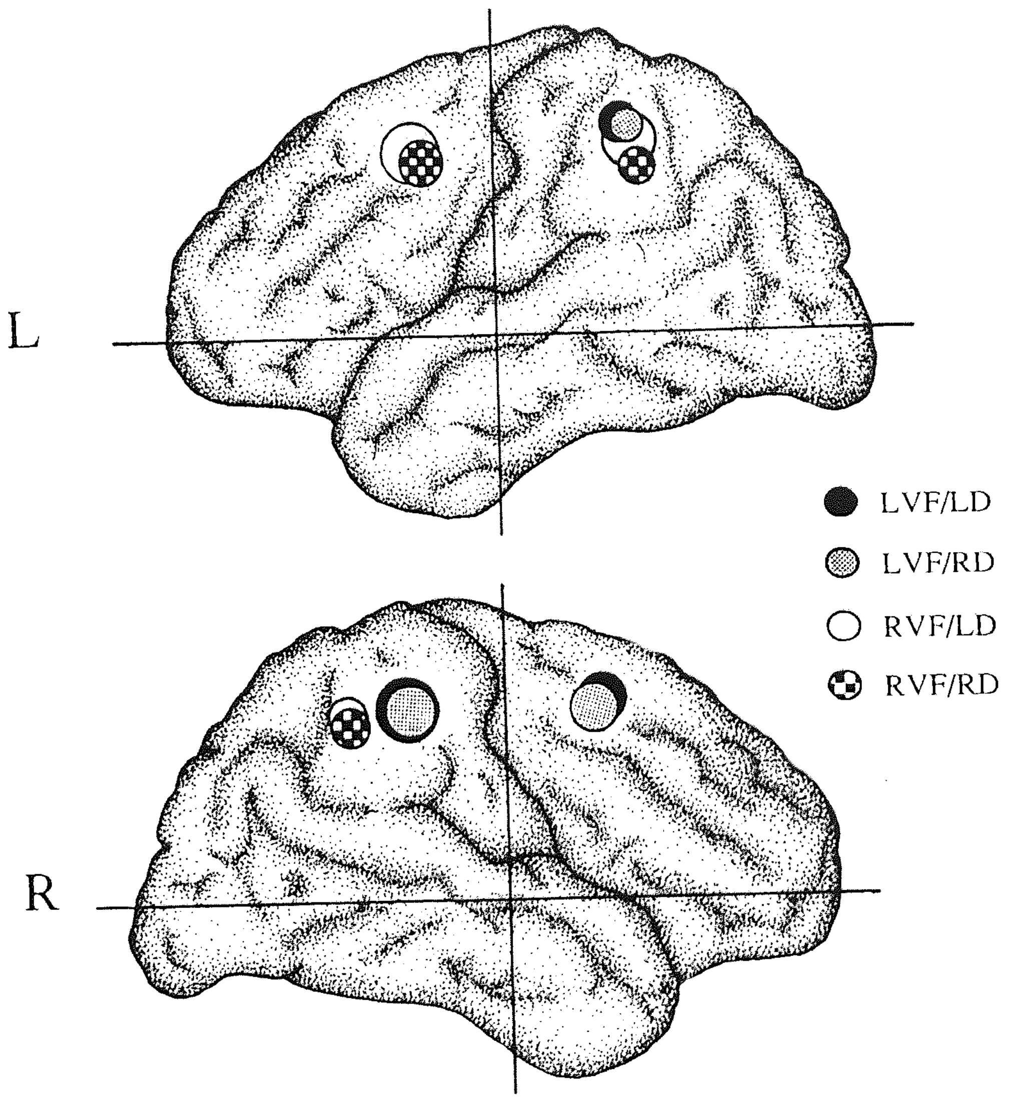
A switch-like filter filters the inputs. The last inputs to go into the sensory store are most likely to be recalled behaviourally, as they have spent less time in the sensory store, and have decayed less than inputs at the beginning of a sequence.

1.9. The Neurological Basis of Attention

There is little doubt that faster and more accurate responses are made to stimuli in expected rather than unexpected locations. Attention enhances sensory processing in specified cortical areas which process attended areas of space (Awh & Jonides, 1998). The frontal and parietal cortices are generally agreed to be involved with attentional processing, in what is termed the 'fronto-parietal' network (for example see: Awh & Jonides, 1998; Corbetta, 1998; Coull et al, 1998; Posner & Dehaene, 1994). The core elements of the spatial attention network have been defined as the posterior parietal cortex (PPC), the frontal eye fields (FEFs), the lateral and medial premotor cortex, the anterior cingulate (AC), and other subcortical areas (Coull & Nobre, 1998). Mesulam (1980 – see Awh & Jonides, 1998) was among the first to implicate the fronto-parietal network in attentional processing. He said that the frontal areas coded spatial-motor representations while the parietal areas coded spatial representations of space. He proposed four primary brain regions, supporting the conclusions of Coull & Nobre (1998): the frontal component, dorsolateral or premotor prefrontal cortex; the posterior parietal component; the anterior cingulate; and subcortical elements, which modulate arousal and the vigilance necessary for attentional processing (Awh & Jonides, 1998).

The parietal lobes are involved with the representation of space that we see, attend to and act in; they are crucial for orienting (Jackson, et al., 1994) and spatial attention to objects (Robertson, 1998). The parietal cortex is implicated in spatial and attentional processing by many researchers (detailed during the course of this section). There are many consistencies between the specific areas thought to be involved, and also with their functions. The posterior parietal cortex (PPC) is the general site of activation during attentional experiments, containing the superior parietal lobe (SPL), the inferior parietal lobe (IPL) and the inferior parietal sulcus (IPS). The PPC is implicated in attentional shifts occurring independently of gaze (Milner & Goodale, 2000). These areas are consistently activated during attentional experiments, and each area is generally linked to particular features of attention. There is also a laterality between the hemispheres, which is less consistent between experiments, although the general principles are commonly accepted.

Figure 1.2: Locations for Shifts in Visuo-Spatial Attention: Locations of Superior Parietal and Frontal Sources. Taken from Corbetta et al (1993, pp1209).



Using a peripheral stimulus in a cue-based paradigm, increased activation was seen in the superior parietal and frontal lobes for invalid relative to valid trials. The valid trials were also performed faster than were invalid trials.

RVF – right visual field
LVF – left visual field
LD – left direction
RD – right direction

1.9.1. The Parietal Cortex

The posterior parietal cortex has been termed the 'parieto-temporo-occipital crossroads' (Critchley, 1953, in (Stein, 1989) due to the connections with other areas of the brain. These connections are centred around the superior parietal lobe and the inferior parietal lobe. The posterior parietal cortex brings together sensory, motor and attentional processing to create a representation of external space and our position relative to that (Stein, 1989).

The anatomical boundaries of the Posterior Parietal Cortex (PPC) are distinct anteriorly, the postcentral sulcus, laterally, to the postero-medial part of the superior temporal sulcus and the posterior portion of the lateral sulcus, and posteriorly, as far back as the parieto-occipital sulcus (Hyvarinen, 1982; Stein, 1989). The PPC is split into the superior parietal cortex (SPL) and the inferior parietal cortex (IPL). The IPL is ventral to the inferior parietal sulcus (IPS), which lies between the SPL and the IPL, while the SPL is dorsal to the IPS (Parent, 1996). The IPL is the cortical association area, with connections to the rest of the parietal cortex as well as occipital and temporal cortices (Parent, 1996).

The SPL (Brodmann's area 5) connects with the secondary somatosensory cortex anteriorly and posteriorly, the motor cortex ipsilaterally and the premotor cortex (Stein, 1989). Subcortically, the main inputs are from the pulvinar and posterior thalamic nuclei, which receive inputs from the ocular motor and neck movement areas of the superior colliculus (Pearson et al, 1978 - in Stein, 1989). The IPL (Brodmann's area 7) connects to the somatosensory, auditory and visual cortices. It also receives projections from the motor and premotor cortices, the frontal eye fields (FEFs), and prefrontal cortex (Stein, 1989). Subcortically the main connections are with the superior colliculus, the pulvinar and from the cerebellum and basal ganglia via the thalamus (Asanuma et al, 1985 - in Stein, 1989). To sum up, the SPL connects somatosensory with motor, and the IPL connects visual, auditory, ocular motor and limb motor areas. The PPC provides connections between auditory, retinal, somatosensory, visual and proprioceptive areas (Stein, 1989). The PPC is therefore an ideal site for attentional processing, bringing all the strings of perception together, highlighting what is relevant in the external world, determining the level of processing needed and then providing the feedback required for appropriate behavioural responses. So, in terms of what these connections mean in terms of processing, the PPC is an integral part of any processing that happens in the brain, be it motor, visual, auditory, proprioceptive, or somatosensory.

Generally, the right parietal cortex is accepted as dominating the response for spatial attention (Corbetta et al., 1993; Awh & Jonides, 1998; Posner et al, 1984) while the left hemisphere is accepted as dominating the response for non-spatial, temporal, and selective attention (Coull et al., 1998, Macaluso & Frith, 2000). This laterality does not presuppose the two hemispheres being exclusively 'in charge' of one type of attentional processing, rather that both hemispheres are more involved in one type of attentional processing than the other. There is also some evidence emerging to back up this theory that both hemispheres are involved in both types of attentional processing, (Coull et al., 1998). An important role of the parietal cortex is in processing that sensory information which relates to behaviour, the planning of actions, and how the intention to respond behaviourally, as a result of attentional influences, is carried out; transforming sensory information into behaviourally relevant motor information (Snyder, et al 2000). The role of the parietal cortex can be thought of as being dominated by visuo-motor components of the task, rather than the explicit visual demands, the parietal cortex being essential for the translation of motor commands into extrapersonal space coordinates, thus visuospatial coordination (Walsh, et al 1999). The parietal cortex is also involved in the orienting of attention (Posner, Walker, Friedrich, & Rafal, 1984) to the contralateral visual field (Macaluso & Frith, 2000).

There is also some evidence that the parietal cortex is involved in peripheral attentional processing, and not central processing (Coull & Frith, 1998; Michie et al., 1999; Harter & Aine, 1984). In a study by Vandenberge (1997 - in: Macaluso & Frith, 2000) the SPL was preferentially activated for discriminations in the periphery, but not for discriminations centrally. For the central task the inferior occipital areas were preferentially activated.

Corbetta et al (Corbetta et al., 1993) used peripheral targets in a visual shifting attention task, using PET. They found that valid trials were performed more rapidly than were invalid trials. They found neural activation in the SPL, the superior frontal cortex (SFC), the inferior frontal cortex (IFC) and the AC (see Figure 1.2). The activation was bilateral in the right visual field condition for the SPL, but contralateral to the field of presentation for all other conditions. The frontal activation was absent during the passive viewing condition, indicating it has an active role in attention, either motor or visual, but not in passive viewing. The SPL activation was present in all conditions, suggesting it is involved in spatial shifting of attention, under both voluntary and automatic conditions (Awh & Jonides, 1998). These and other results suggest that the superior parietal and left premotor and prefrontal areas are involved in the allocation of spatial attention to peripheral locations (Awh & Jonides, 1998).

1.9.2. Lateralization of Function

There is a school of thought that believes that the right parietal cortex is important for attending to both halves of the visual field, but the left parietal cortex is only important for attending to the right visual field (RVF) (for example see Walsh, et al, 1999; Posner & Dehaene, 1994). Also that the right hemisphere is involved in covert, unconscious attentional processing while the left hemisphere is concerned with conscious, overt attentional processing (Gainotti, 1996). It has also been proposed that the right parietal lobe is biased towards global processing, shifting attention between locations, and the left parietal lobe is biased towards local processing, shifting attention between objects, (Posner & Peterson, 1990; Wright, 1998), fitting in with the idea that the right parietal cortex is dominant for whole scene analysis. However, it contradicts the idea of the left parietal cortex being dominant for the right visual field only, but rather puts forward the idea of it being involved with local processing instead.

This is a somewhat odd laterality, indicating that the right parietal cortex is more involved with the process of attention than is the left parietal cortex, at least on some level. It could also indicate that the right parietal lobe has executive control over the attentional processes, and the left parietal lobe is only involved for certain types of processing in the RVF. However, this is not necessarily the case, as is the idea that the right hemisphere is activated for the entire visual field and the left hemisphere only for the RVF. It may be the case that the reverse is true, in terms of covert and overt attentional processing and in terms of the right hemisphere being more active over the whole visual field than is the left hemisphere, as the experiments in this thesis will show, the picture is a little more complicated and is highly dependent on task requirements (Chapters 6 & 7).

There are three key areas of the posterior parietal cortex (PPC), which have consistently been implicated in the process of attention, the superior parietal lobe (SPL), the inferior parietal lobe (IPL), and the inferior parietal sulcus (IPS). The PPC is implicated in spatial perception, particularly that relating to behaviour (Snyder et al., 2000), being part of the dorsal pathway. The PPC also controls eye movements and mediates attentional shifts (Wright, 1998). There are two major cortical pathways from the visual to higher areas; these are the ventral and dorsal pathways (see Chapter 2 for more detail). Both begin in the primary visual cortex. The ventral pathway is directed to the inferior temporal cortex; it is implicated in object visual object recognition. The dorsal pathway is directed to the PPC and is implicated in spatial perception (Webster & Ungeleider, 1998), it is important for spatial perception and visuomotor performance (Desimone & Duncan, 1995). Lesions of the PPC do not impair object discriminations; rather they impair visuospatial processing (Webster & Ungeleider, 1998).

1.9.3. The Superior Parietal Lobe

The SPL has connections to the visual system and to the premotor cortex, making it an important area in the production of visually guided limb movements (Rushworth, et al., 2001). The SPL is commonly considered to be one of the major sites of processing for spatial attention and for spatial processing of external areas (Posner & Peterson, 1990). Activity in the SPL is related to the elaboration of somatosensory information (Rizzolatti, et al 1997), which could suggest that it is activated when behavioural goals involve making an overt, non-linguistic, response. The SPL processes peripheral information preferentially (Macaluso & Frith, 2000), being more active when attention is shifted into the periphery, in particular on the basis of cognitive or sensory cues which are independent of the overt response (Corbetta et al., 1993). There is a great deal of evidence (Corbetta, 1998, 1998; Coull & Frith, 1998) that shows the mechanisms for shifting attention are located here in the SPL and the inferior parietal sulcus (IPS), the strongest activation being in the right hemisphere (Corbetta et al, 1995), this being consistent with the idea of a laterality in the parietal cortex, the specifics of which are detailed above. The SPL is involved with covert orienting, spatial coding, stimulus discrimination (location perception), spatial coding (object perception), and spatial compatibility (stimulus and response) (Le et al, 1998). Lesions in the SPL are associated with symptoms such as visual extinction, which differs from neglect (see below) in that the patients perceive isolated stimuli in the contralesional field, but perception is impaired when accompanying stimuli appear on the ispilesional side also (Awh & Jonides, 1998).

1.9.4. The Inferior Parietal Lobe

The IPL is part of the visuo-motor network specifically dealing with grasping (Rizzolatti et al., 1997). There are at least two main sub-divisions to the IPL with very different connection patterns. One sub-division connects to the occipital cortex and is involved with visual and occulomotor processing, while one sub-division connects to the temporal cortex and is concerned with somatosensory and premotor tasks. Only this first area is concerned with visuospatial attentional orienting (Rushworth, et al., 2001; Rushworth, et al., 2001). Activation in the right IPL, along with the right intraparietal sulcus is significantly higher for spatial orienting conditions (Coull & Nobre, 1998), while the left intraparietal sulcus is implicated in temporal orienting (Coull & Nobre, 1998). Damage to the IPL is considered to be the main cause of unilateral, or hemispatial, neglect, particularly in the right hemisphere (Awh & Jonides, 1998; Milner & Goodale, 2000). Patients with hemispatial neglect have no awareness of the left side of space and/or objects; typically they neglect to report the left half of a visual scene or the left half of the objects within that scene (Milner & Goodale, 2000). This failure in reporting is interpreted as being a failure of the distribution of attention to that particular side of space (Tipper & Weaver, 1998).

Damage to one side of the PPC, usually in the region of the IPL, results in a variety of symptoms collectively known as Unilateral Neglect. These symptoms include visual disorientation; misreaching and neglecting the contralesional side of visual space; disturbances of the visual spatial scheme; and constructional apraxia, the inability to draw or construct objects and pictures (Hyvarinen, 1982). Neglect has successive stages of attentional deterioration (Tant et al, 2002): firstly early, automatic orienting of attention towards the ispilesional side of space deteriorates, the patients lose the ability to do this successfully; then the disengagement of attentional focus from the ispilesional to the contralesional side of space deteriorates; and finally, the patient experiences a general reduction in attentional information processing capacity.

Unilateral neglect is most common after damage to the right parietal lobe, specifically the IPL (Dronkers & Knight, 1988), producing left-sided neglect. Damage to the left parietal lobe can produce neglect symptoms but to a much lesser extent (Jackson et al., 1994), and this is more likely to follow bilateral lesions (Balint, 1909, in (Stein, 1989). This has been taken to indicate that the right parietal lobe contributes more to visuospatial processing than does the left parietal lobe, even in the right visual hemifield (Stein, 1989); the right PPC controls both sides of attentional space whereas the left parietal lobe only controls the right side of space (Hyvarinen, 1982; Jackson et al., 1994). The right parietal cortex is concerned with space-based processing, and damage to this area produces impairment is space-based processing; whereas the left parietal cortex is concerned with both space-based and object-based components, damage to this area produces an impairment in both sets of processing (Egly et al., 1994). Unilateral neglect is most common after right hemispheric lesions in right-handers, however it can be reported after left-hemispheric lesions in right-handers, though the symptoms are generally not as severe and of shorter duration (Dronkers & Knight, 1988). There is little information about attentional disorders, including neglect, in left-handers. Dronkers & Knight (1988) found that a left-handed patients showed classical left-sided neglect, more commonly associated with right-handers, with a right hemisphere lesion. They postulated that, just like a subset of left-handers having a well organised right hemisphere dominance for language, the attentional system may be inversely represented in some left-handers relative to right-handers, the left hemisphere being concerned with the entire visual field and the right hemisphere being concerned with the left visual field only (Dronkers & Knight, 1988). It could also indicate that the left hemisphere is more involved in certain types of attentional processing than has been previously thought.

It appears that both the IPL and the SPL are important for intact attentional processing, functionally reliant while being dissociable (Awh & Jonides, 1998).

The IPS is involved in spatial orienting (Donner et al., 2000), mainly the right IPS, and temporal orienting, mainly the left IPS (Coull & Nobre, 1998). It is also involved in sustained, active, covert attention to the peripheral visual fields (Martinez et al, 2001). Rushworth et al (Rushworth et al, 2001) distinguish motor attention from orienting attention, when referring to attention with relation to bodily movements during the behavioural response to an attentional task. They locate this motor attention in the left hemisphere, despite the response being produced with the left hand in right-handed individuals. They located this effect, using PET, to the anterior portion of the intraparietal sulcus, a region already associated with orienting attention (Rushworth, et al., 2001).

1.9.5. The Frontal Cortex

The frontal cortex is seen as having an executive function regarding attention, being involved in the recruitment and control of brain areas through attention, during cognitively complex tasks (Posner & Dehaene, 1994).

The frontal areas appear to have a particular sensitivity for task-relevant information, with increased activation being evident when tasks are more complex (Banich et al., 2000), making the frontal areas leading candidates for an overall 'executive' role in attention, and online monitoring resource to which all attentional processes are referred. The prefrontal cortex is thought to be involved with expectation; it is possibly the site of interaction between automatic and non-automatic neural processing, allowing for flexibility of adaptations to shifts in context and perspective (Nobre et al, 1999). This online control system is thought to be only active when necessary to override automatic, intrinsic attentional processes (Banich et al., 2000).

The frontal eye fields (FEF) are involved in visual and motor processing, and are central for transforming the outcome of visual processing into behavioural commands (Bichot & Schall, 1999). FEF neurons are not selective for stimulus properties such as orientation and colour; rather they are necessary for the location of the target before the saccadic eye movement occurs. The FEF encode a map of the visual field where stimulus locations are selected for orienting based on behavioural relevance drawn from prior knowledge and stimulus saliency (Bichot & Schall, 1999).

The anterior cingulate is thought to have an executive function of attentional processing (Posner & Dehaene, 1994). It has two important functions: to maintain a focal awareness of the target item, and to exercise some control over the attentional system as a whole. The anatomy of the anterior cingulate shows that there are connections to the posterior parietal lobes, indicating that it is at least involved in the fronto-parietal network. However, as we shall see in Chapters 5 and 7, there has been no evidence of activation of the anterior cingulate during the course of these investigations. This may be due to task demands, being of a covert attentional nature, rather than overt and requiring the input of working memory, another process mediated by the anterior cingulate (Posner & Dehaene, 1994).

Much of the literature on the neurological mechanisms of the brain has been found using studies on non-human species. As a result some of this literature has not been included for personal reasons. However, it is noted that much of the information contained in this review was drawn from articles based on experiments with non-human species; this was unavoidable due to a lack of data from human subjects.

Chapter 2: Attentional Modulation of the Primary Visual Area: Evidence from the Literature.

Visual selective attention is a cognitive function designed to resolve ambiguities in visual coding that arise when multiple stimuli are competing for processing, allocating its limited resources to visual targets. It is an essential brain function, enabling the selection and processing of priority information in the visual field (Heinze et al., 1994). This chapter is concerned with the occipital locus of attentional modulation, with the focus being on the primary visual cortex (V1). A brief discussion of the properties of the visual cortex begins this chapter, followed by a more detailed discussion of the locus of attentional modulation within the visual cortex, and evidence for and against the modulation of the primary visual cortex will be presented.

2.1. The Visual Cortex

The visual cortex is located in the occipital lobe. It receives input from the retina via the lateral geniculate nucleus (LGN). The primary visual cortex is the first in a hierarchy of visual areas. Other names for it include the striate cortex, V1, and Brodmann's Area 17. Like the rest of the human cerebral cortex, V1 consists of layers of cells; about 2mm thick and there are approximately 100 million cells of V1 in each hemisphere (Bruce, et al., 1996). The layers vary in thickness and concentrations of cells vary from layer to layer. Below the layers is white matter, the axons that connect V1 to other areas in the visual cortex, terminating at synapses in the layers they direct to. Cortical cells from all layers form a complex network where fibres run horizontally within layers and vertically between them.

Around 80% of cells in the visual cortex are reserved for processing the central 10 degrees of vision (Drasdo, 1977). This is referred to as cortical magnification, where the centre of the visual field is disproportionately exaggerated in the cortex; a disproportionately large proportion is devoted to a very small area of the retina, the fovea, so that the area which requires the most detailed processing is given the largest share of the available cortex (Bruce, et al., 1996). This bias starts in the retina and carries on throughout the visual system, foveal representations swelling steadily. This is a logical evolutionary step, as the central 10 degrees of visual angle (Drasdo, 1977) are needed for detailed processing of the visual field, outside this area less detailed processing is required, a head turn can bring into focus that worthy of further processing in the periphery.

2.2. The Two Visual Pathways

There are two visual pathways that are generally agreed to stem from V1, the ventral and dorsal pathways (Lamme, 2000; Zeki, 1993). Please refer to Figures 2.1a and 2.1b throughout this section. The ventral pathway terminates in the temporal lobe and is considered to be concerned with form, including colour. The dorsal pathway terminates in the parietal cortex and specialises in spatial vision. These pathways can be seen as cortical prolongations of pathways starting in the retina, the magnocellular, containing M-cells, and parvocellular pathways, containing P-cells. Information comes in though the retina to the LGN, where is it segregated into layers, the magnocellular layers being 1 and 2, while the parvocellular layers are 3-6 (Zeki, 1993).

The magnocellular pathway connects with the dorsal pathway and the parvocellular pathway connects to the ventral pathway. The two pathways remain segregated throughout the visual system, except in V1, reinforcing the idea of them representing two functionally distinct processing pathways (Livingstone & Hubel, 1988). Although information is separated between these two pathways, they are not independent and there is a substantial amount of communication between them (Schwartz, 1999).

The dorsal pathway is concerned with the perception of form, motion, depth, and subtle luminance differences. The cells contained in it are heavily myelinated, and produce a transient response, responding rapidly to stimulation; (McGuire et al, 1989). McGuire et al (1989) showed that areas from the magnocellular division of the visual pathway, from the LGN to the primary and secondary visual cortices up to the higher parietal areas, were heavily myelinated, indicating rapid information processing. Information from the magnocellular pathway gets to the visual cortex around 7-10ms faster than the parvocellular pathway. This allows the visual system to rapidly locate objects and then identify them (Steinman & Steinman, 1998). The dorsal pathway processes the visual location of objects, constructs cognitive spatial maps and provides visual guidance for motor acts initially triggered by the ventral pathway (Mishkin et al, 1983).

The ventral pathway is concerned with the perception of detail, spatial vision, form and colour, highly important in tasks such as reading and detailed visual analysis. The P-cells have a sustained response, responding the whole time the stimulus is in the receptive field (RF). The RFs of the P-cells are smaller than those of M-cells, the P-cells care concerned with detail rather than global features like the M-cells. The axons of P-cells are smaller and thinner than those of M-cells; they are much less myelinated, responding much less rapidly to information, producing a sustained response to stimuli in the visual field. The magnocellular pathway has highly myelinated axons and produces a much more transient response to visual stimuli, enabling this pathway to respond much faster to stimuli in the visual world (Steinman & Steinman, 1998). V1 processes the visual identification of objects and connects to areas that mediate cognitive associations of visual objects with other events, for example motor responses and emotions (Mishkin et al., 1983).

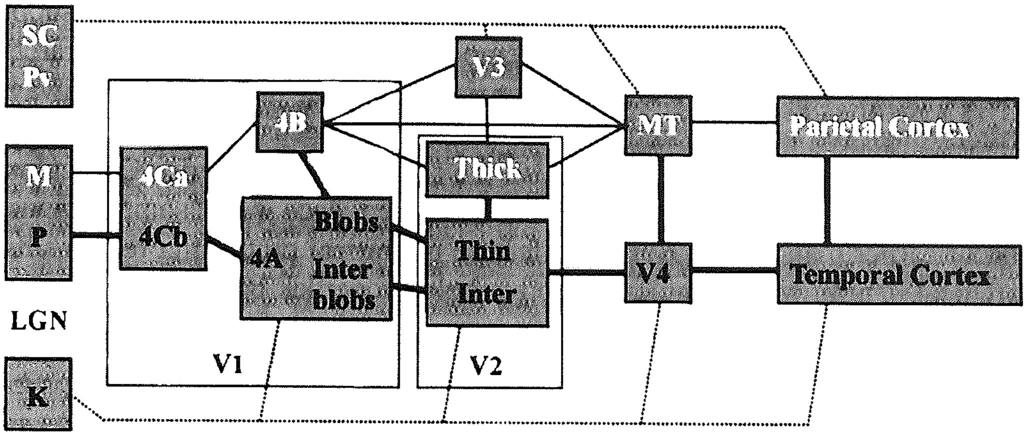
The two pathways have been considered to be mutually exclusive (Zeki, 1993), but evidence is emerging that this may not be entirely the case (Kaplan, 1991; Zrenner, 1991). For the purposes of this discussion the above hypotheses will be adhered to.

2.3. The Primary Visual Cortex

V1 extends over the depth and lips of the calcarine fissure in the occipital cortex, but varies in size and precise location so that generalising between individuals is not possible (Tootell et al., 1998). V1 is the most well defined area of the visual cortex; many agree its anatomical boundaries, both historically and recently (Brodmann, 1909; Stensaas et al, 1974). V1 is highly specialised and deals with elementary processing of input, visual information passes through V1 first, going through V1 to the extrastriate and higher cortical area (Bruce, et al., 1996). V1 deals with a basic level of analysis for incoming information. The cortical areas later in the hierarchy deal with more advanced processing.

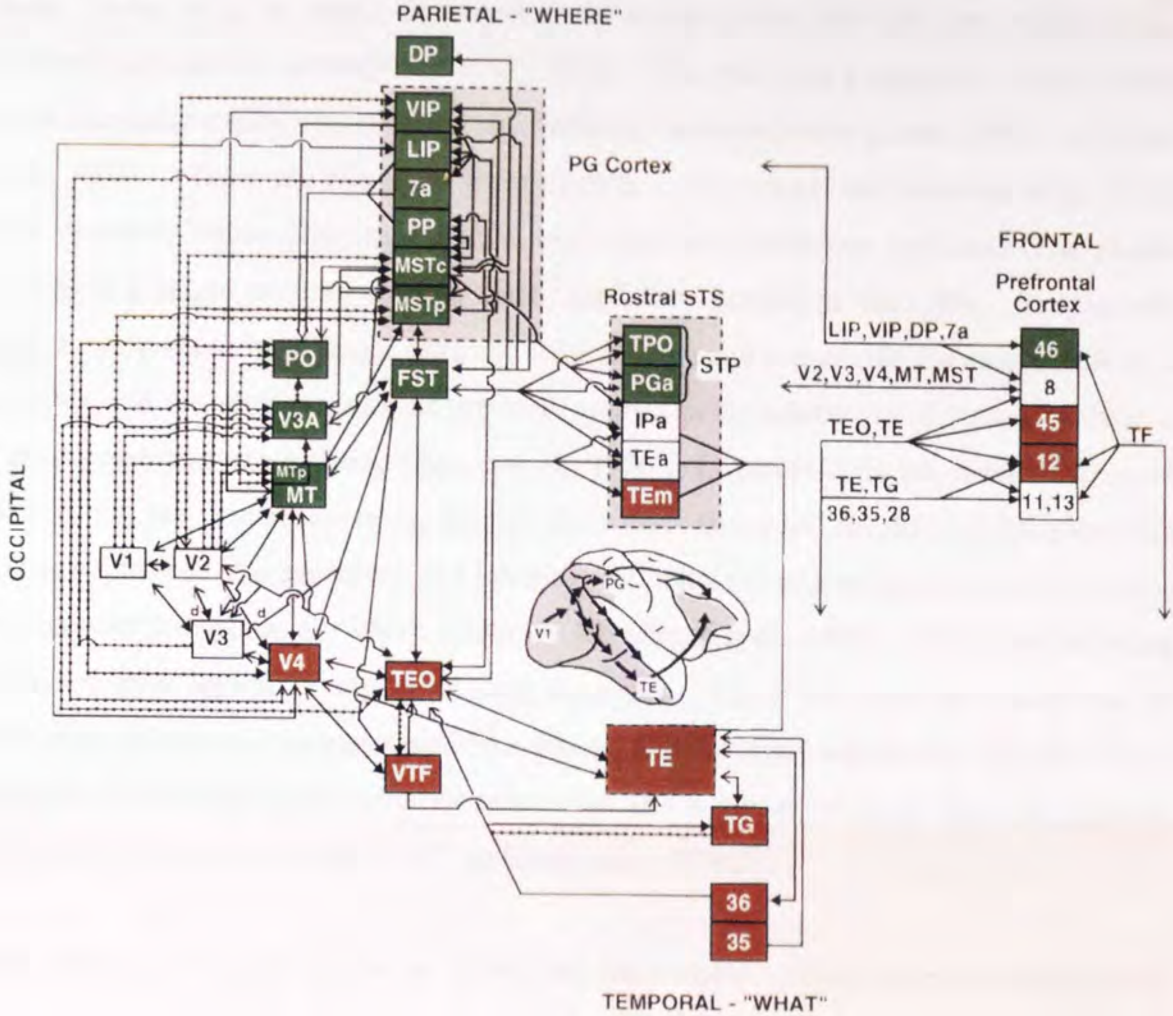
Figure 2.1: The Dorsal and Ventral Pathways Extending from the Visual System Towards the Parietal and Temporal Lobes.

Figure 2.1a Taken from Lamme (2001 pp. 389).



In the Lateral Geniculate Nucleus (LGN) there are different layers of cell types. These cells have different functional characteristics and are the origins of different pathways extending from V1. Twp cortical pathways emerge from these divisions, the dorsal pathway and the ventral pathway. The dorsal pathway extends towards the parietal cortex, is composed of mainly magno-cells (white letters, thin lines) and is concerned with the processing of information about space, movement and action. The ventral pathway extends towards the temporal cortex, is composed mainly of parvo-cells (black letters, thick lines) and is concerned mainly with object identification and perception.

Figure 2.1b) Taken from Webster & Ungeleider (1998, pp.25, colour plate 1).



Heavy arrows relate to feedforward connections and open arrows relate to feedback connections. Solid lines indicate both central and peripheral visual field connections, dashed lines indicate connections from the peripheral visual field only. Red boxes relate to the ventral pathway, while the green boxes relate to the dorsal pathway. White boxes are not specifically associated with either area. As can be seen there are multiple feedforward and feedback connections between the cortical areas.

V1 has a striped appearance under the microscope, hence the name striate cortex, due to the cells forming layers of different densities (see Figure 2.2). Below these layers is white matter, comprising the axons that connect the striate cortex with the rest of the cortex, LGN and sub-cortical areas (Bruce et al., 1996). The cells form a complex network where fibres run horizontally within layers and vertically between them (Lund, 1988 - in: Bruce et al., 1996). There are two main types of cells in V1, simple and complex cells. Cells have receptive fields (RFs) that contain excitatory and inhibitory portions. The simple cells have a single excitatory and a single inhibitory portion in their RFs. Simple cells have a preference for a single attribute of a stimulus, for example the orientation of a stimulus, and this attribute must be precisely attuned to the selectivity of the cell or there is a greatly reduced rate of firing (Bruce et al., 1996). Complex cells are similar to simple cells in that they are selective for stimuli attributes. However, the RFs of complex cells cannot be marked into excitatory and inhibitory regions, rather a suitably oriented stimulus will provoke a response anywhere within the RF (Bruce et al., 1996). V1, as well as being organised into layers, is organised into columns. These columns are comprised of orientation selective cells organised into sections of comparable selectivity. All the cells in one column have the same preferred selectivity, and adjacent columns represent adjacent orientations (Hubel and Weisel, 1977 in Bruce et al., 1996).

Also within V1 are cells known as 'blobs' and inter-blobs'. These were revealed in 1979 by Wong-Riley (Bruce et al., 1996) are situated in all layers except layer 4. It is not entirely clear what role blobs and inter-blobs have in visual information processing. It is possible that they are cortical prolongations of the M and P pathways in the LGN, the blobs being an extension of the P pathway, having a role in colour information processing and the inter-blobs being an extension of the M pathway, having a role in the processing of spatial structure and motion (Livingstone & Hubel, 1988). This is, however controversial as the boundaries between these cells are indistinct, and their responses to stimuli vary smoothly between the two regions (Bruce et al., 1996).

2.4. The Visual Response

The visual system, up to and including V1, is commonly thought of as being a passive and automatic image-processing machine that remains unaffected by cognitive influences (Gandhi et al, 1999). However, the image of a passive processor is not entirely accurate, for V1 is modulated as strongly as any other visual area by attention, just not at the level of the initial inputs, V1 is an active processor and is subject to feedback modulations from higher cortical areas (Gilbert et al, 2000). A certain amount of evidence to support this view comes from the EEG data, in the form of ERP components, specifically P1 and N1 (see Figure 2.3).

P1 is the first positive component post stimulus onset, usually with a latency of around 80-130ms (Martinez et al, 2001), the generator of the P1 has been located to the dorsal extrastriate cortex, possibly having a source in the secondary visual area, V2 (Hillyard & Anllo-Vento, 1998), although this is by no means certain. The P1 component is thought to be linked to the suppression of information from unattended locations (Muller & Hillyard, 2000). The generator of the N1 component is the first negative component post stimulus onset, usually around 150-200ms (Martinez et al., 2001). N1 has been located to many sources, as it is broadly distributed over posterior and anterior regions of the scalp (Eimer, 1998). The N1 component is thought to reflect the facilitation of discriminatory processing of attended locations (Muller & Hillyard, 2000). C1 is the initial component of sensory visual perception, and begins around 50-60ms post stimulus onset (Martinez et al., 1999; Martinez et al., 2001; Heinze et al., 1994). The neural component C1 has been located to the region of V1 (Clark et al, 1995; Gonzalez et al, 1994; Luck & Girelli, 1998; Jeffreys & Ashford, 1972).

Both the P1 and N1 components have regularly been shown to be modulated by attention (for example: Eimer, 1998; Hillyard & Anllo-Vento, 1998; Martinez et al., 2001; Muller & Hillyard, 2000) (see Figure 2.3). The modulation of these components appears to be a general characteristic of the spatial focusing of visual attention across various task situations. Stimuli at attended locations generally invoke larger P1 and N1 components than those at unattended locations (Hillyard & Anllo-Vento, 1998). In contrast, C1 appears to be invariant as a function of spatial attention (Hillyard & Anllo-Vento, 1998) (see Figure 2.3). C1 is consistently found not to be modulated by attentional influences (Gonzalez et al., 1994; Luck et al, 1997; Luck & Girelli, 1998; Mangun et al, 1998). The absence of attentional modulation in the C1 component suggests that attention operates after the level of V1 and any modulation of V1 is due to feedback mechanisms from higher cortical areas, starting at the extrastriate area (Hillyard & Anllo-Vento, 1998; Martinez et al., 2001).

Martinez et al (2001) found enhanced neural activity in an area corresponding to V1, using fMRI. But when they looked for this using ERP they did not replicate this. They found that the P1 component was larger for attended locations but that the C1 component was not. They attributed this to feedback processing mechanisms from higher cortical areas, including the parietal cortex and extrastriate areas. The ERP data from this and earlier experiments (for example: Martinez et al., 1999) argue against the fMRI data in that spatial attention modulates the visual response, but not as early as the initial inputs into V1, rather V1 is modulated by feedback mechanisms. The earliest area to be modulated is the extrastriate area, at a level of V2 or V3.

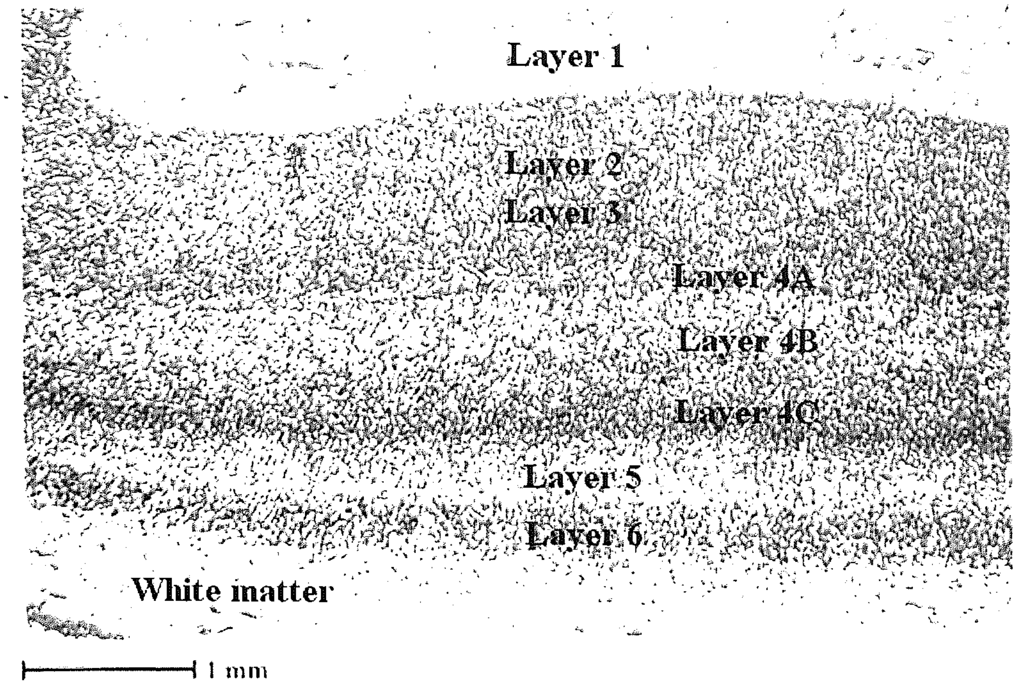
2.5. At What Stage of Processing does Attention have an Effect?

There are many ways that theories (for example see: Corbetta, 1998; Posner, 1980; Treisman & Gelade, 1980) have postulated attention affects the processing of incoming visual information. A major issue in the attentional literature is that of 'locus of selection'. Does attention operate on an 'early selection' basis, where attention operates at the level of perceptual processing; or on a 'late-selection' basis, where attention operates after all stimuli have been fully identified.

2.5.1. Late Selection

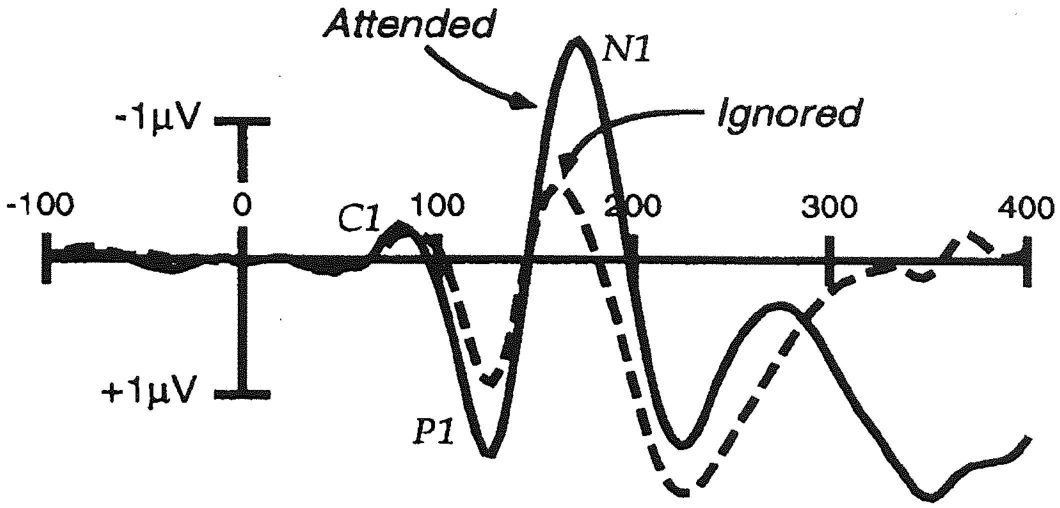
Proponents of this view, (for example: Duncan & Humphreys, 1989), hold that attention does not operate until after stimulus identification is complete. Every item in a display is fully identified, but only attended items are stored in working memory so that they can be reported at a later point (Luck & Ford, 1998). The most common method with these studies is to use indirect measures of priming and interference to draw conclusions about the temporal nature of attention (Luck & Ford, 1998). In particular variations of the Stroop paradigm have been used to show that responses are slower when unattended sources of information conflict with attended sources. These have been given as examples that unattended stimuli are fully identified, for it could not cause interference unless it was (Luck & Ford, 1998). However, these results could just provide evidence that the tasks involved did not draw a high level of attention to start with, and that information about stimuli that were not attended got through the attentional filter (Luck & Ford, 1998).

Figure 2.2: The Primary Visual Cortex as seen under a Microscope. Taken from Hubel & Weisel,(1995, pp 97).



V1 has a stripy appearance under microscope, and is therefore called the striate cortex.
All layers but 1 and 4 contain pyramidal cells.
The layers are formed by different cells clustering together in different densities.
For more detail see (Hubel, 1995).

<u>**Figure 2.3: An Example Occipital ERP Showing the P1 and N1 Components, but not the C1 Component, Being Modulated by an Attentional Condition. Taken from Luck and Ford (1998, pp826)**</u>



The P1 and N1 components are increased for the attended relative to the non-attended task. The C1 component showed no observable difference in the amplitude of the response for the two conditions.

However, it is possible that attention operates at early and late stages of processing simultaneously (Mangun & Hillyard, 1990). There is little evidence for the late selection theories of attentional, there is far more evidence, from neuroimaging and psychophysical data that the early selection theories of attentional selection are accurate.

2.5.2. Early Selection

It has been repeatedly shown that visual spatial attention modulates processing in extrastriate areas, beginning within 100ms post-stimulus onset, exemplified by attentional effects upon the P1 component (for example see: Chawla et al, 1999; Heinze et al., 1994; Luck & Ford, 1998). Low-level feature-based processing occurs for all items in an array, but integrated stimulus representations only form after items are attended to (Luck & Ford, 1998). The Feature Integration Theory (Treisman & Gelade, 1980) is the best example of an early selection mechanism of attention. In this theory there is a basic level of analysis prior to attentional modulation, called preattentive processing, in which the features of the visual scene are recorded, the combining of these features into coherent wholes is a function of attention, the target is then selected on the basis of these conjunctions of features (Banich, 1997). However, selection of a target need not rely on the conjunction of features, the phenomenon labelled 'pop-out' means that the target can be identified on the basis of a single visual attribute, so no conjunction of features is required, this type of processing is preattentive as attention is not required for the successful completion of the goal. For search requiring the conjunctions of features however, attention is obligatory, as the features of the display must be combined before their whole is recognisable.

Unlike late selection theories, there is plenty of supporting evidence for the early selection theories (for examples see Clark et al., 1995; Gonzalez et al., 1994; Luck et al., 1997; Luck & Ford, 1998). The data from ERP studies have shown the earliest component to be modulated is P1 (see above). This has a relatively early anatomical locus and is an indication of an early locus of selection (Luck & Ford, 1998). Even though there is no evidence that attentional processes modulate the earliest component of the visual response, C1, this is not evidence against an early locus of selection. Rather, because attention is still having an effect on temporally early visual components, P1 and N1, selection is still occurring before stimulus identification and perceptual processing are complete (Luck & Ford, 1998).

2.6. At What Point does Attention First Affect the Forward Sweep of Visual Processing?

Many researchers have shown that extrastriate areas are modulated by spatial selective attention (Chawla et al., 1999; Clark & Hillyard, 1996; Hillyard & Anllo-Vento, 1998; Olsen, et al., 2001). In the extrastriate areas V2 and V4, attention modulates a suppressive interaction between two or more stimuli in the same RF; there is a large effect on competing stimuli in the same RF, with the bias being in favour of the behaviourally relevant stimuli. In other words there is a shift in RF sensitivity to the locus of attention (Reynolds et al, 1994; Reynolds et al, 1995). Heinze et al (Heinze et al., 1994) found no evidence that V1 was modulated by attention, in both the ERP and PET data; though both sets of data showed extrastriate areas were modulated contralateral to the direction of attention.

Much of the work into which section of the visual pathway afferent activity is first modulated by attention has reported that extrastriate areas as early as V2 are modulated, but that V1 is not (for example: Chawla et al., 1999; Heinze et al., 1994). However, recent studies have shown that attention may influence V1 during tasks involving difficult visual discrimination (Motter, 1998); in fact V1 may not even be activated without a difficult discrimination task (Lavie, 1995). Responses in V1 to visual stimuli are very small, and it is difficult to produce stimuli that enhance these responses, and experiments which provoke attentionally complex discriminations are more likely to succeed that those that are attentionally simple (Heeger, 1999). Engagement of V1 in attention-related tasks may be due to stimulus discrimination difficulty. The more complex this is the more likely V1 is to be involved (Worden & Schneider, 1996). Gandhi et al (Gandhi et al., 1999) found that attentional effects in V1 increased with increasing attentional demand, with participants relying on cues to optimise performance.

Neuroimaging studies are also beginning to show evidence of activation in or near V1 during non-selective visual discrimination tasks (Watanabe et al., 1998; Watanabe, et al., 1998). There is fMRI evidence to support attentional modulation of V1 (Gandhi et al., 1999; Watanabe et al., 1998). Somers et al (Somers et al, 1999) used fMRI to measure the effects of attentional modulation with a dual task paradigm. The central target, an RSVP letter task, was surrounded by a rotating annulus, which has a radial wedge pattern and rotated clockwise or anticlockwise. The central task was to determine whether two consecutive letter strings were the same or different, and the peripheral task was to determine if the annulus rotated in the same or a different direction in two successive rotations of the same temporal length. They found significantly increased activation, as a result of selective visual attention, in the early visual areas, including V1, for both central and peripheral tasks. This data is consistent with the early selection theories. It also showed that V1 is not a passive area of the visual cortex, it can be modulated as strongly and specifically as the other areas of the visual cortex. Given that they used fMRI, they did admit that there was the possibility of feedback processes being responsible for the modulations found in V1. However, Somers et al (1999) put forward the argument that their study supported the idea that V1 is modulated by attention initially in the feedforward sweep of processing hypothesis. This study is the starting point for the experiments in Chapter 5, where it was used as the basis of one of the experiments designed to show that V1 is indeed modulated by feedback mechanisms only.

Martinez et al (Martinez et al., 1999), using fMRI, found that attention related activity was localised in both striate and extrastriate areas. Specifically for V1, they found that there was an increase in the BOLD signal, reflecting an increase in the regional cerebral blood flow (rCBF), in the calcarine fissure. However, they also found that spatial attention did not affect the amplitude of the neural component C1. The fMRI scans taken by Martinez et al (1999) showed that spatial attention was clearly associated with increased neural activity in V1. But fMRI has a temporal resolution of about 2-4 seconds (Corbetta, 1998) so there is no way of concluding whether the response was due to initial modulation or feedback activity. This is not the only study to have found this discrepancy between the activations of C1 and V1. Luck & Ford (Luck & Ford, 1998) also found that there was attentional modulation of V1 but not of C1.

2.7. Feedback Mechanisms or Direct Modulation?

There is much debate about when the modulation of V1 occurs. It is generally agreed that V1 is modulated by visual selective attention at some point; the question is whether it is modulated in the initial feedforward sweep, or whether feedback mechanisms are responsible for the modulation by visual selective attention. Each side of the argument is suggested by evidence from different analysis techniques. Those using just fMRI or PET argue in favour of attention being modulated initially (for example: Corbetta et al, 1993; Somers et al., 1999), whereas those who use EEG or MEG, or combine the imaging methods with one of these, show that the modulation of attention is most likely due to feedback mechanisms (Clark & Hillyard, 1996; Hillyard & Anllo-Vento, 1998). A quick referral to temporal and spatial qualities of these methods (see Chapter 3) shows us that fMRI and PET have poor temporal resolution, around 1-4 seconds in the case of fMRI (Haxby et al., 1998), and around 40-60 seconds in the case of PET (Corbetta, 1998). For neural sequences that take place in the order of milliseconds, these are quite obviously not going to be suitable methods to use. However, unlike these methods EEG has good temporal resolution, yet poor spatial resolution (Luck & Girelli, 1998), as does PET (Corbetta, 1998); fMRI has relatively good spatial resolution (Haxby, et al., 1998). The method to resolve these discrepancies is MEG, which has good spatial and temporal resolution (see Chapter 3). However, those studies that use a combination of the methods above would have equally good success in drawing conclusions about the sequencing of visual spatial attention.

2.7.1. The Case for Direct Modulation

There are still many researchers that believe V1 to be modulated initially by attentional processes (see DiRusso & Spinelli, 1999; Watanabe et al., 1998; Watanabe et al., 1998), enough for there still to be a debate about the effect of attentional processing on the primary visual cortex.

Motter (Motter, 1993) found that activity of orientation-selective neurophysiology in V1 was enhanced when the monkeys attended to specific orientations, versus a passive condition. Motter (1993) found that V1 showed enhanced selective activation for selective attention to motion, but not for the equivalent stationary stimuli. This shows that the V1 activation, in this case, was due to the local motion component and not location or orientation. However Motter found that activation depended on the aspect of motion attention was directed to (i.e.: local versus object), thus suggesting that attention operates at a higher level of visual processing and uses feedback mechanisms to influence V1 (Watanabe et al., 1998). Somers et al (Somers et al., 1999) claimed their study to be a human version of Motter's (1993) study (for more detail see above and Chapter 5), showing that V1 is modulated by attention initially as well as by feedback mechanisms.

Somers et al (1999) found that V1 was modulated by attention as strongly and specifically as the extrastriate areas.

There are some researchers who, while supporting the idea of direct modulation, are admitting that the techniques they have used, generally fMRI, are temporally inadequate and that feedback mechanisms may account for their results (see: Gandhi et al., 1999; Somers et al., 1999; Watanabe et al., 1998).

2.7.2. The Case for Feedback Mechanisms

The majority of research opinion supports the hypothesis that feedback mechanisms modulate the primary visual cortex. Van Essen et al (Van Essen et al, 1992) showed that there are extensive projections from the higher to lower cortical areas, including V1, MT and MST, showing that the possible influence of feedback on attentional modulation is something that must be taken into account when trying to interpret results from experiments in this area.

Extensive research (for example: Heinze et al., 1994; Luck & Ford, 1998; Martinez et al., 1999; Sengpiel & Hubener, 1999) has now concluded that it is not necessarily the initial inputs to V1 that are being modulated. The neurological response most likely represents a delayed, or re-entrant feedback mechanism, whereby enhanced visual signals from higher extrastriate areas influence V1, representing a top-down processing bias towards visual processing. The lack of response of the neural component C1 to attentional influence indicates that attention operates after this initial stage (Luck et al., 1997) but before perceptual processing is complete (Lavie, 1995), thus still supporting the idea of an early locus of selection for attentional processing.

Steven Hillyard and colleagues (Clark & Hillyard, 1996; Hillyard & Anllo-Vento, 1998; Hillyard et al., 1997) are proponents of the feedback mechanism hypothesis; typically their experiments involve the use of EEG (for details of this technique see Chapter 3). They have consistently found extrastriate areas to be modulated by attention and not the primary visual cortex. Clark and Hillyard (1996) found that selective attention was associated with increased activation in the extrastriate occipital areas, the superior parietal lobe, prefrontal lobe and the pulvinar. They found no modulation of V1. The extrastriate components that were modulated by attentional processing were the P1 component (80-140ms), associated with a source over the ventral-lateral occipital scalp, and the N1 component (140-200ms), associated with occipitotemporal, occipitoparietal and frontal sites. The component C1 (50-90ms) was not found to vary with attention, and was localised to the midline occipital area in the region of the striate cortex, V1. They concluded, along with others (Olsen et al, 2001), that attentional modulation occurs initially in the extrastriate cortex, but through feedback mechanisms in the primary visual cortex. Attentional selectivity was shown to begin at around 80-100ms post-stimulus onset, indicated by the component P1, and continue to around 200ms post-stimulus onset.

Martinez et al (Martinez et al., 1999; Martinez et al., 2001) used fMRI and ERPs and, like Hillyard and colleagues, found that V1 was modulated by attentional influences, but that the component C1 was not modulated. The ERP findings argue against V1 being modulated initially by attention, and the fMRI evidence argue for V1 being modulated by feedback mechanisms from higher cortical areas. Martinez et al argue that this is an essential function of attentional amplification, improving the perception of stimuli at attended locations. They argue for the earliest modulation by attention taking place in the extrastriate areas. V1 has to process a certain amount of information before the higher extrastriate and cortical areas, namely the parietal cortex, are able to discriminate between those stimuli that are behaviourally relevant and those that are not.

Roelfsema et al (Roelfsema, et al., 1998) found that object-based attention was associated with response enhancement at a very early level of visual processing, as early as V1, although there is no reason to suggest that location-based attentional effects would be any different in terms of modulation of the attentional response, the only possible difference would be in terms of timing, the location-based attentional effects being on a somewhat longer timescale (see Chapters 2 and 7). Their experiment involved depth electrodes placed directly into V1, and they subsequently found that there was no modulation by attention in V1 until around 200ms post stimulus onset. The use of depth electrodes gives a very accurate picture of what is happening in a region of the brain, and the results of Roelfsema et al (1998) suggest that V1 is indeed modulated by attention, but not until far later that previously thought, at around 200ms post-stimulus onset.

2.8. The Puzzle of Preattentive Visual Processing

A fundamental challenge to the theories of those who believe visual attention is able to modulate V1 during the initial feedforward sweep is the theory of preattentive visual processing. Treisman (Treisman & Gelade, 1980) brought this idea into the modern framework of attentional thinking, but Neisser (Neisser, 1967) highlighted the idea many years before. This idea states that there is a certain amount of processing which is required before attention can operate. Attention is required to bind together the information, gained through preattentive processing, into a semblance of coherence for use towards behavioural goals. There is much support for preattentive processing (Li, 2000; Wright, 1998), so why has it been ignored in the study of the modulation of V1? Some researchers have even postulated that V1 is modulated initially while supporting preattentive processing (Somers et al., 1999), yet this is a contradiction in viewpoints. The primary visual cortex is the first point of entry into the visual cortex of visual information from the external world. If this is the case then it is simply not possible that the initial feedforward sweep of processing is modulated in V1 itself, preattentive processing takes place here, not attentive processing.

This fits in with the idea of attention limiting processing capacity (see Chapter 1), the idea that there is a limit to the amount that can be processed visually. So, preattentive vision does an initial analysis of the visual field so that attention can focus in on those areas that are behaviourally relevant. This makes a great deal of sense. There has to be a fundamental level of processing before attention is able to operate, for how are we to know if stimuli in the external visual environment are in accordance with our behavioural goals if basic processing to identify these stimuli has not already taken place? If we did not have preattentive processing, we would be attending to all things all the time, which is in direct contradiction to the widely accepted concept of a limited capacity attentional system.

So, if there is a basic level of processing going on before the level of attentive processing, so-called preattentive processing, then this indicates that the initial inputs into V1 are not modulated by attention, thus any modulations found in experimental data are the result of feedback mechanisms from higher cortical areas, namely the parietal cortex and extrastriate areas. Chapters 5,6 and 7 provide support for the idea of attentional modulation of the primary visual cortex via feedback from higher cortical areas.

Chapter 3: Magnetoencephalography (MEG) and Associated Imaging Techniques.

Measurement of magnetic fields outside the human body first occurred in 1963 by Gerald Baule and Richard McFee. They discovered that the magnetic field associated with electrical activity in the human heart could be detected outside of the body by a small copper wire wound round a magnetic core (Kaufman & Williamson, 1986). This sparked the study of what is now termed 'biomagnetism'. MEG first appeared around the 1970s (Fenwick, 1990). The first instrument had 2 million coils of wire around a single induction coil magnetometer, and was used to detect alpha rhythms by a method of signal averaging (Hari, 1993). The single channel systems were cumbersome and a single recording took many hours (Fenwick, 1990). As the multiple channel systems appeared the cost increased, and recording became more complicated as they could not be used outside of a screened room. MEG has advanced significantly since then, and we have progressed to sophisticated full head systems with 151 channels. There will be a description of the sources of the magnetic fields, a more detailed discussion of MEG and a comparison with EEGs (Electroencephalograms). Then there will be a section on fMRI and its applicability to MEG research. Details of analysis methods will be given in the following chapter.

3.1. The Source of the Magnetic Field

The magnetic fields generated in the head are tiny, around 10^{-9} of the earth's magnetic field (Kaufman, et al., 1990). The origin of the magnetic fields is the fluctuations in resting membrane potential of cortical neurones due to synaptic input, i.e.: excitatory and inhibitory post-synaptic potentials. These fluctuations of the resting membrane potentials, called action potentials, cause compensatory current to flow intra- and extra-cellularly, spreading through the network of neurones to the skull and scalp (Rose & Ducla-Soares, 1990). The electrical current produced by these neurons has a magnetic field associated with it, oriented perpendicular to it. The particular cells recorded from are pyramidal cells (see Figure 3.1), the most common cell in the cerebral cortex (Shepherd, 1994). These cells are arranged in parallel, perpendicular to the cortical surface (Romani, 1989), the dendritic fields being non-symmetrical unlike other dendritic fields which are symmetrical, causing an accumulation of all contributions from all cells. It is this that is detected and recorded by the MEG. Radially oriented pyramidal cells are found in the tips of gyri whereas tangentially oriented pyramidal cells are found further from the scalp, in the sulci (Romani, 1989).

EEG and MEG differ in the signal they record from the brain (see Figure 3.2). EEG measures both radial and tangentially oriented sources, but while it can record both individually, it favours the radial sources, so these tend to overshadow the tangential source when both are present in close vicinity as the contribution from the radial source dominates the tangential source so that only the radial source is shown. However, if both sources are present at a distance then EEG may record both (Rose & Ducla-Soares, 1990). The MEG however records the tangential source better than it records the radial source; this is because the radial dipole in a conducting sphere does not produce a magnetic field outside of this sphere (Adelman, 1987). If both sources are present just the tangential source will be recorded.

An EEG records these potentials less effectively than does MEG, as the amplitudes of the currents are reduced by the skull and the scalp, giving low electrical conductivity, while the skull and scalp are transparent to magnetic fields (Malmivuo, et al., 1997). Surface distributions are warped due to differences in thickness and conductivity of the skull and scalp. Thus the currents give voltage potentials that vary in amplitude across the scalp (Rose & Ducla-Soares, 1990). This makes the ERP generators difficult to localise solely on the basis of scalp distribution data as several areas of the brain may be contributing to the resultant ERP waveform at any one time (Luck & Girelli, 1998). This makes the EEG very accurate temporally, but not spatially. In contrast MEG is as accurate as EEG temporally and almost as accurate as fMRI spatially, although this varies throughout the brain.

MEG localisation is more accurate in a direction perpendicular to the dipole source than in a direction parallel to the source, whereas it is the reverse for EEG (Hari, et al., 1988). Also, MEG records better in its best direction than does EEG in its best direction, due the low electrical conductivity of the scalp and it being transparent to magnetic sources (Luck & Girelli, 1998; Rose & Ducla-Soares, 1990).

Figure 3.1: A Schematic Pyramidal Cell. Adapted from Luck & Girelli (1998, pp74).

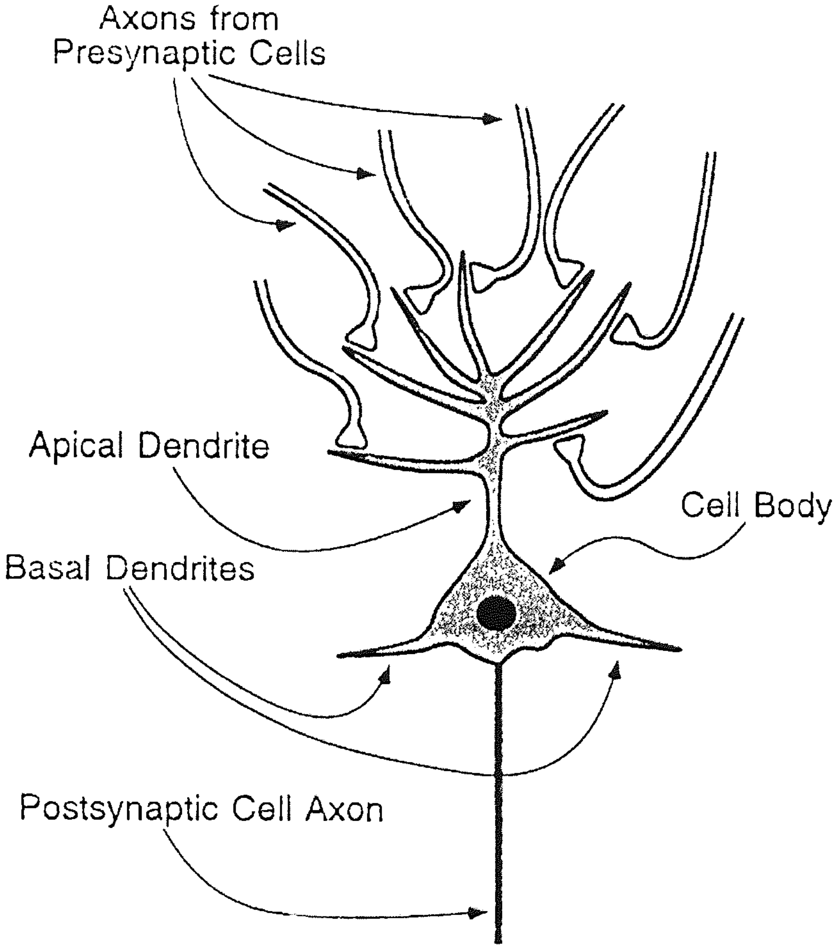
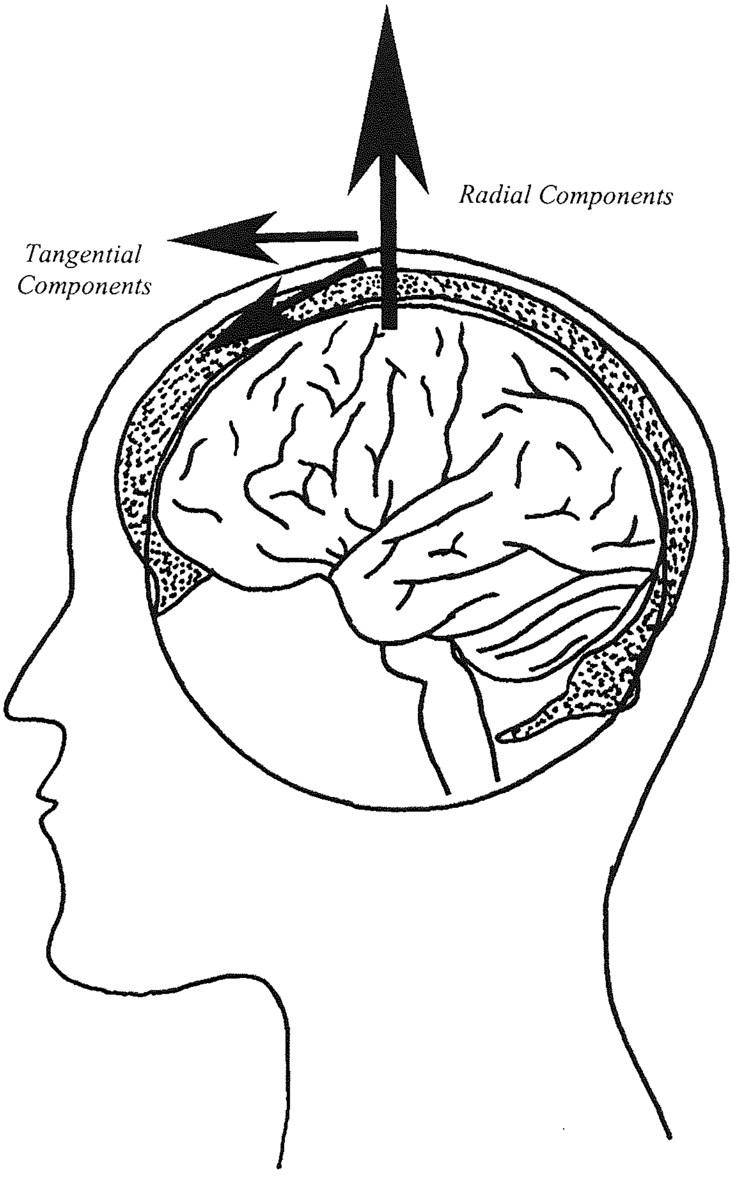


Figure 3.2: Tangential and Radial Components of the Bioelectric Source in the Brain. Taken from Malmuivo et al (1997).



Thus MEG is spatially more accurate than EEG by a few millimetres under favourable conditions as there in no influence on the magnetic signal by the various inhomogeneities of the skull and scalp (Hämäläinen, et al., 1993).

The temporal resolution of EEG and MEG is far better than most other imaging techniques, being in the order of milliseconds rather than seconds like fMRI and PET; it is therefore possible to record rapid, ongoing changes in cortical activity in the brain (Hämäläinen et al., 1993).

There are very few experiments that compare EEG and MEG directly and most of those use saline spheres or saline-filled skulls, less use human heads (Barth et al, 1986; Weinberg et al, 1986; Hansen et al, 1988). Fewer still directly compare EEG and MEG in the same head using the same task. One of these few is Cohen et al (1990 – in: Cohen & Cuffin, 1991). He used depth electrodes and an early MEG system. He showed that in the actual task of source localisation there was no significant advantage of MEG over EEG, average localisation error being 8mm and 10mm for MEG and EEG respectively. However they stated that the 8mm localisation error for the MEG could be readily ascribed to the spherical head model used in the inverse solution; this was used, as no other model was available. More accurate results may have been obtained using MRI scans to localise the dipole sources. By using MRI to incorporate the sources in a realistically shaped head model accuracy is much improved (Scherg, et al., 1998; Wagner et al., 1999). In practice EEG and MEG recordings are generally not done side by side, as up until the last few years there have been no integrated EEG and MEG systems, and standard EEG, metal, electrodes area significant cause of interference for MEG systems. However CTF (http://www.vsmmedtech.com/) have produced a machine in which a 37-channel EEG can be used simultaneously with the 151-channel MEG in the same system.

3.2. Electroencephalograms (EEGs)

The human EEG was first discovered by Hans Berger in 1929 (Bickford, 1987). An EEG measures the electrical activity in the brain that gives rise to the magnetic potentials measured in MEG (Luck & Girelli, 1998). The EEG is acquired by the placement of metal electrodes on the scalp; more rarely depth electrodes are used where the electrode is implanted into the brain (ECoG). The standard data collection method is with scalp electrodes.

3.2.1. Averaging the Evoked Potentials (EPs)

The raw data collected from an EEG is difficult to interpret; specific neural activity underlying cognitive processing makes very little contribution to the overall EEGs. Those neural events that are tied to a particular event such as stimulus onset can be extracted through the averaging process. The neural processes are time locked to the stimulus event and averaged (Luck & Girelli, 1998). The assumption underpinning the averaging process is that the underlying EP is the same each time it is produced but the noise is uncorrelated in time; therefore the amplitude of neural activity that is uncorrelated with the stimulus event has its amplitude reduced towards zero by averaging (Luck & Girelli, 1998). It can be thought of as additive, relative to the background activity; background activity having random amplitudes and polarities, while the EP itself is consistent.

To improve the averaging method, the signal-to-noise-ratio (SNR) is used. This improves as the square root of the number of responses averaged, in other words, for every hundred responses the amplitude of the noise is reduced by a factor of 10 relative to the individual response (Colon, et al., 1983). The SNR is limited in that for it to be effective the underlying EP needs to remain constant, and this is unlikely in the face of physiological factors such as habituation, which influence the response. The SNR includes changes due to fluctuations in variance response. Technically the SNR can be said to be non-stationary. Also, the SNR only allows for background activity to be pure, uncorrelated (stationary) noise, so ongoing general EEG background noise is not included, leading to slightly inaccurate results. Over a long period of time averaging the response can degrade it rather than enhance it. In these circumstances small sections should be averaged and superimposed onto one another (Colon et al., 1983).

The resultant averaged event-related potential (ERP) contains a series of positive and negative deflections from the zero potential, referred to as components, peaks or waveforms. Each peak is labelled positive or negative with a number associated with is relative to its temporal position, for example P1 is the first positive component at around 100ms post stimulus onset (Luck & Girelli, 1998). Standard EEG convention has the negative components plotted upwards and the positive components plotted downwards (Luck & Girelli, 1998).

3.3. Magnetoencephalograms (MEG)

Magnetoencephalography (MEG) is the extracranial measurement of magnetic fields generated by electrical activity in the brain, typically in the uppermost layer of the cortex (Hämäläinen et al., 1993). A magnetometer measures these magnetic fields above the scalp. A single neuron producing an electrical, and therefore a magnetic field, is too weak to be detected outside the head. What is measured is the summation of thousands of cortical neurons (Näätänen, et al., 1994). The magnetometer is positioned close to the surface of the head, measuring the intracranial magnetic fields. The first person to measure magnetic fields in this manner was Cohen (1968), while the measurement of the first visually evoked magnetic field was by Brenner et al in 1985 (Kaufman et al., 1990). There are three main sources of biomagnetic fields: the electric currents associated with the movement of ions in the neurons; the remnants of magnetic moments of contaminants; and the paramagnetic or diamagnetic bodily reaction when subjected to a magnetic field. The first of these is most commonly researched, and this is the intended subject of study. What is measured is the 'evoked field'. The primary areas of the brain are studied by stimulating visual systems, and the evoked response is measured over the appropriate area of the scalp. These responses are quite small and are barely distinguishable from background noise, which can be from sources within or outside of the brain. The noise, in this case is assumed to be stationary so that a single response is 'time-locked' to the stimulus, assumed to be identical after each stimulus. The averaged epoch increases the more responses are accumulated and this is the evoked field. This allows investigations to focus on specific events and manages to cancel out all other activity in the brain and increases the signal to noise ratio (SNR) (Romani, 1989). Shielded chambers provide some protection from magnetic 'noise', produced by the surrounding environment, which is of a higher magnitude that the magnetic signal the MEG is to be detecting. The simplest way to increase the SNR, and thus source localisation, is to increase the number of responses that are averaged (Hari et al., 1988). This however, does mean that recording session must be longer, and this in itself can cause problems as the responses may change over time, and changes to the interstimulus interval (Hari et al., 1988).

3.4. SQUIDs and Gradiometers

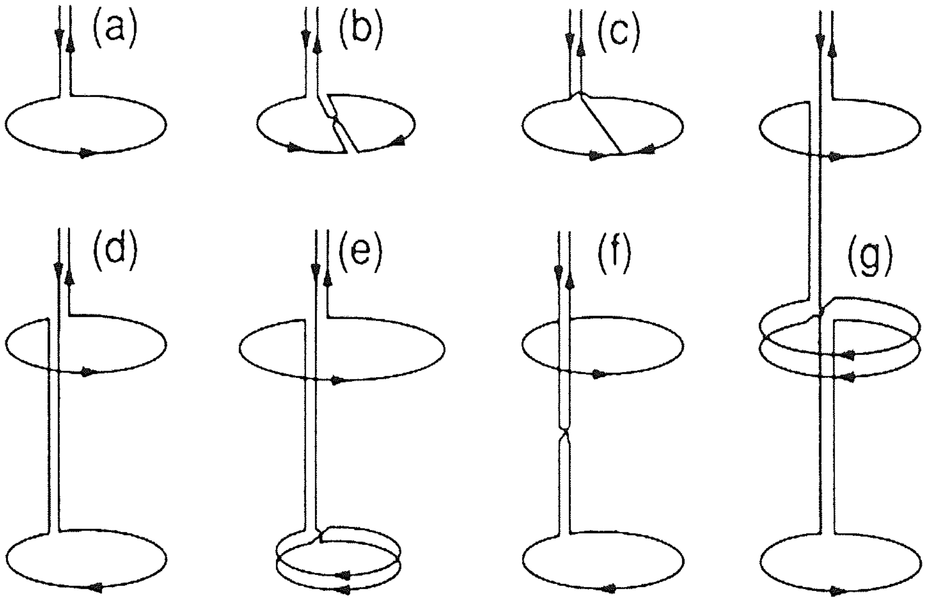
SQUIDs (Superconducting QUantum Interference Devices) and gradiometers (see Figure 3.3) form the basis of the MEG. They are kept inside a dewar surrounded by liquid helium at a temperature of 4.2K (Romani, et al., 1982). The dewar was named after Sir James Dewar who was the first person to liquefy hydrogen in the late 19th century (Kaufman et al., 1990). The SQUID itself was first introduced in the late 1960s by James Zimmerman (Hämäläinen et al., 1993). SQUIDs are the basis of the MEG system. A SQUID consists of: a detection coil, sensing changes in magnetic fields and transforming them into electrical currents; input coils, which transform the electrical current into a magnetic flux; and associated electronics, which transform this magnetic flux into a voltage output at room temperature (Fagaly, 1990). They do not directly measure the magnetic field; rather they sense it using a detection coil of superconducting wire placed near the SQUID (Kaufman & Williamson, 1986). When a cranial magnetic field is applied to the detection coil, a current flows through the circuit keeping the magnetic flux of the coil unchanged. The SQUID senses the flux, produced in the smaller detection coil, and the response is measured by the electronics of the MEG system. This response is strictly proportional to the field applied to the detection coil (Kaufman & Williamson, 1986). The detection coils are superconducting devices, and are thus kept in the dewar, surrounded by liquid helium at a temperature of 4.2K (Fagaly, 1990). As mentioned above the magnetic field in the head is orders of magnitude smaller than anything in the external environment. There are many sources of external noise; magnetic fields are associated with ventilation systems, motors, lifts, cars, computers, and power lines (Romani et al., 1982).

The simplest method of reducing environmental noise is to place the MEG system within a shielded room (Hämäläinen et al., 1993). However, the shielded room in itself is not enough to block out the environmental noise, so additional mechanisms have to be employed. These come in the form of gradiometers. A gradiometer is a detection coil that has been made to be less sensitive to noise, but still highly sensitive to the signal it is detecting. The detection coil is split into sub-coils with an opposite sense of winding. A single gradiometer is known as a magnetometer and responds to applied magnetic fields, regardless of the source (Romani et al., 1982). Regardless of source, the design of the gradiometer in sensors influences the measurements made (see Figure 3.3). Two coils perform a subtraction between a region near the head and one slightly further away, and the difference noted, discriminating between distant sources, noise, in favour of more local sources, the source of interest (Romani et al., 1982). The measured amplitudes are influenced by frequency bandwidth. Gradiometer measurements are in femto-tesla per square root hertz (Ft/sqrt (Hz)). 1st-order gradiometers have the same vertical axis and are insensitive to constant spatial fields in the direction of the coil axis, whereas 2nd-order gradiometers have the same vertical axis and are insensitive to constant spatial fields and gradients in the same direction as the coil axis (Romani & Pizzella, 1990). Hardware gradiometers can seriously reduce the detected brain signal, but synthetic gradiometers are more flexible and only have a small effect on the measured brain signal, being able to increase or reduce it depending on the detection configuration, although this reduction is smaller than signal reductions from hardware gradiometers (Vrba, et al., 1998). Synthetic gradiometers are more compact and their coefficients are independent of the noise and dewar location or orientation (Vrba et al., 1998), and because they significantly reduce the environmental noise and increase the signal to noise ratio, source analysis accuracy is improved (Vrba et al., 1998).

3.5. The Inverse Problem: in both EEG and MEG

The inverse problem is the task of identifying the internal sources which have produced extracranial measurements of magnetic activity, while having this complicated by the idea that there are any number of possible sources for a single measurement (Näätänen et al., 1994). Like EEG the response can be averaged to produce an evoked magnetic potential (EMP), which increases the strength of the response and reduces the random cortical responses, also called noise, making the localisation of responses to specific locations in the cortex easier (Romani, 1989). The solution of the inverse problem is non-unique; there are many configurations of sources that can produce the same measured result; even if there were precise measurement of the electrical and magnetic fields around the head there would still be an infinite number of distributions of activity that would explain the measured potentials (Näätänen et al., 1994). To reduce this problem, a priori information can be added, of which two types are apparent: temporal constraints and spatial constraints.

Figure 3.3: Gradiometers: From Hämäläinen et al (1993, pp. 445).



a) Magnetometer
b) Series planar gradiometer
c) Parallel planar gradiometer
d) Symmetric series axial gradiometer
e) Asymmetric series axial gradiometer
f) Symmetric parallel axial gradiometer
g) *Second-order series axial gradiometer*

The latter arise from the model in which the data is placed. Individual MRI scans can be used to constrain source localisation, in particular with regard to dipole localisation where the activity recorded by the MEG is mapped directly onto a three-dimensional MRI scan, constrained by the spherical model which was derived from the MRI. In SAM analysis (see Chapter 4) the spherical model is still used, but multiple spheres are fitted to the region of the head nearest each sensor. A true cortically restrained model is currently being developed by A. Hillebrand at the Wellcome Laboratory for MEG studies at Aston University (http://www.aston.ac.uk). Theoretically the combination of MEG and MRI is a good one, MEG has far superior temporal resolution while MRI has superior spatial resolution (Scherg, et al., 1998) and so the combination of these two techniques gives very high resolution both temporally and spatially (Cohen, et al., 1993; Ueno, 1999).

Using MRI to attempt to solve the inverse problem improves accuracy due to the head model being more realistically shaped. The most convenient way of doing this is to calculate the theoretical field and the potential patterns generated within it using a suitable source model, generally the MRI image, then the theoretical and experimental distributions are compared and the location is identified to within a few millimetres accuracy (Romani, 1989). fMRI has been used as well as standard MRIs to constrain source localisations in MEG. However, there is some evidence that there are significant difference between fMRI and MEG data and that the combination of these to produce overall localisation is not necessarily the most accurate of solutions to the inverse problem (Ioannides, 1998). It has been found that the foci identified by MEG and fMRI are typically 1 to 1.5cm away from one another. There is now the question of whether MRI signals originate in large or small vessels in the brain (Ioannides, 1998). There is an assumption that the haemodynamic changes associated with fMRI and the neuronal responses associated with MEG are linearly dependent on one another (Ioannides, 1998; Wagner et al., 1999), but whereas there is a strong link, it is unclear as to what this link is (Haxby et al., 1998). The two processes are linked, but on a time scale of seconds rather than milliseconds (Rosen, et al., 1998). However, it has recently been shown that MEG and fMRI experiments show a good deal of correlation between locations (Singh, et al., 2002).

3.6. Magnetic Resonance Imaging (MRI)

Magnetic resonance imaging of the brain started in the early 1990s (Haxby et al., 1998). MRI relies on the use of magnetic fields to perturb the behaviour of atoms, how long atoms take to recover from this perturbation is used to record an image of the underlying anatomy of the tissues. The magnetic field of the scanner forces all the magnetic dipoles of the individual protons to align themselves with the strong magnetic field, the magnetic dipoles are then perturbed by a pulse generated by gradient coils in the scanner (Haxby et al., 1998). After this perturbation the protons wobble back to their original alignment. The MRI relies on three magnetic fields: the static field, the pulse sequence and the gradient field (Banich, 1997). The static field is the constant field produced by the magnet that causes all magnetically sensitive particles to align themselves with the magnetic field. Only if all the particles are aligned can the effects of the perturbation of the static field be measured. The pulse sequence distorts the magnetically sensitive particles. The time taken for the particles to recover from this perturbation is known as the relaxation time, and is measured by a receiver coil. The intensity of the signal measured by the receiver coil provides a measure of the type of tissue being imaged. The third magnetic field, the gradient field, provides a way of measuring particular locations within the magnetic field. The combination of the spatial intensity and the gradient field allows for a three dimensional image to be reconstructed (Banich, 1997).

MRI works by measuring the energy released by protons in atomic nuclei as they return to a resting state after being temporarily perturbed. If enough protons return to a resting state in a coherent manner, the energies produced are summed together and produce a signal strong enough to be detected by a magnetic resonance (MR) scanner (Cohen et al., 1993). Protons in different types of cells emit energy at different frequencies, called the resonance frequency (Haxby et al., 1998), thus providing a method of distinguishing between tissue types in the final image (Cohen et al., 1993). Standard MRIs measure the energy released by the protons of water molecules. This is the most common molecule in biological tissue and provides the strongest signal, and different tissues have different water contents (Cohen et al., 1993).

Functional MRI (fMRI) relies on the blood oxygen level dependent (BOLD) signal, imaging of BOLD changes based on the differences in magnetic properties between oxygenated and deoxygenated blood (Haxby et al., 1998). Oxygenated blood is diamagnetic, it has a negative susceptibility with a weak magnetism in the opposite direction to the applied field and is essentially nonmagnetic, whereas deoxygenated blood is paramagnetic, a positive susceptibility where the atoms and molecules contained have net spin properties and can be aligned in the direction of the applied magnetic field; it acquires a magnetic field in the presence of another magnetic field (Haxby et al., 1998). Changes in blood flow are accompanied by smaller changes in oxygen consumption, leading to oxygen level changes in blood vessels at the active sites in the brain. Oxygen is transported around the blood by haemoglobin. The BOLD signal detects when the blood flow to a region of the brain has changed out of proportion to the oxygen consumption. When this occurs, in either direction, there is a reciprocal change in the level of deoxyhaemoglobin in the surrounding tissues, causing changes in the local magnetic properties (Raichle, 1998).

MRI scans have high spatial resolution of a few millimetres, or sometimes even less than a few millimetres (Haxby et al., 1998), but they have poor temporal resolution, as they are susceptible to changes in regional cerebral blood flow (rCBF) (Raichle, 1998). Functional MRI is much faster than traditional MRI, scans can be taken every 2-6 seconds (Haxby et al., 1998), but there is still a time delay between the perturbation time of the protons or the BOLD response and the underlying neural response. Neural responses are in the order of tens or hundreds of milliseconds, whereas with the BOLD response it can be up to 4-8 seconds before its maximum response is reached (Haxby et al., 1998). fMRI will never be able to distinguish rapid neural responses, simply because it relies on blood flow; but in combination with other methods it can enhance spatial resolution where other methods, such as MEG and EEG, provide the temporal resolution (Haxby et al., 1998).

Chapter 4: General Methods

This section includes the general methods for the MEG experiments. Details of the methods for the psychophysics experiments can be found in the individual methods sections.

4.1. The MEG System

The full head CTF system (Vrba & al, 1998) (http://www.vsmmedtech.com/) in place at The Wellcome Trust MEG Lab at Aston University (http://www.aston.ac.uk/) is capable of simultaneous MEG and EEG recording. It has 151 MEG channels and 37 EEG channels. The tail of the dewar is head shaped and the gap between room temperature and the sensor coils in the helmet is 1.7cm. There are synthetic radial 3rd order gradiometers to provide efficient noise cancellation. The sensors and references are connected to planar DC SQUIDS. Localisation of the head within the dewar is done by affixing 3 small coils to arbitrary points on the head. Tiny electrical currents at different frequencies are passed into the coils and their positions determined from the magnetic signals. This data is stored and then compared to the localisation of the coils done post-experimentally using the bitebar (Singh, et al., 1997). The bitebar defines the head coordinates system, the initial localisation of the coils being to determine the location of the coils relative to the dewar. Post-experimentally, the location of the coils relative to the head is determined using the bitebar. These two sets of data are what are aligned during the coregistration process. The localisation process has an accuracy of ± 2mm (Vrba & al, 1998). The system has 29 reference channels for use in synthesis of higher order gradiometers or adaptive noise cancellation. This allows for gradiometers of 1st, 2nd or 3rd order to be used in real time or offline. Overall the gradiometers within the shielded room provide an environmental noise reduction of $>10^5$ at low frequencies.

The shielded room was made by Vacuumschmeltze GMBH. It is a one layer aluminium and one layer mu metal lined room. The mu metal is the low frequency shield and the aluminium is the high frequency shield. The wires in the system are niobium, including those of the gradiometers. This shielded room is the only one of its kind in the world as it has a window in it to view a computer monitor through. This does not compromise the shielding effect of the room as long as any computer monitors are at least 20cm away from the hole. If this is adhered to there is very little interference. It is also possible to close the hole should a computer screen not be required for the experiment.

4.2. The Experimental Process

The participant was seated in the system and the coils attached to their head with Velcro straps. An inflatable cap was placed on the participant's head to prevent movement inside the system. The participant was then fitted inside the dewar and the seat was raised so that they were in position. The cap was then inflated to prevent movement. Stimuli were viewed through a front-silvered mirror and the button box was placed on the lap of the participant within easy reach of their hands.

The head shape and coil positions relative to the dewar and bite-bar were measured post-experimentally using a Polhemus Isotrack 3-D digitising system. Post-experimentally the subject was removed from the dewar and seated in front of the Polhemus system with their head stabilised using a bitebar (Singh, et al, 1997). The position of the coils relative to the head was then determined using a digital pen. The coils were removed and the head shape was also determined using the digital pen. This head shape was used in the co-registration of the MRI to the data from that session. This final MRI image is viewed in a program called MRIViewer.

4.3. Analysis methods

4.3.1. Coregister

The program Coregister was written by Hillebrand & Barnes, of Aston University, using a program called Align (Nissanov, et al., 1995). The MRI is co-registered with the head shape and coil positions obtained from the Polhemus head digitisation and the experimental run. The new MRI is saved along with the head shape and fiduciary points with the relative data set. This new MRI is used as the basis for viewing SAM data and for the group analysis using SPM99.

4.3.2. Manipulation of the Data Set

There are several ways of manipulating the raw data set, new markers can be added, and the data can be split relative to markers or the recorded triggers. All these commands are part of the CTF data analysis package. The ones used in these experiments are as follows.

addMarker: for identifying a combination of triggers as a single stimulus, the binary codes for the triggers are used to add a new marker into the dataset.

averageDS: creating a new, averaged, dataset for a specific combination of markers, for example in Chapter 7 the valid dataset was produced with a combination of markers 1,3, and 5, whereas the invalid dataset was produced with a combination of markers 2 and 4.

newDS: creating a raw data set rather than an averaged one. The SAM analysis requires raw data, and in these instances, for example Chapter 7 the data had to be split into left-orientation and right-orientation. Markers were added to signal the orientation of the stimulus and the dataset was split in two using this command.

MarkerScript: a program created by Hillebrand (2000) to take the raw marker data from the experiment and transform it into a CTF formatted marker in the raw dataset. This was used to create the markers for left and right orientations in Chapter 7.

4.3.3. Synthetic Aperture Magnetometry (SAM)

SAM is an analysis package in the CTF software (http://www.vsmmedtech.com/) that takes the raw data and turns it into a power map for all the sensors over all regions of the brain, by minimising the noise and thus maximising the event related signals. SAM derives maps of the root mean square source activity from unaveraged MEG data during specified time intervals and locations. The source power for every brain coordinate is estimated by minimising the signal power due to noise (Robinson & Vrba, 1998). SAM improves the signal to noise ratio (SNR) of MEG signals by combining signals from sensor arrays using weighting factors, giving MEG a resolution sensitive enough to examine single neural events. The weighting factors (time, frequency of response, Hz) are chosen by the experimenter to give the response at a specific location in the cortex. SAM is based on traditional linear beamformers, first used in radar systems. The beamformers used in SAM analysis probe along each 3-dimensional location in a specific location. The direction of analysis is rotated along the tangential plane and the orientation where the level of activation is maximised becomes the solution for that particular location. This is done for all 3-D locations in the brain. For small SNR the SAM response for two sources is about the same, the signal space of the vectors is blurred due to noise and the two sources are indistinct. For higher SNR the two sources become distinct as the response to the noise decreases while increasing to the specific source (Vrba, 2002). SAM assumes that each neural source has a unique time course and that all other covariance is noise. For any neuronal source the weights can be calculated so that the weighted sum of the M<EG channels provides millisecond by millisecond estimates of neuronal activity at any point in the brain (Barnes et al., 2001).

The functional brain image is generated by plotting the source power and its noise variance as a colour scale, representing brain activity at each voxel in the image of the region of interest. Higher density/lighter colours represent higher levels of activity and vice versa. In the CTF version of the program, the blue-pink end of the spectrum denotes negative activity, in other words a decrease in activity relative to the normal resting brain state, while the red-yellow end of the spectrum denotes higher levels of activity relative to the normal brain state, positive activity. The image created is then fused with the anatomical image to be displayed. The 3-D images are statistical parametric maps of brain function and can be normalised and averages, enabling group studies and analysis to be carried out. SAM is not an inverse solution, and it does diminish the time resolution of MEG data, however this is resolved by selecting an active region and recovering the millisecond time course trace data. For more detailed information about SAM analysis please see (Robinson & Vrba, 1998; http://www.vsmmedtech.com/, and Vrba & Robinson, 2000).

4.3.4. MRI3DX

This software was designed by Krish Singh of Aston University, (http://www.aston.ac.uk/psychology/meg/mri3dX/). This is an integrated tool for the visualisation and analysis of structural and functional imaging data. With this software it is possible to transform images into bi-commissural Talairach space (Talairach &

Tournoux, 1988), achieve 3-D rendering of the scalp and cortical surface, and segment the 3-D image for deeper cortical viewing.

Functional data and SAM files, once converted, can be imported and viewed superimposed onto 2-D or 3-D individual brain images. The Talairach coordinates can be viewed simply by clicking on a point in the brain. This activates the coordinates and the name of the region in which the point selected is located. A page number for the slice selected is also displayed in the corner of the 2-D images; this corresponds to the pages in the Talairach book (Talairach & Tournoux, 1988).

4.3.5. SPM 99

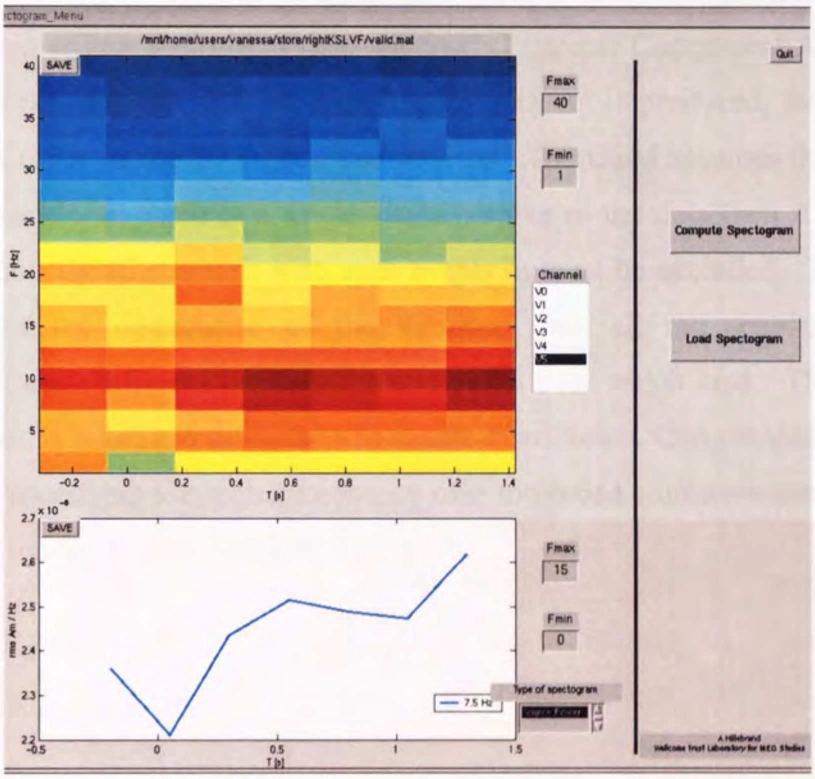
Statistical Parametric Mapping (SPM) is a voxel-based program, designed using MATLAB, which produces images that are normalised to a template brain, produced by averaging the brains of all participants involved in the experiment. It was originally developed by Karl Friston (Friston et al., 1995), and is now developed by the Wellcome Department of Cognitive Science in London (http://www.fil.ion.ucl.ac.uk/). The SPM99 program can produce a template brain, provides automated non-linear spatial normalisation, normalisation of the template brain into Talairach coordinates, image segmentation, and coregistration with SAM images that have been pre-converted. The activation effect in the averaged SAM images is divided by the standard error to produce a t-statistic. This t-statistic is normalised across brain images and scans, meaning that different t-statistics are equivalent and can be compared across separate conditions. This pseudo-t-value is not an absolute, quantitative statistical measure; rather when the conditions and parameters used to analyse the brain image data are identical they provide a relative measure of significance. It is therefore possible, within the study, to assume levels of significance relatively between conditions, provided all parameters are identical across conditions. In this thesis this was the case, so all assumptions of significance based on the pseudo-t-values are relative, not absolute. The relative differences cannot be assumed to imply true statistical significance, even though it is probable that they would achieve true significance; the results must be treated qualitatively and not quantitatively. Again, as with the MRI3DX program, the Talairach coordinates can be viewed simply by clicking of a point in the brain, which reveals the coordinates and the name of the region, in which the point selected, is located. A page number for the slice selected, as before, is also displayed in the corner of the 2-D images; this corresponds to the pages in the Talairach book (Talairach & Tournoux, 1988).

4.3.6. Spectrograms

The Spectrogram program uses MATLAB and the basic Spectrogram functions in the MATLAB signal processing toolbox. Voxels in the brain, showing significant task-related power changes, are chosen based on the SAM images viewed in MRIViewer, and the coordinates of those voxels are placed in a text file. It is possible to choose the location of the virtual electrodes to be produced in the Spectrogram output, specific coordinates can be given for virtual electrodes. The text file is used to create virtual electrodes viewed in the DataEditor program. The Spectrogram program analyses the time series of each of these virtual electrodes using a moving window Fourier Transform. This generates a time-frequency spectrogram (see Figure 4.1). Source power for frequencies (F) is along the y-axis and source power for latencies is along the x-axis (T - for time). Both are in 'rms Am/Hz'. The average source power over time for a chosen frequency band is shown below in 'rms Am/Hz', a virtual electrode at that point in the brain (Singh, et al., 2002). In Figure 4.1 the upper half of the display shows the frequency of the response in Hz, red indicates a large positive response relative to baseline activity whereas dark blue denotes a large negative response relative to baseline activity. The lower half of the display shows the power trace from the virtual electrode, created using a specified frequency range and averaging all responses within that range, to create a single virtual electrode; the implication here is that were there to be an electrode placed exactly over the specified coordinates this would be the average response trace produced. The time in seconds (T(s)) is shown along the x axis, this shows the time scale over which the responses were averaged, with zero denoting the stimulus onset, thus negative values are pre-stimulus onset and positive values are post-stimulus onset. From a spectrogram it is possible to see where in the frequency range the main responses lie, and also whether the activity is greater or less than baseline activity. From the Virtual Electrode data it is possible to see what the response would be like at a specified location should an electrode be placed over that exact area, and so provide data for more precise interpretation of the data in the selected area of the brain. This data can help interpret when a response occurs post-stimulus, which can help in the interpretation of results, in particular in terms of feedforward and feedback mechanisms in the occipital cortex. Unfortunately the

Spectrogram program at present will not allow for millisecond sectioning of the timescale and so more detailed interpretation would only be possible once this is possible. Also, it should be noted that the spectrogram program only allows for single subject data to be used. Thus all the comparisons in the thesis are of single subject data. Between subject comparisons are made within subjects.

Figure 4.1: Example of a Spectrogram.



/mnt/home/users/vanessa/store/rightKSLVF/valid.mat

Fmax 40

Fmin 1

Fmax 15

Fmin 0

The Spectrogram output window as it appears on the screen.

4.3.7. General Linear Model (GLM)

This analysis program was not actually used in this thesis, as it is not possible to use multiple markers at present. However, future publications are likely to contain this data.

The GLM program was designed by Ian Holliday of Aston University to help with testing the size of any effects found in the MEG datasets and was based on a paper by Friston (Friston et al., 1996). This program does a multivariate analysis comparing two regions of the brain within a specified time window. Principle Component Analysis (PCA) is done on the raw data set, and an approximate data set is produced, then the program uses a MANCOVA on the 20 biggest components. The GLM assumes the same variance on all 12 channels, so there is a single random spike in the data then it will upset the results, consequently all channels with such events in must be excluded. The processed data file contains the distribution of the variance over all the sensors, which sensors are significantly different between the two states over which area. The significance of such variance is measured using the Chi-square distribution. One problem with the GLM model is that specifying too high a frequency over too broad a time window provides a set of data that is too big to be calculable.

Chapter 5: Study 1 – Dual Attentional Task Showing Lateralized Activation in the Parietal Lobes

5.1. Introduction

It is generally agreed that there is attentional modulation of the primary visual cortex; the dispute is over how and when this modulation occurs. There are two possible explanations for this: those who say that the modulation is through feedforward mechanisms, in other words, that the initial input into V1 is modulated by attention, and those that say the modulation is through feedback mechanisms, the initial input not being modulated or that any attentional influence is through feedback from higher extrastriate visual and parietal areas.

The 'feedforward' explanation takes its evidence from groups mainly specialising in fMRI studies (see: Somers, et al 1999;Watanabe, et al., 1998, Watanabe, et al., 1998; Roelfsema, et al 1998), while the 'feedback' explanation takes its evidence from research groups specialising mainly in EEG studies (see: Martinez et al., 1999; Martinez, et al, 2001; Clark & Hillyard, 1996; Heinze et al., 1994; Mangun, et al, 1998). For technical comparisons of these methods see Chapter 3. This study uses MEG to resolve these discrepancies and try and find a solution to the 'feedforward-feedback' dilemma of attentional modulation in V1.

Somers et al (1999) used fMRI to measure attentional modulation in the visual cortex, specifically V1. They showed that modulations in activity were spatially specific between attended and non-attended regions, with suppression as well as enhancement being evident. V1 was modulated as strongly as other areas in the visual cortex and the properties of this modulation were similar to those found in higher areas, suggesting common mechanisms across the visual cortex. Their data showed that V1 was modulated as strongly and effectively as other areas of the visual cortex. The conclusion was that this was consistent with 'early' selection models of attention as V1 was most likely being modulated in a feedforward fashion and was not a passive part of the visual cortex. Given that Somers et al (1999) were using fMRI it was impossible for them, and others using the same method, to comment on the sequencing of events occurring on the timescale of milliseconds.

Selective attention is where a location or object is highlighted for further processing. Selection may be through a bias for behaviourally relevant processing coming from the higher cortical areas, what is known as 'top-down' processing, or it may come from automatic actions, learned or innate behaviours that have become automatic, or 'bottom-up' processing. 'Top-down' influences rely on feedback mechanisms to direct and bias attentional selection; the information flow through the cortex must obviously reach the higher areas before it can exert its influence, and this does not usually happen until after information has entered the earlier cortical areas such as V1 (Lamme, 2000). However, this is not necessarily true of 'bottom-up' influences. It is most likely that 'bottom-up' processes are modulated right from the start of the information flow, thus at the very earliest cortical areas, such as V1. This then suggests that V1 is modulated by attentional influences, but only if this influence is reliant on 'bottom-up' mechanisms. This idea relies on attention being active before the initial feedforward sweep of information processing has begun. If the influence relies upon 'top-down' mechanisms then this reasoning would suggest that V1 is not initially modulated by attention, but rather later by feedback mechanisms. If 'bottom-up' influences are modulated by feedforward mechanisms, there must be a point at which 'top-down' mechanisms in a repetitive task become 'bottom-up' mechanisms through the habituation and learning that happens during the task as it becomes more familiar. If this were the case, then it would seem plausible that feedback mechanisms hand over attentional modulation to feedforward mechanisms at some point, as the habituation occurs. It is fair to say that the majority of behaviours are modulated by top-down influences at first; therefore, as these are highly likely to be modulated by feedback mechanisms, and it can therefore be concluded that this is the overriding mechanism by which attention influences behaviour, at least in terms of visual processing.

Leaving aside the question of evolution and brain development, it is reasonable to suggest that we are unable to selectively attend to objects and locations if we have not already performed basic processing across the visual field. This can be shown in the 'Pop-Out' phenomenon, first shown by Anne Treisman (Treisman & Gelade, 1980). In this situation the target item 'pops out' of the visual field before any attentional selection has occurred. Even though instructions have been given to attend to that item, it is still a preattentive process. This is the case even when a 'serial search' task is undertaken, if the target is not the distinctive item and must be searched for in the rest of the display, it is still this distinctive item which draws the eyes first and is processed earliest, before any attempt has been made to find the target item. This would suggest that basic processing of the visual field has already occurred by the time attentional influences are active, and that processing can then be biased rapidly, and in parallel, through feedback modulation. Thus V1 can receive data that is not being modulated by attention, in a completely 'bottom-up' process driven by stimulus attributes rather than behavioural goals. This is the fundamental difference between preattentive and attentive processing, the former requires simply that the objects and locations in the visual field exist, it is driven by their attributes, whereas the latter is driven by behavioural goals, primarily those connected with the control and execution of movement. This 'Pop-out' phenomenon is not universally accepted, Duncan (Duncan & Humphreys, 1989) sees visual search rather as a continuum of search efficiency wherein familiarity is increased to targets and decreased to non-targets. This produces a continuum of search efficiency. However, this theory still incorporates a level of processing that is, in essence, preattentive; a level of processing that occurs before any attempt is made to bias the input signals in favour of behaviourally relevant targets. If such a process as 'preattentive' vision exists then it is obvious that processing, in the visual cortex at least, is split into 'preattentive' and 'attentive' processing. This makes it impossible for the feedforward hypothesis to survive. How can the initial input in V1 be modulated by attention if there is a 'preattentive' processing stage first?

Parietal areas are also heavily involved with the process of attention. The parietal cortices form part of the 'fronto-parietal' attentional network, documented in many imaging experiments (for example: Corbetta, et al, 1993; Coull, et al, 1998). There is no dispute over whether or not the parietal cortices are involved in attentional processing, but it has been suggested that there is a hemispheric asymmetry in the type of processing each hemisphere in involved in. The right hemisphere has been shown to be more involved with spatial information, whereas the left hemisphere is said to be more involved with temporal tasks (Macaluso & Frith, 2000; Coull & Nobre, 1998). This does not preclude both hemispheres being involved in both types of information processing; both types of information are likely to be processed in each hemisphere (Coull & Nobre, 1998), rather this notion of hemispheric specialisation implies that each hemisphere is organised to deal preferentially with one type of information processing. The right parietal cortex is important for attending to both halves of the visual field, but the left parietal cortex is only important for attending to the right visual field (Walsh, et al, 1999). It is also thought that the parietal cortices are not just involved in simply the visual demands of attention, but rather in the visuo-motor demands of attention, the behavioural relevance of stimuli is what is required for attention to be focused on a particular item in the visual array (Walsh et al., 1999).

The fronto-parietal network acts to modulate interactions between attention and selective monitoring of targets. The frontal part of this network is said to provide an 'executive' function, being used in the control and monitoring of attentional focus and attentional memory (Coull et al., 1998; Posner & Dehaene, 1994). These frontal areas are thought to include the prefrontal cortex, which works to hold online representations of events in the immediate past, 'attentional memory', and the anterior cingulate, which has the role of the 'executive' in awareness and control (Posner & Dehaene, 1994). The 'executive' function of this network has two distinct roles: to keep track of processes being undertaken in the attentional network, including an awareness of the target and providing memory information; and also to exercise control over the system but having connections to the parietal lobes and involving ''attentional memory' in sustained and selective attention (Posner & Dehaene, 1994). In the parietal cortex there are specific areas that have been associated with attentional influences. The inferior parietal sulcus (IPS) is said to be active during tasks requiring sustained covert attention to spatial locations in the peripheral areas of the visual field (Martinez et al., 2001) but this area is only active during the task and not during passive viewing, suggesting it is used in the attentional control of incoming sensory information to earlier cortical areas. Other areas implicated in this role are the prefrontal cortex, pulvinar, and the superior colliculus (Martinez et al., 2001), areas linked to the fronto-parietal attentional network.

The 'Spotlight' analogy states that attention is like the beam of a torch, the centre is highly salient, and the edges are less salient (Brefczynski & DeYoe, 1999). This theory states that information in the centre of the spotlight is processed faster and more accurately than information further out in the periphery. The 'Spotlight' analogy would suggest that if a stimulus is circular and encompasses the whole visual field, with the subject having instructions to attend to the centre of the display, the information at the centre of the stimulus would be processed faster and more effectively than that on the outside. This model would also suggest that if these two areas of the stimulus were in competition that the central area would have priority through being most salient in the attentional lens.

Therefore a dual attentional task with central and peripheral components would be a suitable way to study such a hypothesis.

This study is firstly an experiment based on that by Somers et al (1999), and secondly an extension on this study. Their experiment used a circular grating with a central RSVP letter task. This study replicates this and then improves on it by removing the language component and replacing the RSVP letter task with another grating. We also improved this original study by using MEG rather than fMRI. This gives an improved temporal resolution, enabling more accurate conclusions about the temporal sequencing to be made (Ueno, 1999). The extension of the experiment was done to put both sets of stimuli in one perceptual domain rather than two. This makes it possible to conclude on temporal sequencing of attentional events. When the two tasks are in different perceptual domains there is the risk of confusing differences between the processing of different domain with differences in attentional processing. The behavioural manifestations of this attentional modulation will be measured through reaction times.

We expected to find attentional modulation of early visual areas, but in the form of feedback mechanisms rather than feedforward mechanisms.

5.2. Methods

5.2.1. Experiment 1: Peripheral Grating Task vs. Central Letter Task

5.2.1.1. Apparatus

Stimuli were produced using a VSG5.021 grating generator (CRS Ltd.). The viewing monitor was an EIZO T562-T 17" colour monitor, calibrated and gamma-corrected using a computer-controlled photometric procedure (Optical, CRS Ltd). Responses were made on a button box with 0.25mm contact switches.

5.2.1.2. Stimulus Parameters

Stimuli were presented on a uniform grey background, calculated to be the midpoint between the black and white of the stimuli. The letter strings were comprised of the letters 'O, C, D, Q, U' in one string and 'H, M, L, X, T' in the other. The font used was Times Roman, 78 point, generated from the preinstalled fonts in the VSG package. The letters were 12mm in height on the computer screen, and constituted 0.02° visual angle. The grating was a 16 cycles per 360 degrees sinusoidal luminance grating of 90% contrast and 28.9Cd/m^2 mean luminance. The width of the grating was 1.17° visual angle, with a total radius of 2.86° visual angle (see Figure 5.1).

5.2.1.3. Participants

Participants in the MEG version all had normal, or corrected-to-normal, vision. There were 4 females and 2 males. The mean age was 32.5 years, age range 22-45. All participants were right-handed. For the psychophysics part of the experiment there were 10 participants, 5 males and 5 females. The mean age was 33.8 years, age range was 22-45. All participants were right-handed and all had normal, or corrected-to-normal, vision.

5.2.1.4. Timing Parameters

The stimuli were onscreen throughout the experiment. For the central task each letter on screen for 200ms and a 50ms gap between letters, with 1 second between letter strings. The peripheral grating rotated twice for 1 second, a gap of 1 second between each rotation. Total trial length was 3 seconds. There was a 10 second gap at the end of each block of 10 trials in the MEG version of the experiment to allow for a 'passive viewing' phase. The time taken to complete the task was 25 minutes.

5.2.1.5. Procedure

There were two tasks: a central task and a peripheral task. The central task involved watching two letters strings and the participant had to decide if the two letter strings were the same or if they were different. The peripheral task was to watch the outer grating rotate and decide if the two rotations were in the same direction or not. The two elements of the display, the letters and the gratings, were present onscreen throughout the experiment and were synchronous with each other. A right button press indicated a 'different' response and a left button press indicated a 'same' response. The task was alternated every 10 trials, starting with the peripheral task. The change was indicated with a centrally located 'P' or 'C' presented in the Times Art Nouveau font, 54 point, from the VSG preinstalled fonts, 12mm in height on the computer screen. There were 100 trials per condition, making 400 trials in total. The 'same' and 'different' conditions were randomised. Participants fixated on the centre of the display throughout the experiment. Participants were instructed to fixate on the centre of the display and the attend to the central or peripheral stimuli when cued to do so by the 'C' (central) and 'P' (peripheral) appearing in the centre of the display every 10 trials. The instructions were to press the left button if the two rotations/letter strings were in the same direction/contained the same letters, and to press the right button if they were different. Limited practice was given to ensure the participants were clear about the task but still found the stimulus novel and the changes between rotations unexpected. Post-experimentally it was explained to the participants that what was being looked for was a difference in the timing of response to the different conditions and whether there were any delays as a result of the distraction presented by the other stimulus. All participants were told their performance results in terms of percentage accuracy and relative performance in the different conditions. Participants reported that no strategies were employed as they were discovered to be a hindrance in completing the task rather than a help.

5.2.1.6. Psychophysics

As there were more participants doing the psychophysics than the MEG version, a slightly different timing mechanism was used, as no passive phase was required in the analysis. Therefore the 10 second gap at the end of each block of 10 trials was removed.

5.2.1.7. MEG

Participants sat 2.1m away from the screen and viewed the screen through a front-silvered mirror in a magnetically shielded room, the monitor being situated outside the room. For more details on the MEG methods see Chapter 4. Participants were positioned in the MEG system and the head localised, to obtain the position of the coils with respect to the dewar, within the dewar. The first half of the experiment was run, taking around 15 minutes. There was then a break of a few minutes while the second half of the experiment was set up; the participant remained in the MEG. The second experiment then took around 15 minutes. The participant was then removed from the MEG system and their head digitised using the Polhemus software (see Chapter 4) to localise the coils with respect to the head.

5.2.2. Experiment 2: Peripheral and Central Gratings Tasks.

There was only one difference between the experiments, the central task, being a grating in the second experiment, instead of letters.

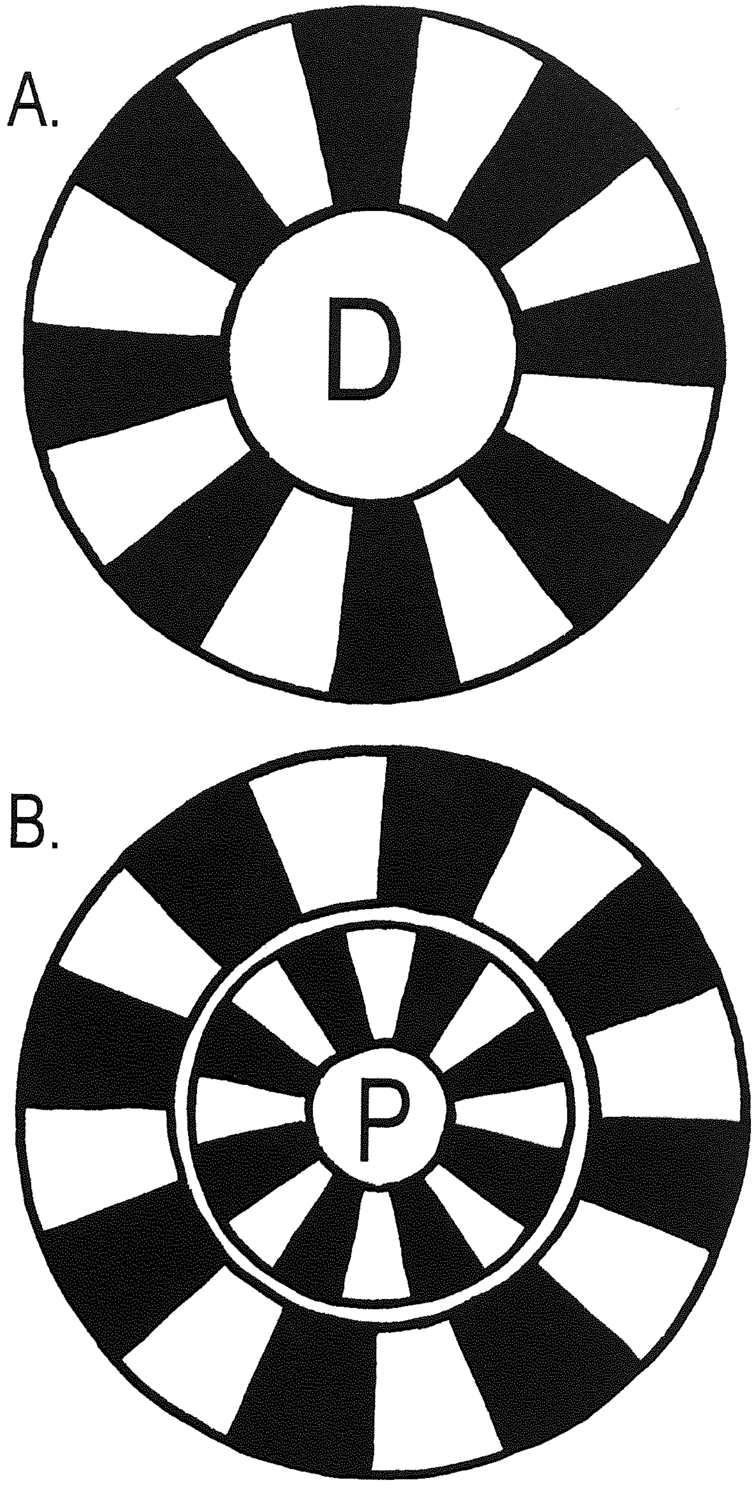
5.2.2.1. Stimulus parameters

The inner grating was 1.12° visual angle in width with a total radius of 1.6° visual angle. The grating was a 16 cycles per 360 degrees sinusoidal isoluminant grating with a contrast of 90% and 28.9Cd/m^2 mean luminance.

5.2.3. Analysis methods

The data from the Polhemus system was co-registered with the participant's MRI scan using the 'Coregister' program in the CTF software (see Chapter 4). The data was analysed using Synthetic Aperture Magnetometry (SAM) (Vrba & Robinson, 2000). A baseline was chosen (the second half of the 10 second pause, 7-10 seconds post stimulus onset) and this was compared with the active time window (0-3 seconds post stimulus onset) for both experiments. Four different frequency bands were analysed, 0-10/10-20/0-15/5-15/Hz. The SPM99 program (see Chapter 4) was used to average the MRIs to form a template brain. The SAM images were then averaged into a global image and placed on the template brain. The results are based on these averaged group images. Spectrograms and virtual electrodes were also computed for selected areas, areas for this analysis were chosen on the basis that the early visual areas were the most important in terms of timings. The co-ordinates were obtained from individual subject SAM data viewed in the MRI Viewer program (see Chapter 4). All Spectrogram and Virtual Electrode data was on single participants, it was not possible to average data by this method at this time. The majority of consistent activity was found in the 5-15Hz ranges. This is evident in the Spectrogram output.

Figure 5.1: The Stimuli.



A) Experiment 1. Peripheral gratings of 16 cycles per 360 degrees. Central task of 2 letter strings of 5 letters each. Central and peripheral tasks were responded to separately but were onscreen the entire experiment.

B) Experiment 2. Peripheral and central gratings each of 16 cycles per 360 degrees. Central and peripheral tasks were responded to separately but were onscreen the entire experiment.

For both experiments the central and peripheral task were indicated with a 'P' or 'C' in the central fixation spot, in the delay between trial blocks, indicating 'peripheral task' and 'central task' respectively.

5.3. Results

Table 5.1a: Psychophysical Results

Means of Correct Responses (in milliseconds)	**Experiment 1 mean**	**sd**	**Experiment 2 mean**	**sd**
Centre-Same	484.78	280.66	397.25	203.56
Centre-Different	364.57	199.43	387.03	248.64
Periphery-Same	396.83	196.69	357.48	176.79
Periphery-Different	439.84	215.44	392.73	231.56
Means of Errors (in milliseconds)				
Centre-Same	839.43	252.03	961.86	888.91
Centre-Different	639.63	238.14	518.29	405.61
Periphery-Same	1401.86	1886.63	509.96	374.61
Periphery-Different	515.21	257.2	520.22	323.93

Table 5.1b: Psychophysical Results

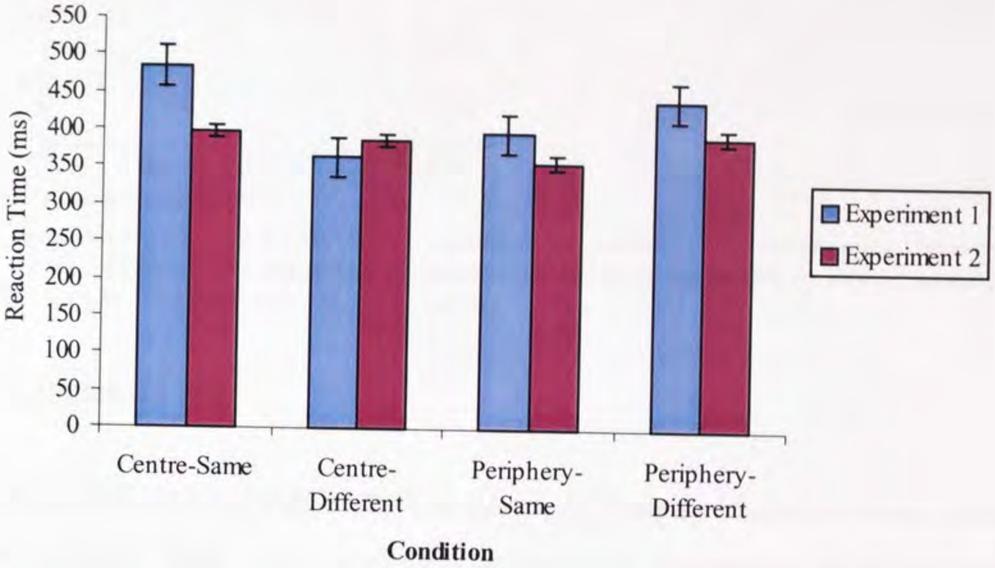
Experiment 1 Condition	**F-value**	**df**		
Same vs. Different (S vs. D)	14.696	1	p<0.001	*significant*
Centre vs. Periphery (C vs. P)	0.389	1	n-s	*non-significant*
S vs. D x C vs. P	51.215	1	p<0.001	*significant*
Experiment 2 Condition				
Same vs. Different (S vs. D)	1.547	1	n-s	*non-significant*
Centre vs. Periphery (C vs. P)	2.746	1	n-s	*non-significant*
S vs. D x C vs. P	4.154	1	p<0.05	*significant*

There were no significant interactions or effects in the Errors results. There were very few errors, 2.6% of responses on average overall, between all ten participants. They made very little impact on the results; however, they have been separated out for accuracy

The 'different' condition was generally faster than the 'same' condition, whereas the 'centre' condition had faster reaction times (RTs) for the 'different condition than the 'same' condition. The 'peripheral' condition had slightly slower RTs for the 'different' condition than the 'same' condition, but the 'same' condition was faster in the 'centre' condition and the 'different' condition was faster in the 'peripheral' condition (see Table 5.1a and Figure 5.2).

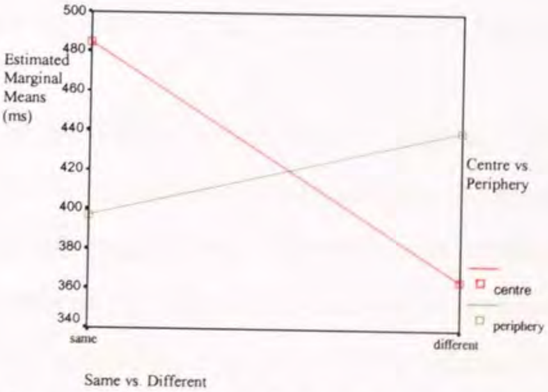
There was a significant interaction between the two variables, same/different and central/peripheral (see Table 5.1b and Figures 5.3a and 5.3b). There was a crossover effect wherein for the 'centre' condition the 'same' responses were much slower than the 'different' responses, and for the 'peripheral' condition the 'same' responses' were faster than the 'different' responses, though the difference was not as big as for the central condition.

Figure 5.2. Reaction Times Show a Difference Between Experiments 1 and 2.



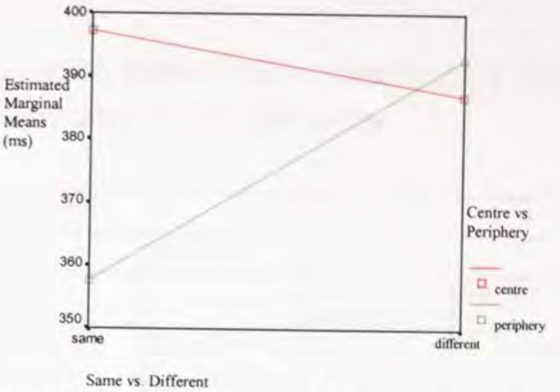
This figure shows a difference between the two experimental conditions, Gratings and Letters (Experiment 1) and Dual Gratings (Experiment 2). There is a significant difference for the 'Same vs. Different' comparison for Experiment 1 but not for Experiment 2, but there is a significant difference for the interaction of 'Same vs. Different' and 'Centre vs. Periphery' for both experiments. The 'central vs. Periphery' contrast revealed non-significant results in both experiments. A difference was expected, but a difference between the two experiments was not expected. The speed of the responses for Experiment 2 were more similar than those of Experiment 1, which showed variation in the speed of responding for the different categories.

Figure 5.3a: Crossover Effects for Experiment 1.



This figure shows that for the 'Same' condition the 'central' condition is responded to slower than the 'peripheral' condition, whereas for the 'Different condition this is reversed, with the 'central' condition being responded to faster than the 'peripheral condition, but about the same amount. This interaction is significant to p<0.001

Figure 5.3b: Crossover Effects for Experiment 2.



This figure shows whereas for the 'Same' condition the 'central' condition is, again, responded to slower, and for the 'Different' condition the 'peripheral' condition is responded to slower, although by a much smaller margin. This interaction is significant to $p<0.05$.

5.3.1. Imaging Data

For detailed results see Table 5.2. The following imaging results are based upon the Group SAM analysis. There was mainly left hemispheric dominance in the activations in the majority of conditions for both experiments. The early visual areas, V1/V2/V3, showed left dominance throughout except in the 'peripheral' conditions in Experiment 2, where activation showed right hemisphere dominance. The parietal lobes showed left dominance throughout both Experiments for all conditions. For Experiment 1 there was bilateral activation with a left dominance, whereas for Experiment 2 there was mainly left hemisphere activation only. All other areas activated showed bilateral activation with a left dominance. This hemispheric dominance was unexpected as the stimulus was present in all four visual quadrants (Figures 5.4 and 5.5).

At the time of writing there was no way of determining the significance of the difference in levels of activation between the different conditions at the present time, so the data is purely qualitative. However, with reference to the pseudo-t-values produced in the SPM analysis (see Tables 5.3 and 5.4) it is possible to predict possible directions of significance. In Experiment 1 there is a large increase in activation in the SPL, IPL and Cuneus, in the left hemisphere relative to the right hemisphere, this is repeated in Experiment 2.

In Experiment 1 there is an increase in the SPL, IPL and Cuneus in the peripheral conditions relative to the central condition. In Experiment 2 the reverse is seen but to a much smaller degree, the peripheral condition shows less activation than does the central condition for the areas of interest.

Table 5.2: Group SAM Data Results: 'Area' denotes area activated, while a cross indicated which hemisphere the activation was in.

SAM Data							
Area	**Condition**	**Experiment 1**			**Experiment 2**		
		Left Dominance	**Bilateral**	**Right Dominance**	**Left Dominance**	**Bilateral**	**Right Dominance**
V1 (Area 17)	Centre-Same	X	X	-	X	-	-
	Centre-Different	X	X	-	X	X	-
	Periphery-Same	X	X	-	-	-	X
	Periphery-Different	X	-	-	-	X	X
V2/V3 (Cuneus) (Areas 18-19)	Centre-Same	X	X	-	X	-	-
	Centre-Different	X	X	-	X	X	-
	Periphery-Same	X	-	-	-	X	X
	Periphery-Different	X	-	-	-	X	X
Superior parietal Lobe (SPL)	Centre-Same	X	X	-	X	-	-
	Centre-Different	X	X	-	-	-	-
	Periphery-Same	X	X	-	X	-	-
	Periphery-Different	X	X	-	X	-	-
Inferior parietal Lobe (IPL)	Centre-Same	X	X	-	X	-	-
	Centre-Different	X	X	-	X	-	-
	Periphery-Same	X	X	-	X	-	-
	Periphery-Different	X	X	-	X	X	-
Superior frontal Gyrus (SFG)	Centre-Same	X	X	-	X	X	-
	Centre-Different	X	X	-	X	X	-
	Periphery-Same	X	X	-	X	X	-
	Periphery-Different	X	X	-	-	X	-
Medial frontal Gyrus (MFG)	Centre-Same	X	X	-	X	X	-
	Centre-Different	X	X	-	X	X	-
	Periphery-Same	X	X	-	-	X	-
	Periphery-Different	X	X	-	-	X	-
Pre-central Gyrus (PrCG)	Centre-Same	X	X	-	X	X	-
	Centre-Different	-	-	-	X	-	-
	Periphery-Same	-	X	-	-	X	-
	Periphery-Different	X	-	-	X	X	-
Post-central Gyrus (PoCG)	Centre-Same	X	X	-	-	-	-
	Centre-Different	-	-	-	X	-	-
	Periphery-Same	-	X	-	-	-	-
	Periphery-Different	-	-	-	-	-	-

Table 5.3: The Pseudo-t-values for Experiment 1.

The levels of activation were slightly greater on the left hemisphere than on the right hemisphere for the main areas of interest. In particular the SPL and Cuneus showed consistently increased levels of activation over the left hemisphere. There is also increased activation for the peripheral vs. central conditions in the majority of situations. It is thought that these differences would obtain a low level of significance under qualitative analysis.

Frontal areas are not represented, as the focus of the experiment was the parietal and occipital lobes. There were significant levels of frontal activity in all conditions.

Cuneus	**Left Hemisphere**		**Right Hemisphere**	
	Pseudo-t-values	**Co-ordinates (x,y,z)**	**Pseudo-t-values**	**Co-ordinates (x,y,z)**
Central-Same	3.62	-8.9/-83.0/17.8	3.32	18.9/-75.8/23.9
Central-Different	3.72	-10.9/-85.9/17.0	3.45	19.9/-82.0/16.8
Central vs. Neutral	3.77	-8.0/-75.9/23.0	3.96	18.9/-75.8/23.9
Peripheral vs. neutral	4.96	-16.9/-82.1/15.9	3.72	13.9/-82.0/16.8
Peripheral-Same	4.67	-21.9/-85.8/18.9	3.01	14.9/-86.2/10.9
Peripheral-Different	4.361	-17.9/-86.1/12.4	2.69	15.9/-86.2/11.5
SPL	**Left Hemisphere**		**Right Hemisphere**	
	Pseudo-t-values	**Co-ordinates (x,y,z)**	**Pseudo-t-values**	**Co-ordinates (x,y,z)**
Central-Same	4.07	-22.9/-43.0/57.2	3.06	23.9/-41.0/57.1
Central-Different	4.03	-34.8/-34.2/56.8	3.3	15.9/-45.8/59.2
Central vs. Neutral	4.66	-21.9/-42.8/60.9	4.45	15.9/-40.8/60.8
Peripheral vs. neutral	4.89	-20.9/-37.9/60.6	4.74	23.9/-37.9/60.6
Peripheral-Same	4.27	-26.8/-58.2/45.1	3.97	26.8/-58.2/45.1
Peripheral-Different	3.61	-26.8/-53.9/53.2	4.02	28.8/-53.9/53.2
IPL	**Left Hemisphere**		**Right Hemisphere**	
	Pseudo-t-values	**Co-ordinates (x,y,z)**	**Pseudo-t-values**	**Co-ordinates (x,y,z)**
Central-Same	3.67	-38.8/-60.5/37.9	3.34	33.8/-60.2/43.4
Central-Different	3.86	-34.8/-57.1/46.9	4.37	26.8/-56.9/50.5
Central vs. Neutral	4.6	-29.8/-50.0/52.0	4.74	36.8/-43.2/52.6
Peripheral vs. neutral	4.56	-34.8/-64.2/42.6	4.45	26.8/-64.3/39.9
Peripheral-Same	4.17	-31.8/-61.1/46.1	4.04	26.8/-64.3/39.9
Peripheral-Different	3.42	-26.8/-73.6/30.2	3.01	31.8/-72.4/33.8

Table 5.4: The Pseudo-t-values for Experiment 2.

There is consistently an increase in activation for the left hemisphere over the right hemisphere, in the areas of interest, in particular the SPL. There are more similar levels of activation for the central and peripheral conditions than in Experiment 1; however, there is a slight reversal of activation dominance, in that the central conditions appear to have a higher level of activation than do the peripheral conditions. This is due to the task conditions being more visually demanding. It is thought that a low level of significance might be obtained under qualitative analysis.

Frontal areas are not represented, as the focus of the experiment was the parietal and occipital lobes. There were significant levels of frontal activity in all conditions.

Cuneus	**Left Hemisphere**		**Right Hemisphere**	
	Pseudo-t-values	**Co-ordinates (x,y,z)**	**Pseudo-t-values**	**Co-ordinates (x,y,z)**
Central-Same	4.48	-10.9/-82.9/18.7	2.37	10.9/-82.9/19.6
Central-Different	3.9	-10.9/-82.1/15.0	3.2	17.9/-81.9/19.6
Central vs. Neutral	5.06	-8.9/83.0/16.9	3.23	10.9/-82.9/19.6
Peripheral vs. neutral	3.04	-12.9/-84.8/19.7	3.5	13.9/-85.0/15.2
Peripheral-Same	1.95	-8.0/-83.8/20.6	2.42	9.9/-83.8/19.7
Peripheral-Different	3.31	-10.9/-86.8/18.9	3.04	13.9/-86.9/16.2
SPL	**Left Hemisphere**		**Right Hemisphere**	
	Pseudo-t-values	**Co-ordinates (x,y,z)**	**Pseudo-t-values**	**Co-ordinates (x,y,z)**
Central-Same	2.93	-21.9/-37.0/58.8	2.95	31.8/-36.9/60.6
Central-Different	3.36	-23.9/-42.7/62.7	3.12	17.9/-42.7/61.8
Central vs. Neutral	3.99	-24.8/-42.7/62.7	3.56	13.9/-42.5/65.5
Peripheral vs. neutral	3.2	-19.9/-50.7/57.6	2.5	24.8/-50.7/58.5
Peripheral-Same	2.91	-40.7/-45.0/54.6	2.44	43.7/-44.9/57.3
Peripheral-Different	3.2	-30.8/-44.9/57.3	2.4	30.8/-44.7/61.0
IPL	**Left Hemisphere**		**Right Hemisphere**	
	Pseudo-t-values	**Co-ordinates (x,y,z)**	**Pseudo-t-values**	**Co-ordinates (x,y,z)**
Central-Same	3.77	-48.7/-33.3/35.6	3.71	54.7/-34.5/31.1
Central-Different	3.36	-37.8/-50.9/53.9	3.04	41.7/-50.2/49.3
Central vs. Neutral	4.19	-36.8/-55.0/50.47	3.46	39.8/-55.3/44.9
Peripheral vs. neutral	4.23	-35.8/-54.2/45.8	3.3	42.7/-51.3/45.7
Peripheral-Same	3.24	-40.7/-55.4/43.1	2.68	43.7/-50.5/42.9
Peripheral-Different	4.1	-38.8/-56.3/44.1	2.64	44.7/-56.4/41.3

5.3.2. Virtual Electrodes and Spectrogram Results

All of this data was processed using the same parameters and time windows. The 50Hz range was filtered out of all data; this being the power line, and the time range for all was 0-2 seconds. It is therefore possible to make inferences about relative levels of activation within the results; although, as with the SAM data, this is purely qualitative, no quantitative measures were available at the time of writing. For more detail about this technique see Chapter 4. The locations of these virtual electrodes were chosen as they had the most significant activation in the areas that were relevant to the paradigm we were working in.

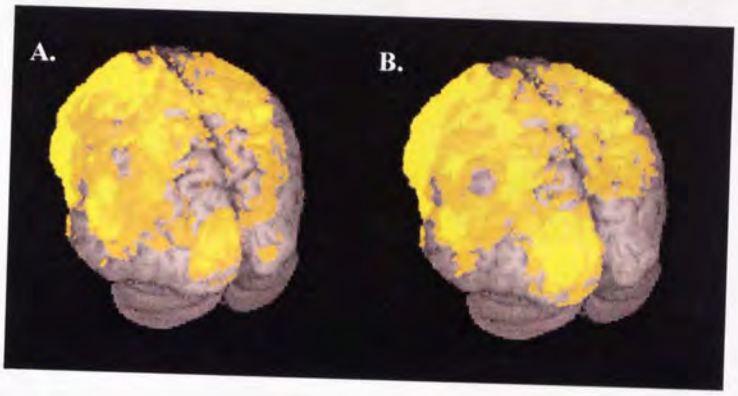
The Spectrogram results show that the activity was in the 0-20 Hz band, with little activity outside of this. The data of more than one participant if compared, and the time scales along the x axis show a slight variation, due to the Spectrogram program itself being unable to process all data sets with the same parameters at the time of writing, slight variation in temporal recordings produced differences in time scale that were unavoidable.

The virtual electrode data showed that there was generally a decrease in activation until around 250-500ms, after which there were increased in activation at around 800-1200ms (see Figure 5.6). For more detailed results see Appendix A, the details are not included as there are not thought pertinent to the main point of the discussion, namely the lateralized effect of the parietal response.

Figure 5.4: Experiment 1 – 3D Images of Activation over the Occipital and Parietal Lobes.

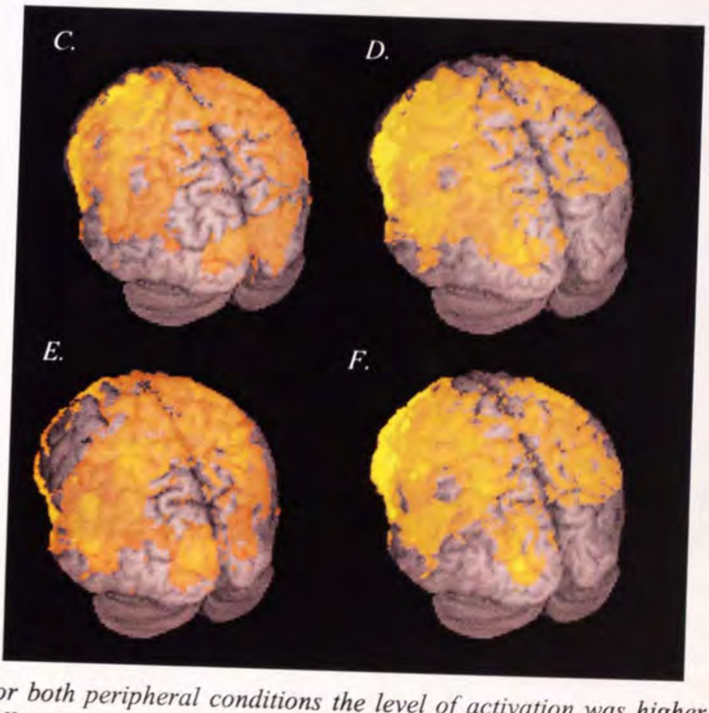
For all images, the Fun Integration Depth was 0.05. The Amplitude cut-off (AC) was between 3.1 and 3.9. A higher AC value indicates a higher level of activation was evident and a higher cut-off value was required for localised activation to be visible. The concentration of colour indicates the strength of the response, a higher concentration of yellow indicates a strong response. The closer to orange and red the colour gets indicates a weaker response. Colours in the yellow-red range indicate a positive response relative to the resting baseline activity.

A: Comparison: central condition vs. neutral. AC = 3.8
B: Comparison: peripheral condition vs. neutral. AC = 3.9



The peripheral condition shows an enhanced level of activation in the parietal and extrastriate areas, in particular the left hemisphere, indicating that the parietal lobes in particular are more involved with peripheral than central vision.

C: Comparison: central-same condition vs. neutral. AC = 3.1
D: Comparison: peripheral-same condition vs. neutral. AC = 3.5
E: Comparison: central-different condition vs. neutral. AC = 3.1
F: Comparison: peripheral-different condition vs. neutral. AC = 3.6

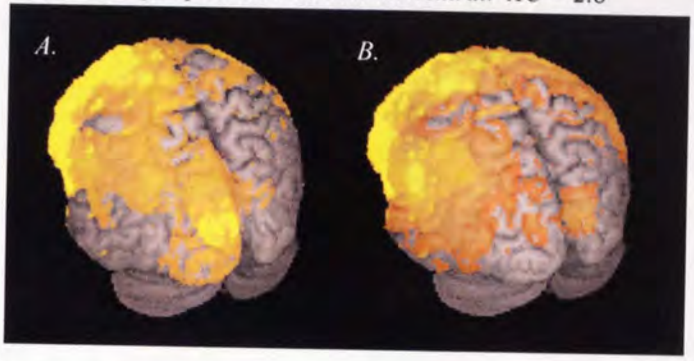


For both peripheral conditions the level of activation was higher than for the central conditions. For the different conditions there was a slightly higher level of activation, in particular in the left hemisphere, than the respective same conditions. The occipital activation in the peripheral conditions was more localised in the left hemisphere, there was more bilateral activation in the central conditions.

Figure 5.5: Experiment 2 – 3D Images of Activation over the Occipital and Parietal Lobes.

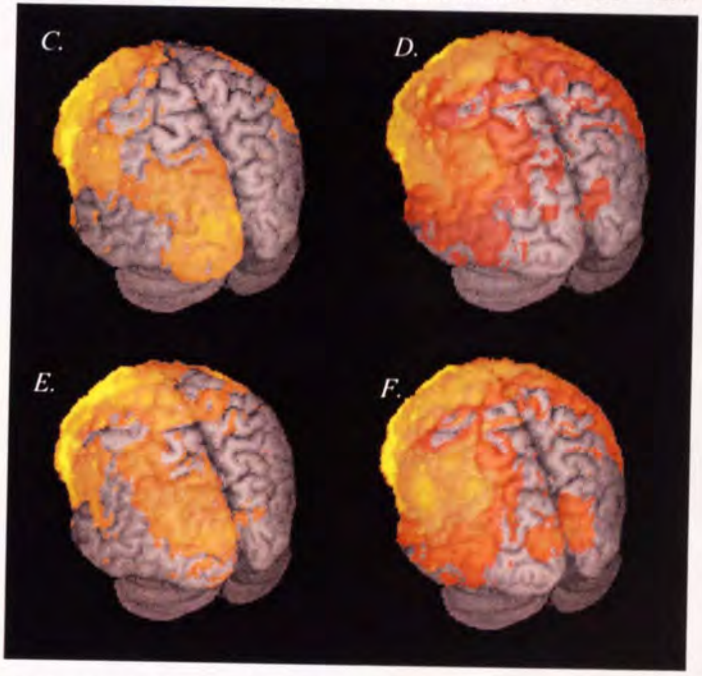
For all images the Fun Integration Depth is 0.05. The Amplitude cut-off (AC) was between 2.0 and 3.4. A higher AC value indicates a higher level of activation was evident and a higher cut-off value was required for localised activation to be visible. See Figure 5.4 for colour representation information.

A: Comparison: central condition vs. neutral. AC = 3.4
B: Comparison: peripheral condition vs. neutral. AC = 2.8



For this experiment the central condition evoked higher levels of activation than the peripheral condition. There is, however, more extensive parietal activation in the peripheral condition, indicating that there is still the possibility of the parietal lobes being more involved in peripheral than central visual processing. The occipital activation is greater for the central condition. This is likely to be due to the nature of the stimulus, which was more visually demanding than the equivalent stimulus in experiment 1.

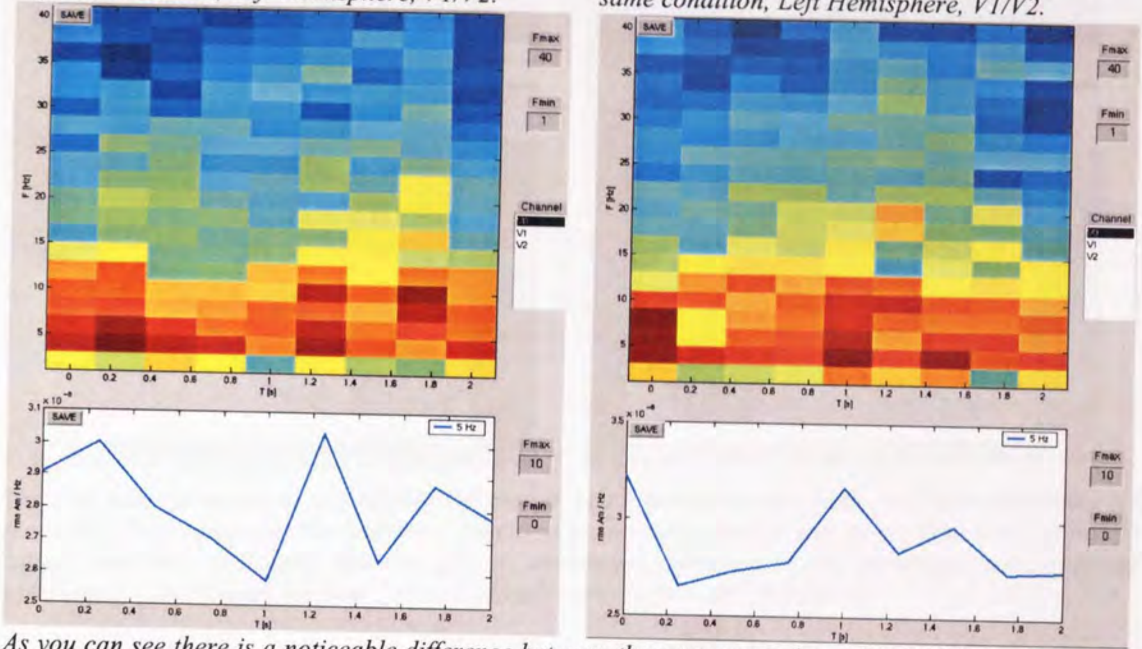
C: Comparison: central-same condition vs. neutral. AC = 3.0
D: Comparison: peripheral-same condition vs. neutral. AC = 2.0
E: Comparison: central-different condition vs. neutral. AC = 3.0
F: Comparison: peripheral-different condition vs. neutral. AC = 2.4



There was more activation in the central than peripheral conditions. For both peripheral conditions the level of activation was more extensive over the left parietal lobe than for the central conditions. For the different conditions there was a slightly higher level of activation, in particular in the left hemisphere, than the respective same conditions. In the central conditions there was a higher level of activation over the left occipital lobe than for the peripheral condition. This is due to the nature of the task; see above. Occipital activation for the peripheral task was bilateral, unlike in Experiment 1, see above, where it was bilateral in the central conditions and unilaterally left in the peripheral conditions.

Figure 5.6: Some examples of Spectrograms showing the neural response to the stimuli in the early visual areas.

For more detail on what is shown by a Spectrogram, please see Chapter 4. Red indicates high levels of activation relative to baseline activity, whereas blue indicates no/decreased activity relative to baseline activity.



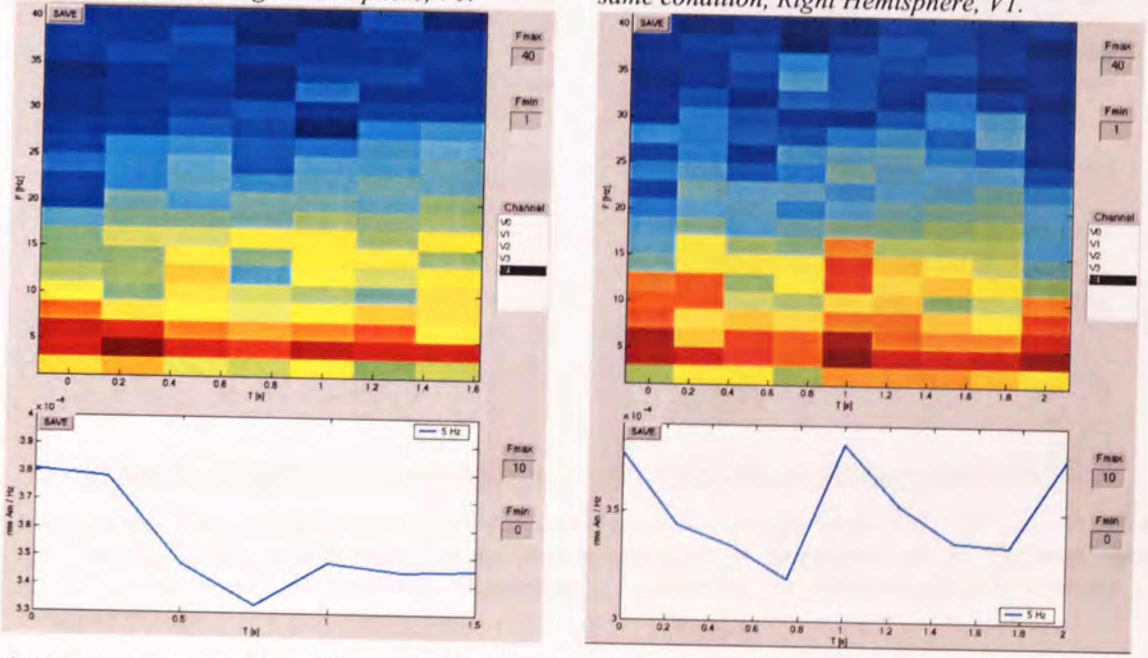
A.Participant IEH, Experiment 2, the peripheral different condition, Left Hemisphere, V1/V2.

B.Participant IEH, Experiment 2,the peripheral same condition, Left Hemisphere, V1/V2.

As you can see there is a noticeable difference between the response to 'same' and 'different' conditions for the peripheral conditions, with the attentionally more demanding 'different' condition producing the largest response, slightly later than the 'same' response. Coordinates for both virtual electrodes are -5.59/1.67/2.04 (x/y/z)

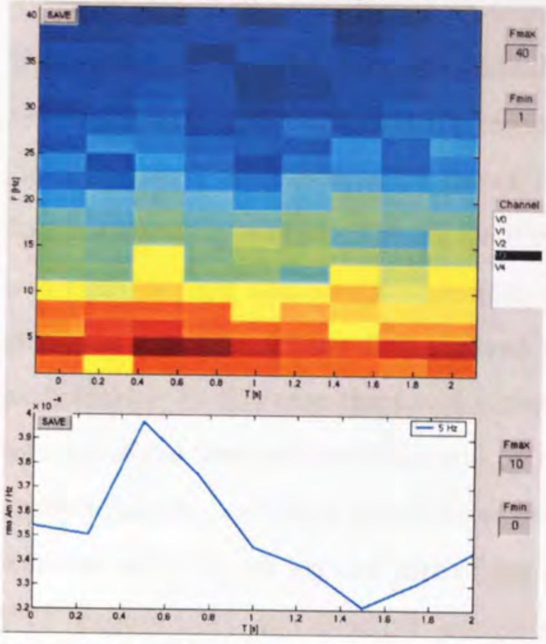
C.Participant SW, Experiment 2, the central different condition, Right Hemisphere, V1.

D. Participant SW, Experiment 2, the central same condition, Right Hemisphere, V1.

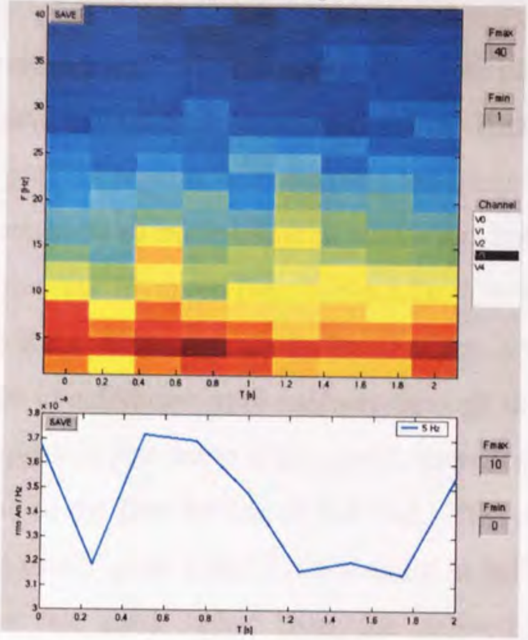


As you can see, the reverse difference is seen here for the central conditions, the 'same' condition exhibits a larger response than does the 'different' condition. This could be because the central response always exhibits a large response, so an attentionally modulated response would be smaller than expected (see Discussion). Coordinates for both virtual electrodes are -2.73/-1.05/-0.04 (x/y/z)

E. Participant SW, Experiment 1, the peripheral different condition, Right Hemisphere V1/V2.

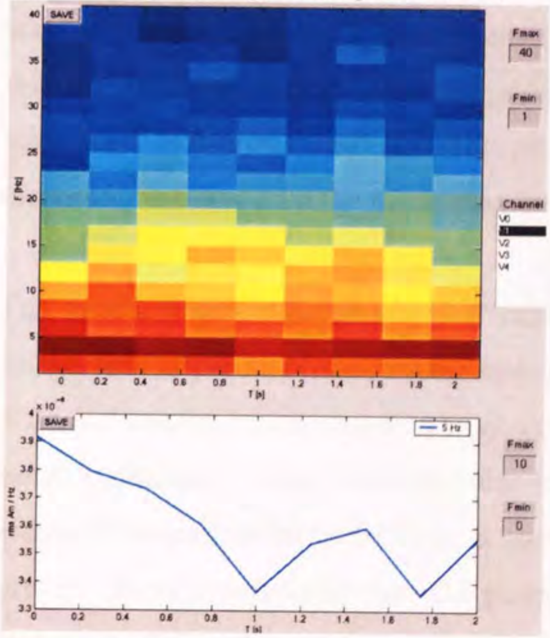


F. Participant SW, Experiment 1, the peripheral same condition, Right Hemisphere, V1/V2.

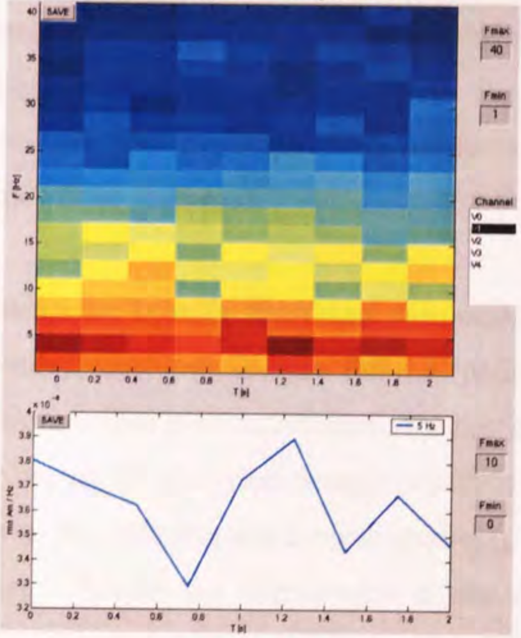


These peripheral responses are slightly different in this experiment, with both conditions exhibiting a large response. The response to the 'different' condition is somewhat clearer and larger than the response for the 'same' condition, indicating there is still an attentional influence on the peripheral component of this experiment. Coordinates for both virtual electrodes are -5.36/-1.09/2.45 (x/y/z).

G. Participant SW, Experiment 1, the central different condition, Right Hemisphere V1/V2.



H. Participant SW, Experiment 1, the central same condition, Right Hemisphere V1/V2.



Here you can see the same pattern as for the central condition in Experiment 2 (C, D). The responses are somewhat less clear but still indicate a decrease in amplitude of the response to the 'different' condition relative to the 'same' condition (see Discussion). Coordinates for both virtual electrodes are -5.36/-1.09/2.43 (x/y/z).

5.4. Discussion

The results of the two experiments exhibited broadly similar distributions in both the psychophysical and neuroimaging results (See Tables 5.1a, 5.1b, and 5.2). There was mainly bilateral activation in the frontal and parietal regions with a strong left hemispheric dominance easily visible. The occipital regions showed more bilateral activation, but there was a left or right dominance depending on the task involved (see Table 5.2). The virtual electrode data (see Figure 5.6) showed that there were, again, similar findings between participants. In this case there was a decrease in activation until halfway through the first rotation of the first section of the trial, with a peak in activation at this point, there was then another peak in activation 500ms after the end of the first section of the trial. This pattern was the same for the second part of the trial (see Figure 5.6). Traditionally in MRI and PET experiments active-active comparisons are used rather than the active-passive comparisons used here. This course of action was decided upon due to the desire to look at the stimulated activity in the brain relative to the baseline activity. However, caution is used when interpreting this data, and no conclusive interpretations are made relating changes in the operation of attention when it is entirely possible that a component of the task may be responsible for the activation changes observed. However,, as will be evident, the data produced indicate a strong possibility that in most cases the changes are due to attentional influences and not task components. The psychophysical results will be discussed first, and then the neuroimaging data will be discussed.

The results from the psychophysical experiments are broadly consistent with each other. In the first experiment the central task provided more interference for the 'peripheral-different' condition whereas the peripheral task provided more interference for the 'centre-same' condition. There must be more interference for the 'centre-same' condition than either of the peripheral conditions, at odds with the idea that the central condition would provide more interference than the peripheral. Maybe the interference is also due to 'same' or 'different', and the result of the conjunction of these two factors. This is shown in the fact that there was a significant interaction between the two variables. In the 'centre' condition the interference from the periphery slowed the 'same' condition down more than the 'different', whereas in the 'peripheral' condition the interference from the centre affected the 'different' condition more than the 'same' condition. In the second experiment, the 'centre-same' condition was again the slowest, but this time the 'peripheral-same' condition was the fastest. The interference appeared to be most effective from the periphery for the 'same' condition, for the 'different' condition the RTs were similar from both 'centre' and 'periphery' conditions. There were no individual effects, but there was a significant interaction where the same pattern as in Experiment one was observed, the 'centre-same' condition being slower than the 'centre-different' condition, but the 'periphery-same' condition being faster than the 'periphery-different' condition. Again, it is not possible to say that the idea of the centre condition provided more interference than the peripheral condition, if anything the reverse if more likely as the RTs for the central conditions were, overall, slower than the peripheral ones. Interference from the periphery slowed the centre conditions down more than interference from the centre slowed the periphery down.

For both experiments the expected psychophysical results were found for the peripheral conditions, that being that the 'same' condition was responded to faster than the 'different' condition. However, for the central condition there was the unexpected finding that the 'same' condition was slower than the 'different' condition for both experiments. This may be a function of Inhibition of Return (IOR) (Tipper, et al, 1988). When there is an equal likelihood of a stimulus appearing at all locations attention is first drawn to one location but it then inhibits this location, as the target is not there, therefore it must be somewhere else. This inhibition can last for over a second (Tipper et al., 1988), and so the following response, if the target does appear in this location, is subsequently delayed. In this case the response was equally likely to be 'same' or 'different', but participants were waiting for a 'different' response; so, for the central task, the first letter string/direction of motion would have been inhibited as a possible response based on this assumption. This would indicate that IOR, in this case at least, was a function of central vision only and is not present in the periphery at all. The 'same' response was made with the left button on the button box. This indicates that the right-handers would be, theoretically, at a disadvantage for responding to the 'same' conditions in terms of handedness. This was clearly not the case as the 'same' trials produced lower RTs, this could indicate that the response was dominated by an expectation of the condition by the participant, the 'same' trials being expected and the 'different' trials being unexpected. In terms of the lateralization of the attentional response, this would indicate that the 'same' response was consciously expected by the subject and subsequently processed by the right parietal lobe, where overt attentional processing is presumed to take place (see Chapters 6 and 7). According to this idea, the 'different' response would be unanticipated and therefore processed using the left parietal lobe, considered to be dominant for automatic, covert attentional processing (see Chapters 6 and 7).

It was interesting to note that where there were errors in the psychophysical data they were drastically slower than the correct responses, varying from around 150ms to 800ms slower. This shows that the attentional interference in the processing could have had a large effect and the 'catch-up' processing had to be repeated. It could also be interference in the memory portion of the task; the participants may have occasionally had momentary lapses of concentration and thus not remembered the original direction of motion/letter string. It is more likely to be the latter as there were very few mistakes; they were not consistent so there is no way they could be due to the attentional part of the task, as if they were then they would be more frequent and all participants would have exhibited them. This was not the case so therefore the errors are most likely to be due to momentary lapses in concentration.

The first experiment used letters so there would, logically be a left dominance in brain activity here as the task required language abilities to distinguish the letters and decide on a 'same/different' response, memory for letters in the majority of English speakers would be an automatic response. However, with the second experiment yielding virtually identical results, this is not necessarily the case. Letter recognition may not have been required in the actual processing needed for a response. The language centres in the brain need not be involved at all; the second experiment included no language conditions at all and yet it yielded comparable results. It would appear that all that was needed for this task was the ability to spatially distinguish features as being the same or different, and not to know what those features were in terms of language. Even though the participants will have recognised the letters and would have easily been able to name them, the response will already have been determined by this stage of processing. This suggests that there is a common process at work serving two disparate perceptual and cognitive systems. The reaction time is not dependant on this separable system, being dependent on the attentional task itself rather than the brain processes serving the processing of the task. The location of this common process would logically appear to be the parietal lobes, in particular the SPL and IPL, given that there was the most variation in activation for these areas (see Figures 5.4 and 5.5). The frontal lobes would also play a major role, although their role is seemingly consistent across the task conditions as there was little variation in the levels of activation related to condition. This links with the idea that there is a fronto-parietal network of attention and it would appear that there is a modulation in attention related to task condition, and not a modulation related to the differences in tasks themselves. This again supports the idea of a common process for visuo-spatial perception.

The left hemisphere, which is generally the dominant hemisphere in right-handed individuals, is concerned with processing language, and analytical functions, whereas the right hemisphere is concerned with spatial concepts (Coull & Nobre, 1998; Macaluso & Frith, 2000). In these experiments the left hemisphere was dominant. This was not anticipated as this was a spatial attentional task and previous studies have found the right hemisphere to be dominant in such cases (Coull & Nobre, 1998). However, it can be argued that this was a temporally dominant task as there was the need for 'attentional memory' to remain active while the subject remembered over time what response to make. As no language concepts were involved in experiment 2, it may be that language is the driving force here; or rather that the precursor to language processing (that of feature recognition) is processed in the left hemisphere and that this is what is observed here, the process of feature recognition plus the motion perception. However, Experiment 2 did not involve multiple letters, rather the stimuli was constant and the only difference between conditions was the direction of motion. This lateralization is most likely due to the task demands. The task is a decision-making task, using overt attentional mechanisms and memory. Participants had to pay attention to the stimulus until it was time to respond, having remembered the chosen, appropriate response when the stimuli paused. This was a purely spatial task with no higher elements of language processing influencing the response. The responses were dependent on spatial processing and the conjoining of features in the display – in other words parallel processing of visual features, a basic process that can be influenced by attention (Treisman, 1991; Lavie & Driver, 1996).

But were we actually measuring a modulation by attention? The attentional influence comes with having to make a decision based on conflicting information, particularly in the second experiment. The participants had to decide whether the inner or outer circular grating was turning in the same or different direction in Experiment 2. The direction of motion for the two gratings was randomly synchronised with each other; the conflict would have arisen when there was confusion over which direction a grating was turning as the other grating in the task had been turning in the opposite direction all along. This is particularly the case with the peripheral condition where there was the central task running at the same time, and the subject had to attend to the peripheral only. The central task had the role of the distracter. It is possible to hypothesise, based on the 'Spotlight' analogy, that the central condition will have had less distraction than the peripheral condition. It would be thought that a central task with peripheral distracters would be easier to do than a peripheral task with central distracters as we rely on our central vision for the majority of our visual input, the peripheral distractions can be ignored easily. Whereas for peripheral vision the central task will naturally be competing more heavily for processing priority, it will involve more competition for attentional resources. However, this did not appear to be the case and the distractions posed by the two tasks were in the form of an interaction with the other variable, task response. This data therefore suggests that the 'Spotlight' analogy is flawed. If this theory were an accurate representation of how attention acts then we would have expected the central task to interfere with the periphery more than did the periphery with the central. Evolutionary explanations state that motion in the periphery may be important and requires the central vision being turned towards it, which would suggest that motion in the periphery is as strong a pull for attentional resources as central information. This is more in line with the results of this experiment, where task response interacted with target position.

However, the tasks in these two experiments do appear to be influenced by attention. The two sets of responses, 'same' or 'different' produce different RTs and brain activity. In the 'different' condition there appeared to be more activity in the parietal and occipital areas than in the 'same' condition, for both experiments. Frontal activity remained relatively unchanged over both conditions, though there was slightly more activation in the 'same' conditions than the 'different' conditions for the first experiment (see Figures 5.4 and 5.5). This shows that the regions undergoing attentional modulation were located primarily in the parietal and occipital areas for both types of stimuli; the source of the modulation was most likely the parietal cortex, as this is where it is thought the source of the attentional processing in terms of the fronto-parietal network (Posner & Dehaene, 1994), specifically the superior parietal lobe (SPL) and the inferior parietal lobe (IPL); the occipital cortex was most likely modulated through feedback mechanisms. The frontal cortex dealt with the behavioural response to the stimulus and this will have been unchanged regardless of the condition, as every condition required the same response, a button press. The frontal cortical area activated could also have been involved in the attentional memory need in the task.

Somers et al (1998) concluded that their data showed evidence for the initial modulation of V1. This data does not support this. V1 is modulated as strongly as other visual and parietal areas (see Figures 5.4-5.6) but there is nothing in Figure 5.6 to suggest that V1 is modulated initially by attentional influences; all virtual electrodes show an immediate decrease in activation until around 200ms post-stimulus onset. While is cannot be stated that there is conclusively no modulation, nor can be stated that there is. Along with previous research (see Chapter 2) it seems unlikely that V1 is initially modulated by attentional influences, and that any modulation comes in the form of feedback mechanisms.

The medial surface of the superior frontal gyrus is the supplementary motor area and is involved in mechanisms influencing automatic grasp reflex, bimanual coordination and voluntary movement; it is also thought to be involved in learned, skilled motor sequences. This could be where the coordination of the response was processed. The caudal part of the medial frontal gyrus is the frontal eye fields (FEF), the centre for voluntary eye movements. The FEF are independent of visual stimuli and participate in the initiation of saccades, they are also implicated in coordination of movements required for accurate gaze changes. This area could be processing the fixation of the gaze in the centre of the screen (a requirement given in the instructions to the participants). It is an impossible task to keep the eyes motionless for seconds at a time (Bruce, et al, 1996), so the constant re-fixating of gaze will be the cause of activation in this area.

The precentral sulcus is the primary motor area, so obviously the initiation of the finger response was processed here. The postcentral sulcus is the general somatosensory processing area and will have been activated as the participants felt for the response button, no head movement to look being possible, the participants had their head securely positioned under the dewar, so finding the button was done by touch alone. Participants were told to keep their fingers on the buttons at all times, however, due to the repetitive nature of the task there will have been a natural desire to remain focused, and moving the fingers will have constituted part of this. Even though only one finger was required to respond, these two areas were mainly bilateral activation, with left hemisphere dominance.

This possibly indicates that even though the response was only one finger or the other, both fingers were primed to respond, indicating a genuine 'unknown' quantity of the response prior to finalisation of the motor sequence. The dominance of the left hemisphere may be due to the participants expecting the stimulus to be 'different' more than they expected it to be the 'same', the right button indicating a 'different' response. In the second experiment the postcentral sulcus was only activated in the 'centre-different' condition, unilaterally left, in all other conditions activation was absent. The precentral sulcus was bilaterally activated in all conditions. This could be due to the participants resting their fingers on the buttons in this phase of the experiment, rather than resting them elsewhere on the keypad and having to feel for them at each response

It has been found that the posterior parietal cortex is activated in tasks involving working memory (Snyder, et al, 2000; Coull & Frith, 1998). Both hemispheres are involved with this, although there is evidence for the left hemisphere being dominant for temporal tasks and the right hemisphere being dominant for spatial tasks (Macaluso & Frith, 2000). This view is not supported in this task as there was a strong spatial content to the task but not much temporal content other than the speed with which intentions to respond were altered. Yet the responses were left hemisphere dominant throughout. This would suggest that the left hemisphere is involved in this spatial task. In terms of the spatial component, the inferior parietal sulcus (IPS) has been found to be more concerned with spatial processing, and the superior parietal sulcus (SPS) with non-spatial processing (Coull & Frith, 1998). If the hemispheric divide between temporal and spatial attentional mechanisms is to survive there has to be an acceptance of the information showing that there is both spatial and non-spatial processing within each hemisphere (Coull & Frith, 1998), even if the balance is skewed in favour of one in each hemisphere (Walsh et al., 1999). The dominance of one hemisphere over another in terms of processing will, naturally, depend on the nature of the task itself. In this case overt attention was used along with working memory and intention. There is a case to be made for covert spatially selective attention and intention being processed in the left hemisphere, specifically the SPL and IPL (Parson & Holliday, 2001). In particular, the IPL has been shown to have neural circuits dealing with the acquisition of visual information and its subsequent transformation into behaviourally relevant movements (Rizzolatti, et al, 1997). It may also be the case that overt attention and intention are linked in the same hemisphere, based on these results.

It has also been found that the SPL is more involved in peripheral processing than central processing, which is dominated by inferior occipital areas (Coull & Frith, 1998; Macaluso & Frith, 2000). In this task there were both central and peripheral components, and all these areas were activated, supporting this idea of separable systems for central and peripheral visual processing. If the central task caused more interference than the peripheral task when the other was the focus of attention, a difference in activity should be seen between the areas being processed and the areas being selectively ignored. For the central task, the SPL activation should be less active than the inferior occipital areas, while in the peripheral task the inferior occipital areas should be less active than the SPL. Although, if it is the case that the central task provides more interference than does the peripheral task, the inferior occipital areas should be more active in the peripheral condition than is the SPL in the central condition. The activation in the imaging data showed no consistent differences in activation in line with these RT results. As this discrepancy of interference did occur, but only in the form of interactions with task response, and no differences in the imaging data were found, no conclusions about central processing and peripheral processing areas can be made.

The intention to respond is important in the understanding of what is happening in this experiment. An important role of the posterior parietal cortex (PPC) is processing behaviourally relevant sensory information and intention comprises a large part of the transient response, consistent with the role of the PPC in sensory motor transformations (Snyder et al., 2000). In these experiments the subject had no idea whether the task would elicit a 'same' or 'different' response, so was primed to respond to either, however, the expectations of participants leant more towards the 'different' response. Yet, when the response was called for there had to be a change in intention from the option to respond to either to the specific intention to respond correctly (Snyder et al., 2000). The participant was only allowed to respond to one task at a time, yet both were on screen throughout the experiment. This will have created confusion in the intention to respond through conflicting information in another part of the visual field interfering with the processing of the response. The conflicting information of the two tasks, particularly in Experiment 2 will have created confusion over the correct response and delayed the process of responding. This will have lead to the intention to respond a certain way being changed, possibly several times, as the 'attentional memory' was recalled.

However, another possibility is that this left hemispheric lateralization is due to response selection, participants had to select one of a number of responses. Previous research (Rushworth, et al., 2001) has found that left parietal and premotor cortices are involved with response selection whereas the right parietal and premotor cortices are involved with single detection responses.

5.5. Conclusions

There was generally a decrease in activation for the early visual areas until ~ 250-500ms, exemplified in the virtual electrode data (see Figure 5.6), indicating that the level of activation decreases post-stimulus, thus indicating that the enhancing properties of attentional processing are not active until after this time. This would indicate that there is no initial increase in processing for the response early on in the visual pathway, namely V1 and V2. These results seem to suggest that the modulation of V1 and V2 is in the form of feedback from higher areas, the extrastriate and parietal areas, at a time later than the initial feedforward sweep of information processing. The parietal activation was left hemisphere dominant for both experiments, indicating a higher involvement of this hemisphere in spatially oriented tasks than has been previously thought. The left hemisphere lateralization observed is possibly to be due to a number of factors, response selection, temporal and spatial attention and the intention to respond, all of which have been shown to be lateralised in the parietal cortex, specifically to the left hemisphere.

The results from these two experiments therefore supports Somers et al (1999) in that the early visual areas, in particular V1, are modulated by attention, however, it does not support their theory of initial modulation in V1.

Chapter 6: A Cue-based Attentional Paradigm Revealing the Implication of a Lateralized Attentional Effect

6.1. Introduction

Theories of attention generally fit into two categories: space-based accounts and object-based accounts. Space-based accounts stem from the idea that the flow of information to higher processing stages can be controlled by limiting the inputs from earlier, sensory processing stages. Posner likens attention to a 'Spotlight', where stimuli in the centre of the 'beam' are processed fastest and most efficiently and there is a gradual tail-off in processing power further towards the edge of the spotlight, or a 'Zoom lens', where there are said to be differing levels of resolution (Vecera, 2000). Eriksen and Yeh (Eriksen & Yeh, 1985) assert that the Zoom lens analogy is closer to how attention operates: as the power of the lens is increased, the field of view decreases, higher processing resolution compensates for a smaller processing area, and also, the larger the lens then less detailed the processing of the information contained within.

Object-based accounts work on the premise that stimuli are selected for further processing on the basis of feature processing done in a preattentive stage of processing. The features are processed, but only those that fit the behavioural requirements are processed further and formed into objects per se in our awareness. Neisser (1967) was the first person to describe, in detail, preattentive and attentive stages of attention. The preattentive stage segments the visual field into separate objects on the basis of gestalt properties, for example spatial proximity and shared movement, such processes are continually ready to process information in the external world, and are indifferent in context and meaning (Neisser, 1967). The attentive stage is a 'focal attention' stage where the selected information is analysed in more detail (Duncan, 1984).

Attention is not a single process; attentional processing can be broadly classified into two categories. Covert attention is stimulus induced, tied to sudden changes or novel stimuli in the visual field; there is no conscious thought or cognition involved, it is a completely involuntary process. Covert attention can be seen as transient, having rapid engagement and dissipating quickly; being fully activated in about 50ms and dissipating in about

250ms (Posner & Cohen, 1984), and is linked with early, 'bottom-up', processing. Overt attention, on the other hand is related to 'top-down' processing, and is a conscious, voluntary process.

Attention is summoned by a cue, without a cue attention is not drawn to a location or object, and without attention there is no awareness of the target: attention is fundamental to conscious awareness of external environments (DeSchepper & Treisman, 1996; Lamme, 2000). Obviously there is a behavioural advantage to knowing when a stimulus is to occur (Coull & Nobre, 1998), and in experimental terms the heightened awareness is evident through reduced response times to the presentation of stimuli requiring a response from participants.

To examine these two forms of attentional process two types of experimental design have been developed for use in attentional experiments: those using endogenous cues and those using exogenous cues. A cue that is interpreted and used voluntarily to direct attention, such as an arrow (Posner, et al, 1978), is said to be endogenous. This type of cue is not entirely necessary in itself, as similar results have been found where participants are asked to directly 'pay attention' to a particular location. However cues that depend on inducing attentional selection through sensory stimulation, are said to be exogenous, for example a light flash. Exogenous cues facilitate stimulus detection when sensory information is used as advance information about target position (Jonides, 1981).

Spatial cuing is a common way to study visual spatial attention (see Chapter 1). The use of spatial cues to cue stimulus locations enhances stimulus processing in the absence of eye movements, reflecting the activation of mechanisms to shift attention to the stimulus location before its appearance (Corbetta, 1998). There are two ways in which cues can be said to facilitate stimulus analysis: firstly visual analysis is done more rapidly at the attended location as time is needed for attention to reorient itself to a new location when a cue proves false (Corbetta, 1998; Posner, 1980), and secondly attention may directly influence visual processes by enhancing sensitivity to the attended location, which could be one explanation of improved sensory thresholds found in attended locations (Corbetta, 1998). Shifting attention is thought to involve 3 internal processes: disengagement from the original focus, movement to new location, and engagement with a new focus (Posner, et al, 1984). The reason that invalid cues, where the cue is a false indicator of the position of the stimulus, produce much longer reaction times (RTs) is due to the attentional system having to utilise all three of these processes in re-orienting the focus of attention, whereas with valid cues, where the cue is a true indicator of the position of the stimulus, require only the final stage of engagement, providing enough time has been given to orient to the cued location. If no cue is given for a target location, so called 'neutral' trials, only the last two stages are required (Posner, et al, 1984). Posner and co-workers (Posner, et al, 1978) found that invalid trials produce significantly longer processing times than do either valid or neutral trials, also that the valid cue facilitated the RT relative to the neutral trial. They (Posner, et al, 1978) developed the 'Cost-Benefit' paradigm, based on this evidence, which states that the response will be facilitated if attention is already drawn to the location of the target, the benefit, and inhibited if attention is directed away from the target, the cost.

There has been little reason to think that attentional processing can be influenced by laterality of processing demands such as handedness. This aspect of attention has been little researched. However, given the idea that the contralateral hemisphere is dominant in terms of behaviour, it would seem reasonable to suggest there are differences in the behavioural responses of left- and right-handers. Exactly what these differences may be has been little researched, yet it is a fundamental assumption in the limits of experimentation, which use only right-handers as standard. There would be no reason to exclude left-handers from research if there was not this assumption of a difference in processing lateralization. This indicates that there is a valid pool of data here that has yet to be collected; there is no reason why experiments should not have more than one category of handedness.

It has been commonly accepted that there are both structural and functional asymmetries in the human brain since Broca, in 1861, found that lesions producing language disorders were generally located in the left hemisphere (Galaburda et al., 1978). Since then we have learned that many behaviours and processes are dominated by one hemisphere. The two hemispheres of the human brain are markedly different anatomically, as has been found in many studies since Broca in 1861. For example, McRae et al (1968) found that the left and right lateral ventricles varied with the handedness of the subjects. In right-handed subjects the left occipital horn of the ventricles was longer than the right occipital horn in 60% of cases, while the right occipital horn was longer in only 10% of cases. In left-handed and ambidextrous subjects, 38% had a longer left occipital horn and 31% had a longer right occipital horn (Galaburda et al., 1978). This indicates that there is a greater degree of asymmetry in right-handed individuals, with left-handed individuals showing a greater degree of symmetry.

Another consistently found asymmetry that has been associated with handedness is in the sylvian fissure, which has been found to be asymmetrical at the posterior end; the right fissure curls upwards posteriorly and ends higher than the left fissure (Geschwind & Galaburda, 1987). In terms of handedness there is a bias among self-reported right-handers to have a higher right sylvian fissure than do left-handers (Hochberg & LeMay, 1975, in (Geschwind & Galaburda, 1987). However, the left fissure of the ascending limb of the sylvian fissure, part of Broca's speech area, is more branched than the right, indicating more infolding, and therefore more cortex, than the corresponding area on the right (Eberstaller, 1884, in (Geschwind & Galaburda, 1987).

The asymmetries recorded over the last 150 years are along a continuum, there are no absolute differences between left- and right-handers, individuals fall along a continuum of handedness (Annett, 1970, in (Geschwind & Galaburda, 1987). The general findings from these anatomical studies is that left-handers show a greater degree of symmetry than do right-handers, and that the left-handers is more likely to show reverse asymmetries, albeit less striking. For left-handers showing asymmetry in the same direction as the right-hander the difference is of a lower magnitude than in the right-hander (LeMay & Geschwind, 1978, in (Geschwind & Galaburda, 1987). However this does raise issues of measuring handedness, how do we measure something that is along a continuum? In this instance the measure that has been taken is the hand that the participant writes with is the measure of handedness.

What research there has been into handedness in the area of attention has shown that there is a difference in the responding of left- and right-handers. Left-handers have been shown to have an asymmetry of processing favouring the left hemisphere while right-handers have been shown to have an asymmetry favouring the right hemisphere (Pierce, et al, 1996; Eviator, et al, 1997). In a study by Pierce et al (Pierce, et al, 1996), using the cost-benefit paradigm, only right-handers were found to have significantly slower RTs in invalid conditions. Right-handers were also found to respond slower to targets on the left after an invalid cue, whereas left-handers suffered greater costs and benefits in the valid and invalid conditions for target on the right than on the left. This fits in with idea of the non-dominant hemisphere being dominant in processes involving attention, to be explored later.

It is not really clear in the literature what the timing of covert attention is, when it is activated, when it's influence decreases, and when it stops altogether. Posner and Cohen (1984) are one of a small number of researchers who have put time limits on this process. A study of different timings based on the information given by Posner and Cohen (1984), see above, would give rise to more information on what is happening. Employing the Cost-Benefit paradigm would also be of use, as this is known to utilise covert attentional resources, thus one could theoretically, based on this paradigm, gain more information into the timing of covert attention and what influence cues have on such processes.

The first aim was to examine the timing of covert attentional processing with a view to moving this experiment into a neuroimaging study. We wished the response from the cue to be fully ended before the target appeared. Thus the full effect of the 'Cost-Benefit' paradigm (Posner, et al, 1978) would need to be observable in the reaction times. If this were not the case then this experiment would not be transferred to a neuroimaging study. In the first experiment different timings between the cue and the target were employed to investigate the effect this had on the expected results. Three times of 70ms, 100ms and 300ms were employed. Covert attention is fully activated by 100ms and the initial effects are dissipated by 250ms (Posner & Cohen, 1984), so thus 70ms would be during early activation, 100ms would be during full activation, and 300ms would be when the initial effects of attention have dissipated. This study incorporates the cost-benefit paradigm of Posner et al (Posner, et al, 1978) adding two new forms of trial, but rejecting the neutral trial, as there is more than enough evidence to support a neutral trial being the midpoint between the valid and invalid trials. This was done to see if there was a continuum of processing costs between the valid and invalid conditions. Firstly a 'partially-valid' condition was designed, where the cue is semi-co-located with the target, and then a 'partially-invalid' condition was designed, where the cue was adjacent to the target (see Figure 6.2).

The second aim was to examine the differences in reaction times between left- and right-handers. We needed to check any differences between left- and right-handers for further imaging research. In the second experiment handedness was examined in the context of the same task, using the timing that produced the most consistent RTs in the first experiment. In Experiment 1 we expected to find a continuum of processing cost between the valid and invalid trials, the partially-valid conditions showing less cost than the partially-invalid condition. We also expected there to be a difference between the timing conditions. In Experiment 2 we expected to find a difference in the lateralization of responses between left- and right-handers, it was unknown what this difference would be but it was expected to be in line with the results of Pierce et al (Pierce, et al, 1996), involving decreased RTs for the dominant hand in each participant group.

6.2. Methods: Experiment 1

6.2.1. Apparatus

Stimuli were produced using a VSG5.021 grating generator (CRS Ltd.). The viewing monitor was an EIZO T562-T 17" colour monitor, calibrated using a computer-controlled photometric procedure (Optical, CRS Ltd). Responses were made on a button box with contact switches, 0.25mm pressing distance. Lighting conditions were limited to one overhead spotlight located posterior to the participants and angled so there was no glare on the viewing monitor.

6.2.2. Stimulus Parameters

Stimuli were 2c/deg sinusoidal luminance gratings of 90% contrast and 28.9 Cd/m^2 mean luminance bounded within a square region 1.2 x 1.2 deg (Figure 6.3). The gratings were presented tilted ± 2 deg off vertical in the lower right (or left) quadrant of the visual field. Participants fixated on a 0.25deg white square. Gratings were presented 2.0 deg eccentric to the fixation at 30, 45, 60 degrees along radii from the fixation (Figure 6.1). Stimuli were preceded by a brief cue of 100ms duration, which was a white outline box matched in size to the stimulus. The cue appeared at 2.0deg eccentric from the fixation in 5 locations along radii from the fixation of 30, 37.5, 45, 52.5, 60 degrees, thus stimuli could be co-located, partially overlapping, just touching, and separated. The locations denoted the top left hand corner of the cue or grating. Stimuli were presented on a uniform grey background of 28.9 Cd/m^2, calculated to be to midpoint between the black and white of the stimuli.

6.2.3. Participants

The 9 participants, 6 females and 3 males, had a mean age 28.4 years, with an age range of 23-44. All had normal or corrected-to-normal vision. All were right-handed dominant. This was measured by observing which hand was used to write with, no handedness inventories were used.

6.2.4. Timing Parameters

The stimulus cycle commenced with the presentation of the fixation point for 100ms. A cue appeared 500ms after the onset of the fixation point, followed by a target at a variable onset time, which remained onscreen for 100ms. The screen was blank for up 2 seconds or until the participant responded. The gap between the cue offset and the target onset times was one of 70ms/100ms/300ms. In any run of the experiment only one time was used; participants did only one of the timing parameters at a time. There were 1300 trials per run, taking approximately 50minutes, with breaks of 1-2 minutes every 15-20 minutes. Participants only did one timing condition per session.

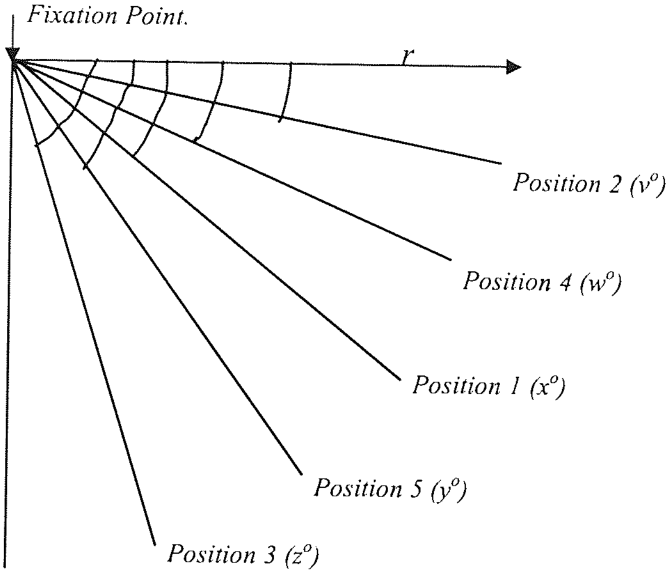
6.2.5. Procedure

Participants sat 2.1m away from the screen and looked at the fixation throughout the trials (see Figure 6.4). The task was to judge the direction of tilt of the stimuli, signalling their choice with a button press. A right button press indicated a 'right orientation' response and a left button press indicated a 'left orientation' response. There were 4 categories of stimuli: valid (cue and target were co-located), partially-valid (cue and target overlapped), partially-invalid (cue and target were located next to each other), and invalid (cue and target spaced apart). There were 13 trial types in all: 3 valid, 4 partially-valid, 4 partially-invalid, and 2 invalid (Figure 6.2). Trials were randomly generated with equal probability giving an average of 100 trials being produced for each of the 13 trial types (Figure 6.2). Participants were giving adequate practice at the task in pilot sessions to achieve at least 80% accuracy in the identification of target grating orientation before proceeding to the main data collections. Typically participants achieved this performance level after one 30-minute session. Participants were instructed to fixate on the fixation point in the top left-/right-hand corner of the screen and to respond to the target only; they were instructed to not respond to the cue. The instructions were to press the right button if the target grating was oriented to the right, based on the top edge o the grating, and the left button if the target grating appeared to be oriented t the left, based on the top edge of the grating. Post experimentally the participants reported that the cue either 'was distracting' or that the task was 'difficult'. Few participants thought they had achieved over 80% accuracy when most achieved over 90%, indicating an automatic response that required little or no conscious input. Once all sections of the experiments were complete, it was explained to the participants what the significance of the cue was in relation to the target and what it was hoped it would do to the responses generated. All participants were told the results of their performance in terms of percentage accuracy and whether or not their responses conformed to the expected patterns. Participants did not report using any strategies to help them with the task.

Figure 6.1: The Positions of the Target and Cue Relative to the Fixation Point.

The targets and cues were positioned with the top left hand corner touching the end of the line shown.
Target Gratings were in positions 1, 2, and 3.
Cue Outline boxes were in positions 1, 2, 3, 4, and 5.

Target and Cue Positions.



$r = E^o$ *eccentricity*

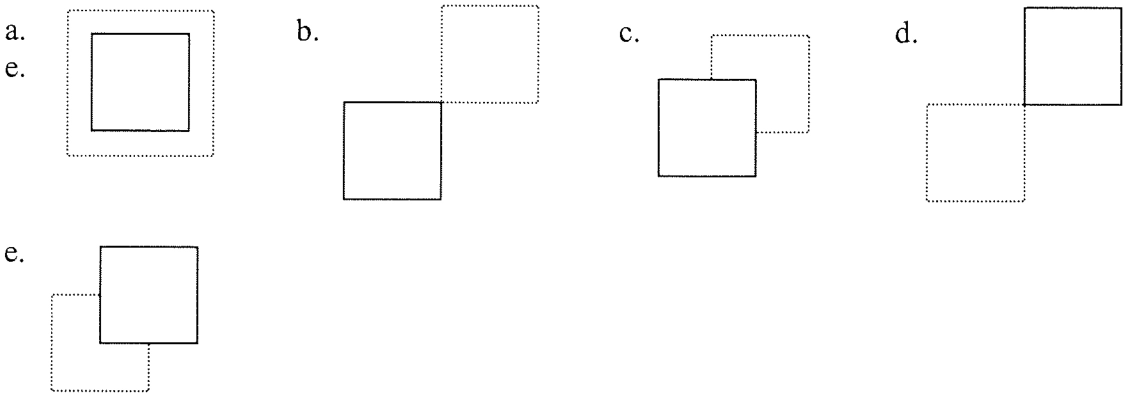
$v^o = 30$
$w^o = 37.5$
$x^o = 45$
$y^o = 52.5$
$z^o = 60$

Figure 6.2: The Positions of Targets and Cues Relative to Each Other.

The dashed line represents the cue and the solid line represents the target.

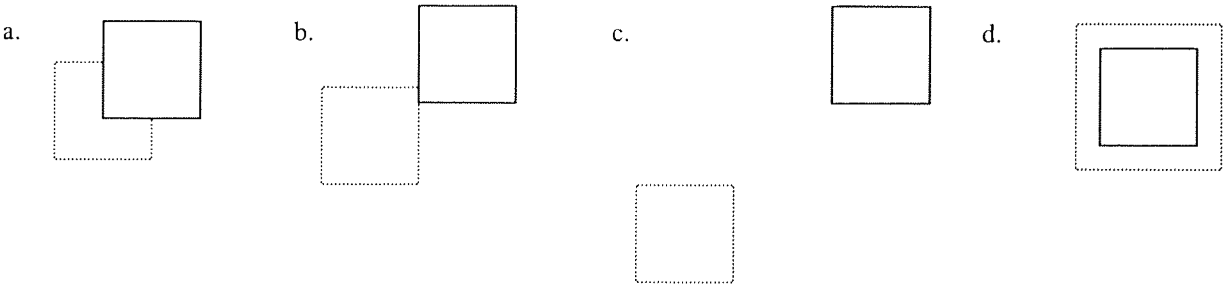
1. When target is in position 1:

Item a represents the valid trial (the cue was no bigger but is drawn so as to be visible). Items b and d are the partially-invalid trials.
Items c and e are the partially-valid trials.



2. When the target is in position 2:

Item d represents the valid trial (the cue was no bigger but is drawn so as to be visible). Item a is the partially-invalid trial.
Item b is the partially-valid trials. Item c is the invalid trial.



3. When the target is in position 3.

Item d represents the valid trial (the cue was no bigger but is drawn so as to be visible). Item a is the partially-invalid trial.
Item b is the partially-valid trials. Item c is the invalid trial.

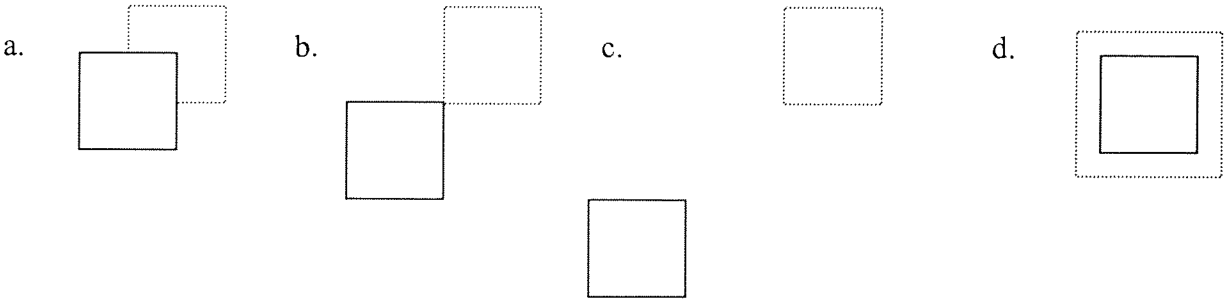


Figure 6.3a: The Stimulus.

The gratings was a sinusoidal luminance grating of 2c/deg at 90% contrast and 28.9 Cd/m^2 mean luminance bounded within a square region 1.2 x 1.2 deg. The gratings were ± 2 deg off vertical in the lower right (or left) quadrant of the visual field. Shown here in position one (see Figure 6.2.). Not drawn to scale.

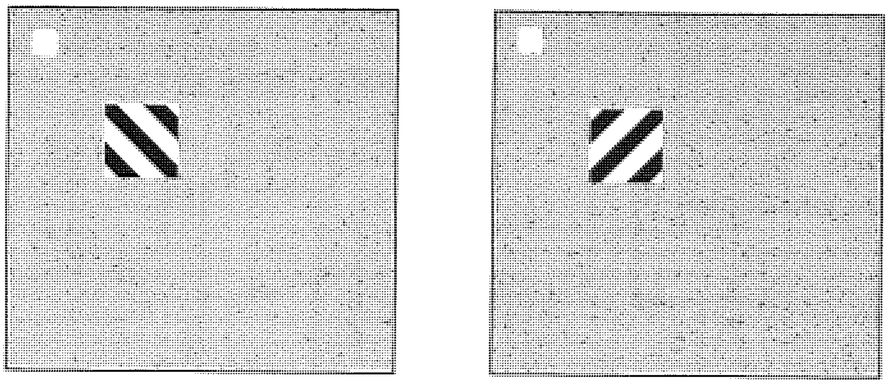


Figure 6.3b: The Cue

The cue was a white outline box the same size as the target. Shown here in position one (see Figure 6.2.). Not drawn to scale.

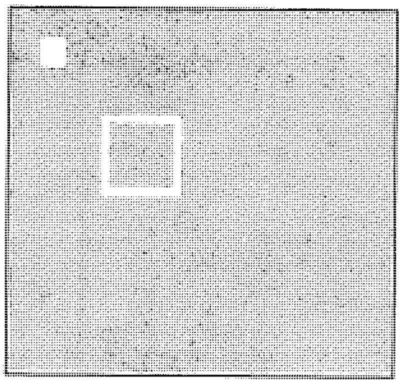
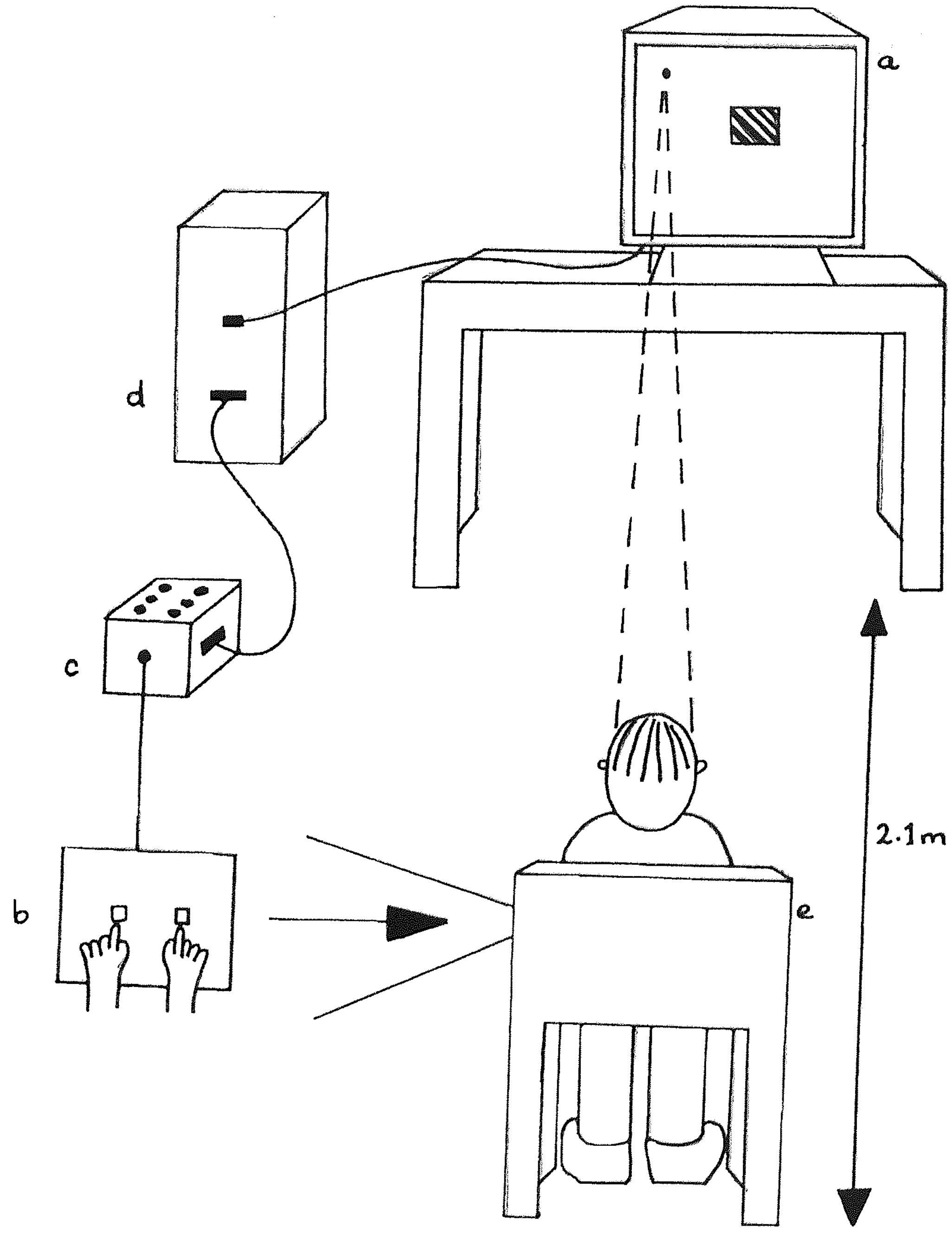


Figure 6.4: Stimuli Layout. The experiments in Chapter 7 had the same layout but with the participant seated in the MEG system inside the shielded room.



A) The monitor, an EIZO T562-T 17" colour monitor. B) The button box rested upon the subject's lap. There were 2 x 0.25mm contact switches with which the Participants responded. The Participants rested their fingers on the buttons until a response was required. C) The connector box between the button box (B) and the computer (D). E) The subject sat 2.1m away from the monitor and fixated on the top corner of the screen. The two runs consisted of the fixation point being on the left, making the right visual field the focus, ad with the fixation point on the right, making the left visual field the focus. Participants responded to the target by deciding if the grating was oriented left or right and then pressing the appropriate button.

6.3. Results for Experiment 1

Table 6.1: Summary of Reaction Times for all Conditions

TYPE	SIDE	ORIENT	70ms	sd	100ms	sd	300ms	sd
valid	LVF	LEFT	447.55	104.46	430.21	109.64	480.98	142.98
partially-valid			445.82	115.98	432.6	112.85	496.97	147.71
partially-invalid			467.91	120.33	435.9	112.75	502.88	143.31
invalid			500.45	127.58	514.74	154.03	523.67	139.74
valid	LVF	RIGHT	475.23	120.81	403.4	68.34	457.15	126.56
partially-valid			479.84	146.62	410.72	95.59	469.05	120.42
partially-invalid			489.78	125.84	415.69	83.74	481.72	135.7
invalid			503.66	116.65	484.86	128.02	500.32	134.6
valid	RVF	LEFT	516.44	172.78	485.79	135.69	491.78	143.53
partially-valid			517.94	177.98	414.57	73.414	500.41	147.29
partially-invalid			542.7	185.09	428.87	82.559	519.74	155.75
invalid			566.84	194.96	508.22	145.25	523.01	153.21
valid	RVF	RIGHT	433.84	110.56	452.05	121.54	460.71	135.68
partially-valid			442.35	119.45	421.84	93.25	467.84	130.78
partially-invalid			475.68	139.42	415.72	71.96	471.86	125.37
invalid			475659	126.41	480.4	114.44	489.94	147.57

The effect of presentation side, orientation of the stimulus and time offset on processing time are shown in Table 6.1 and summarised graphically in Figures 6.5 - 6.7. The data was subjected to a repeated measures 2x2x4 ANOVA, the results of which are summarised in Table 6.2.

6.3.1. Results Summary

For the 70ms condition orientation appeared to be the deciding factor when determining the speed of response. For the same orientation in the same visual field (for example the LVF-left condition) is faster than for different orientations in the same visual field (for example the LVF-right condition). For the 100ms condition the overriding factor influencing the RT appeared to be visual field, the LVF being faster than the RVF. For the 300ms condition there appeared to be an interaction of sorts, with the conditions involving left orientations giving slower responses than those involving right orientations, but with the LVF producing the faster RTs than the RVF in each case.

The valid conditions produced the faster RTs, the invalid the slowest, with the partially-valid and the partially-invalid producing RTs midpoint between the two, in the expected order (see Table 6.1). For the 100ms condition, this pattern was observed only in the LVF conditions. For the RVF conditions, the valid conditions, while not as slow as the invalid condition, was distinctly slower than either the partially-valid or partially-invalid conditions.

6.3.2. Results

The interaction between side of presentation and trial type in the 70ms condition ($p<0.001$) showed that the trial types, on average, produced slower RTs in the RVF than in the LVF. The other conditions were in the expected order, valid fastest followed by partially-valid. The side of presentation and orientation also showed an interaction, the orientation, which was oriented to the fixation point, was faster on the corresponding side, ($p<0.001$), so on the LVF the left orientation was faster, and on the RVF the right orientation was faster

For the 100ms timing condition there was an interaction between side of presentation and trial type ($p<0.001$). The LVF showed the valid trial produced the fastest RTs, followed by the partially-valid and partially-invalid conditions, the invalid condition producing the slowest RTs, whereas the RVF showed the valid and invalid conditions producing the slowest RTs. Overall the LVF had faster RTs than the RVF ($p<0.05$). In this timing condition the right orientation had faster RTs over both sides of presentation ($p<0.001$). Although participants were faster at responding in the 100ms condition, the results of the RVF condition makes it an unsuitable timing condition for further research in this instance, however, further research into this timing difference alone would be useful, however that is beyond the scope of the current studies.

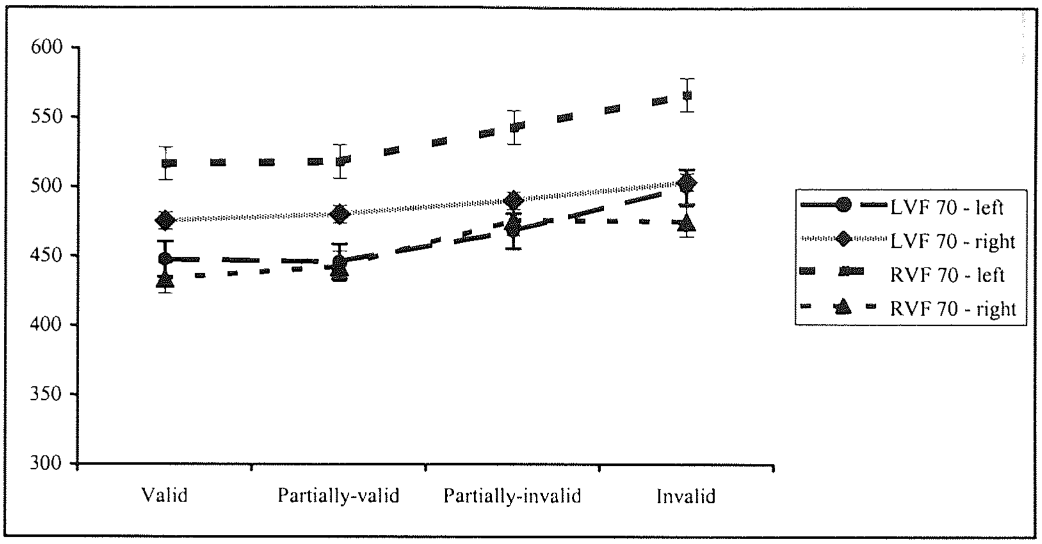
For the 300ms timing condition, showed the most consistent progression of trial types over time with no overlap between the conditions indicating no interaction of hand or trial type over time. The finding that the left orientations gave slower responses than those involving right orientations, but with the LVF producing the faster RTs than the RVF in each case, was significant ($p <0.001$).

The results detailed above can be seen more clearly in Figures 6.5 - 6.7.

Table 6.2: Results of the Within-Subjects ANOVA for all Three Timing Conditions.

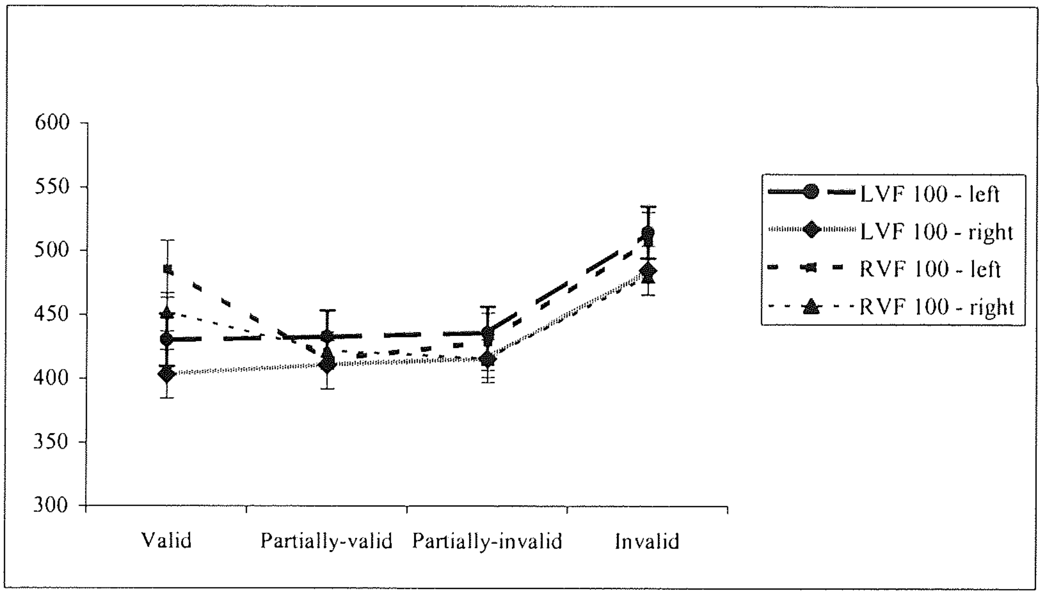
comparison	**70ms df**	**F-value**	**p-value**	
trial types	3	24.512	0.0001	significant
orientations	1	115.728	0.0001	significant
side of presentation	1	1.579	0.21	non-significant
trial types * orientation	3	4.263	0.005	significant
side of presentation * trial type	3	7.394	0.0001	significant
side of presentation * orientation	1	307.256	0.0001	significant
side of presentation*orientation *trial type	3	2.255	0.081	non-significant
comparison	**100ms df**	**F-value**	**p-value**	
trial types	3	178.306	0.0001	significant
orientations	1	66.402	0.0001	significant
side of presentation	1	8.706	0.003	significant
trial types * orientation	3	5.141	0.002	significant
side of presentation * trial type	3	16.906	0.0001	significant
side of presentation * orientation	1	2.372	0.124	non-significant
side of presentation*orientation *trial type	3	2.486	0.059	non-significant
comparison	**300ms df**	**F-value**	**p-value**	
trial types	3	92.793	0.0001	significant
orientations	1	71.598	0.0001	significant
side of presentation	1	4.32	0.038	significant
trial types * orientation	3	1.842	0.138	non-significant
side of presentation * trial type	3	6.268	0.001	significant
side of presentation * orientation	1	11.196	0.0001	significant
side of presentation*orientation *trial type	3	2.228	0.083	non-significant

Figure 6.5: Reaction Times for the 70ms Timing Condition



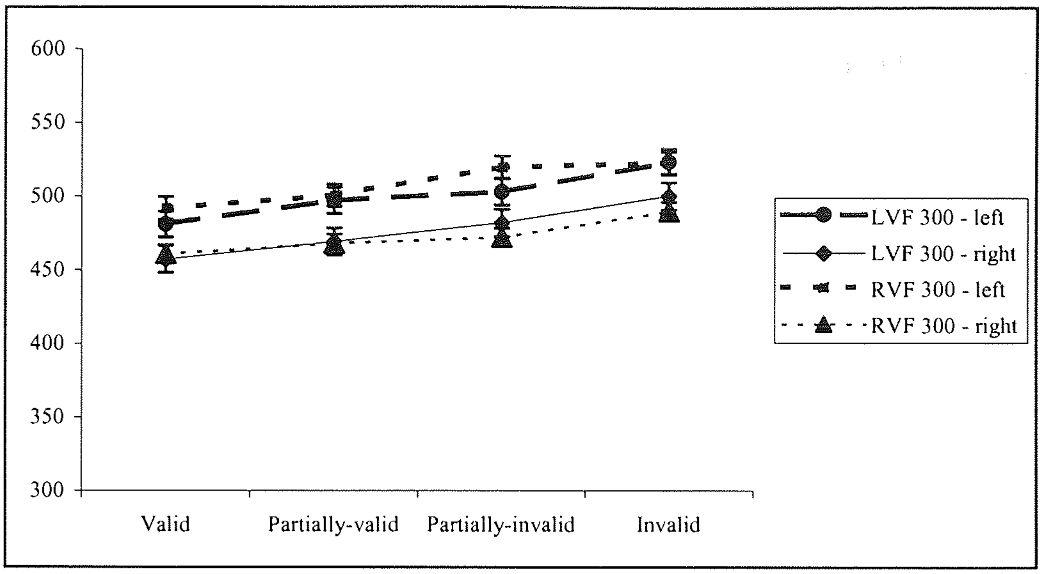
The RVF-left and LVF-left conditions were responded to the fastest, the slowest being the RVF-left condition. The expected pattern of valid being slower than invalid was observed, with the partially-valid and partially-invalid falling at midpoints between the two extremes.

Figure 6.6: Reaction Times for the 100ms Timing Condition



A different pattern was observed here, with the partially-valid and partially-invalid conditions being responded to faster than either the valid or invalid conditions. The invalid condition was still the slowest, but only just. The LVF-right condition was the fastest this time, and there was no observable slowest condition.

Figure 6.7: Reaction Times for the 300ms Timing Condition



A more consistent pattern was observed here, with the valid being the most rapidly responded to condition, the invalid being the slowest and the partially-valid and partially-invalid conditions coming at expected time intervals between the two extremes. The right oriented conditions were fastest, whereas the left-oriented conditions were slowest, across both visual fields. This timing condition showed the most consistent responses, in all aspects of the responding.

6.4. Methods: Experiment 2

The timing parameter of 300ms was chosen, as the results produced were the most consistent across the required parameters for all participants, therefore any differences would be due solely to differences in participant responding.

All methods were the same as for Experiment 1, except for the following.

6.4.1. Participants

There were 9 right-handed participants, 6 females and 3 males, mean age 28.4 years, range 23-44. There were 7 left-handed Participants, 6 females and 1 male, mean age 22.7 years, age range 18-30. Handedness was measured by observing the dominant hand used when writing their details down. No handedness inventories were used. All had normal or corrected-to-normal vision.

6.4.2. Timing Parameters

A cue appeared 500ms after the onset of the fixation point for 100ms, followed by a target 300ms later, which was onscreen for 100ms after which the screen was blank for 2 seconds or until the participant responded. There were 1300 trials per run, taking approximately 50 minutes, with breaks of 1-2 minutes every 15-20 minutes

6.5. Results for Experiment 2

Reaction times for both left- and right-handers can be found in Tables 6.3 and 6.4; all were calculated with the errors excluded. There was a general effect of handedness, with the left-handers having results dictated by visual field, and the right-handers having results dictated by orientation of the stimulus. The results of the 2x2x2x4 ANOVA can be found in Table 6.5; again, errors were excluded in the calculations.

Tables 6.3 and 6.4 show the mean RTs for all conditions. The right-handers had faster reaction times (RTs) overall, mean RT 494.25ms, than the left-handers, mean RT 497.54ms, but only just. The data for trial type showed the valid trials produced the fastest RTs, mean RT 480.87ms, and the invalid trials had the slowest RTs, mean RT 516.93ms, for both left- and right-handers ($p<0.001$). The partially-valid and partially-invalid had times between these two extremes, the partially-valid trials, mean RT 486.903ms, being slightly faster than the partially-invalid trials, mean RT 498.88ms.

There was an interaction between handedness and orientation ($p<0.001$). The right-handers responded, on average, faster for right orientation conditions, mean RT of 486.66ms, than the left orientation conditions, mean RT 501.84ms. However, the left-handers responded, on average, faster at the left orientation conditions, mean RT 492.27ms, than the right orientation conditions, mean RT 502.81ms.

There was an interaction between handedness and side of presentation ($p<0.001$) with the left-handers responding slower than the right-handers for the RVF, but around the same, although slightly faster, for the LVF. There was a significant difference between the two orientations for left-handers, around 50ms, but only a small difference for the right-handers, around 20ms ($p<0.001$) (see Figures 6.8 and 6.9). The left-handers responded faster on the RVF regardless of orientation, however, the right-handers responded faster for the right-orientation regardless of the side of presentation ($p<0.001$). The results of the analysis can be found in Table 6.5. This last point is the most important finding for this particular experiment, the lateralization based on different aspects of the visual field for left- and right-handers.

Table 6.3: Mean Reactions Times for Left-Handers

Hand	Side	Orientation	Trial type	Mean RT (ms)	sd
Left	Left visual field (LVF)	left	valid	499.93	73.9
			partially-valid	501.3	76.14
			partially-invalid	517.57	93.22
			invalid	534.32	94.35
		right	valid	515.74	90.21
			partially-valid	518.81	90.03
			partially-invalid	530.47	97.09
			invalid	567.01	115.33
	Right visual field (RVF)	left	valid	453.51	66.86
			partially-valid	459.06	66.53
			partially-invalid	477.16	75.68
			invalid	495.35	83.13
		right	valid	457.67	59.6
			partially-valid	462.53	64.33
			partially-invalid	470.94	69.9
			invalid	499.32	87.47

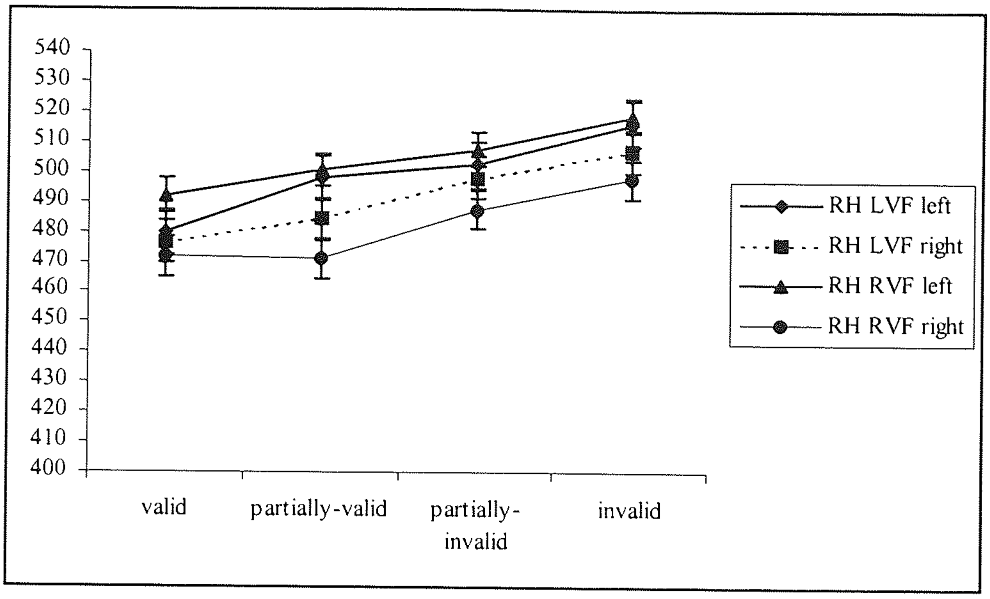
Table 6.4: Mean reactions Times for Right-Handers

Hand	Side	Orientation	Trial type	Mean RT (ms)	sd
Right	Left visual field (LVF)	left	valid	479.91	63.21
			partially-valid	497.94	60.73
			partially-invalid	502.16	64.34
			invalid	516.21	60.38
		right	valid	476.61	64.65
			partially-valid	484.26	62.75
			partially-invalid	498.05	68.77
			invalid	506.93	72.81
	Right visual field (RVF)	left	valid	491.94	63.2
			partially-valid	500.53	65.92
			partially-invalid	507.4	68.78
			invalid	518.66	80.19
		right	valid	471.66	53.33
			partially-valid	470.82	55.12
			partially-invalid	487.31	63.19
			invalid	497.66	62.79

Table 6.5: Results of the Within-Subjects ANOVA.

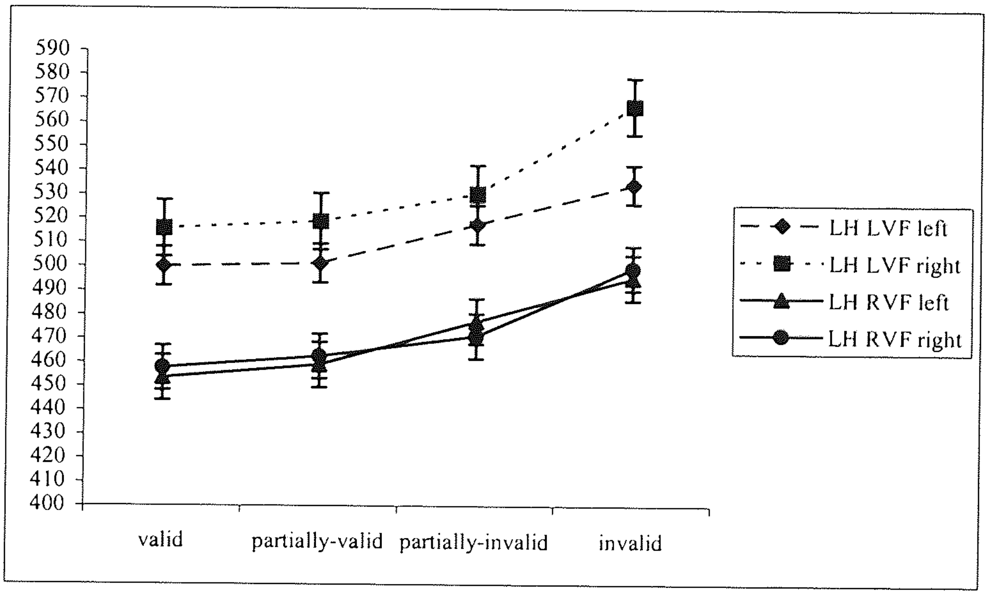
Comparison	df	F-value	p-value	
Handedness	1	227.884	0.0001	significant
orientation	1	192.363	0.0001	significant
side of presentation	1	116.202	0.0001	significant
trial type	3	39.261	0.0001	significant
handedness * orientaiton	1	338.518	0.0001	significant
handedness * side of presentation	1	78.845	0.0001	significant
orientation * side of presentation	1	5.476	0.02	significant
handedness * trial type	3	9.584	0.0001	significant
orientation * trial type	3	0.97	0.406	non-significant
side of presentation * trial type	3	6.846	0.0001	significant
handedness * orientation * side of presentation	1	24.351	0.0001	significant
handedness * orientation * trial type	3	9.061	0.0001	significant
handedness * side of presentation * trial type	3	3.383	0.018	significant
orientation * side of presentation * trial type	3	4.481	0.04	significant
handedness * orientaton * side of presentation * Trial Type	3	0.195	0.9	non-significant

Figure 6.8: Right-Handers, RTs for all conditions



There is a much closer range of RT for the right-handers than left-handers, with all RTs being in the same region of time. The right-oriented conditions were responded to the fastest, whereas the left-oriented conditions were responded the slowest, for both visual fields, as was found for the 300ms timing condition in Experiment 1. Expected RTs were observed for the valid, partially-valid, partially-invalid, and invalid conditions.

Figure 6.9: Left-Handers, RTs for all conditions



There was a split in RT for the left-handers. The RVF conditions were responded to the fastest regardless of orientation, and the LVF conditions were responded to the slowest regardless of orientation. There was a bigger difference in this split than there was for the orientation split observed in the right-handers. Left-handers were significantly slower for the LVF condition than were the right-handers overall, but significantly faster for the RVF conditions. Expected RTs for the valid, partially-valid, partially-invalid, and invalid conditions were observed, although these were slightly increased between conditions relative to the RTs for right-handers.

6.6. Discussion

6.6.1. Experiment 1

In Experiment 1 there was a significant difference between timing conditions, with all cue-target latencies showing a significant effect of trial type and orientation (see Table 6.2). The expected continuum of increasing RT with increasing costs was found. However, the 100ms condition revealed a significant ($p<0.001$) inhibition for the valid trial type in some conditions (see Tables 6.1 and 6.2). There was greater variation between conditions in the 70ms condition, the 300ms timing condition showing the least variation across conditions, hence its usage in Experiment 2. The 70ms timing condition showed the same orientation and hemisphere (e.g. LVF and left orientation of gratings) to be faster than the different orientation and hemisphere (e.g. LVF and right orientation of gratings). The other two timing conditions did not show this. In these two conditions it was seen that trials on the LVF produced faster RTs than those on the RVF.

The results from the 100ms condition showing the valid condition was responded to slower than either the partially-valid or partially-invalid conditions, may be explained by Inhibition of Return (IOR). Posner et al (1985 - in Egeth & Yantis, 1997), first described IOR. The phenomenon of IOR is that when attention is drawn to a location during serial search tasks, it temporarily inhibits it, preventing a return to a visited location. Whether IOR is location or object based is much discussed, however, Tipper et al (Tipper & Weaver, 1998) have found that it can be either or both. In this case, the cue may have drawn attention to the location and then inhibited it, so that when the target appeared there was a delay in processing as the inhibition had to be removed before the target could be processed. This leads to the idea that there is an automatic IOR mechanisms that operates after all visual stimuli, the evidence here pointing to between 80 and 250ms after onset of the first stimulus. The IOR, on the basis of this data, is likely to be location based, as the partially-valid trial type was faster than the valid trial type, indicating that only the cue location was inhibited, and the half of the target that was outside this area was processed quicker than the target fully inside the area. This indicates that the attentional 'beam' did not move very far after inhibiting the area of the cue, the partially-invalid trial type still produced slower RTs than these two trial types, and the invalid was slower still.

The results of this experiment do not support the idea that the attentional effect is all over by 250ms post stimulus onset (Posner & Cohen, 1984). The 300ms timing condition yielded the most consistent results and produced the pattern of RTs expected from the Cost-Benefit paradigm. Here it seems that the cue has a significant effect on subsequent responding beyond the time frame proposed by Posner (Posner & Cohen, 1984). Further studies using time intervals longer than 300ms post cue offset are required before conclusions can be made about how long the cue can facilitate attentional allocation.

Were we measuring covert attention? The behavioural goal of the participants was to identify the orientation of the target, they were not told about the reason for the cue being present, simply that it was going to be there. There was no behavioural advantage to attending consciously to the cue as it produced less than the 80% accuracy required for inclusion of data. Research into peripheral and central cues, such as those used in these experiments, shows that peripheral cues are more effective at drawing attention automatically, and that central cues actually require a conscious shift in attention (Egeth & Yantis, 1997). The peripheral cues are characterised by a fast, transient response while the central cues are characterised by a slow, sustained response (Egeth & Yantis, 1997). The peripheral cues used in these experiments were drawing covert attention automatically.

6.6.2. Experiment 2

In Experiment 2 a lateralization of responses between left- and right-handed participants was found. This was anticipated, however the way in which lateralization appeared was not anticipated. Left-handed participants responded faster to the RVF while the right-handers responded faster to the LVF. The left-handers were shown to have a large advantage in the RVF, regardless of the orientation (see Figure 6.9) whereas the advantage for the right-handers in the LVF was less pronounced, indicating more bilaterality of responding in right-handers. The right-handers also had an advantage for the right orientation, using the dominant hand, regardless of visual field (see Figure 6.8).

In these experiments the effects of lateralization are evident in two respects. There are two different kinds of lateralization to consider here, sensory-perceptual lateralization, and motor-processing lateralization. It is conceivable that the dominance of the hemispheres, which leads to the phenomenon of left- and right-handedness, could also give rise to differences between these two types of lateralization. It is conceivable, therefore, that the left-handers may have somewhat reversed lateralization to those of right-handers. It is also possible that there is only one form of lateralization that is different between these two subject groups, the motor-processing lateralization. The sensory-perceptual lateralization, which involves attentional processing, may be identical with no regard for hemispheric dominance in other forms of processing, such as handedness.

There is much debate about exactly how cognitive processing is lateralized across the hemisphere. Both hemispheres have access to the same incoming information, and it is relayed to the opposite hemisphere almost immediately, why then, the differences in performance in Experiment 2?

There are many processes that are lateralized across the hemispheres, which fall into the sensory-perceptual domain (for a review see: Hugdahl, 2000). The right hemisphere has been found to be dominant in the processing of spatial and global elements, coordinate judgement decisions and discriminations at higher frequencies. The left hemisphere has been found to be dominant with language and local elements, temporal processing, categorical judgements, and the processing of information at lower frequencies (Hugdahl, 2000). Unfortunately none of this explains the results here. Assuming that the dominant hemisphere for motor control in right-handers is the left and for left-handers it is the right, we appear to have results that can be interpreted in this format, with reference to the two types of lateralization described above. The results show that left-handers have a distinct advantage for processing entering the left hemisphere, their non-dominant hemisphere, when using the above assumption. While the right-handers have an advantage for processing involving their dominant hand, again using the left hemisphere. Anatomical connections that cross the midline are at a great competitive disadvantage compared with those that originate in the same hemisphere (Sato, 1988 in: Desimone, 1998). This could provide some evidence for the lateralization effects in right-handers, and the reversal of said effects in left-handers; the connections required for the processing of motor-processing events may be reversed anatomically in left-handers relative to right-handers, the sensory-perceptual being the same, and thus subject to the inter-hemispheric transfer of information.

What is happening in the left hemisphere that gives rise to these results? Some have found that there is a lateralization of attentional processing, the covert, automatic attentional processing being located in the right hemisphere, while the overt, conscious forms of attentional processing are located in the left hemisphere. (Gainotti, 1996) Is it then possible that it is the other way round? We know that these experiment were employing covert attention, and there is a tendency for the left hemisphere is provide an advantage is the speed of responding. Could it be that covert attention is located in the left hemisphere, ostensibly the parietal lobe (see Chapter 7), regardless of the motor-processing lateralization? If this is the case, then the results seem to suggest an advantage when the left hemisphere is the non-dominant hemisphere. This would seem logical as any dominance may lead to conscious processing in an area designed for automatic processing, thus hindering any processing occurring in that location. Therefore the fact that covert attention is present in the non-dominant hemisphere, based on the assumption made above, provides a processing advantage for left-handers over right-handers. Right-handers, on the other hand, having their dominant hemisphere as the left-hemisphere, have a disadvantage with regards to covert attention, but an advantage with regards to the motor-processing lateralization, their right-hand being dominated by the hemisphere which is dominant for the attentional task.

It has been found (Springer & Deutsch, 1998) that left-handers have a greater bilaterality than right-handers. This last point is not held up in these results as the right-handers were found to have more bilaterality in this task, evident in the more similar RTs (see Tables 6.4 and 6.5), the left-hander's had a larger advantage for the RVF than did the right-handers for the LVF.

If neuroimaging data also found that there was this lateralization of activation for the two groups of participants it would mean that left-handers would have more reversal of processing in the two hemispheres than previously thought (Hugdahl, 2000). It is possible that the neuroimaging data would show that this lateralization of processing, and may even highlight the two types of lateralization, detailed above.

6.7. Conclusions

The results here indicate first that the initial aims of the experiment were supported. However, only under certain timing and experimental conditions was the idea of the Cost-Benefit model (Posner et al, 1978) concurred with. Under the 100ms condition there was 'spatial' IOR influencing the valid condition. There is more work to be done to work out exactly when the process of covert attention is activated and when its influences decreases, but the data here does not support the earlier work of Posner (Posner & Cohen, 1984) in this area. The influence of handedness shows that there may be a left hemispheric advantage in this covert attention task, indicating there is possibly a difference in the lateralization of processing between left- and right-handers. Two possible forms of lateralization were proposed, sensory-perceptual and motor-processing, the second of which is reversed for left-handers as opposed to right-handers, while the first is unchanged and is a universal lateralization, not dependant on the motor-processing mechanisms. This work highlights the need for more research into the timing of covert attention, and IOR, and into the lateralization of the sensory-perceptual and motor-processing mechanisms in left- and right-handers.

Chapter 7: A Cue-Based Attentional Paradigm Using MEG Showing Lateralized Attentional Processing in the Parietal Lobes

7.1. Introduction

We cannot covertly attend to something that does not change; a vital property of attention is to highlight changes in the external world, bringing them into the conscious domain. In terms of evolution change can signal possible threat of danger, so if some things do not change, for example trees or rocks, then they are of no perceivable danger and are ignored perceptually as a result. These items fade and become 'invisible' until attention is once more drawn to them again by some form of cue, or the sudden presence, 'onset', or absence, 'offset', of an object in the visual array. Visual stimuli will go unnoticed unless they are signalled, or cued, in some form or another (Posner & Gilbert, 1999).

Attention (see Chapter 2) is summoned by a cue, without a cue attention is not summoned and therefore there is no awareness of the target (DeSchepper & Treisman, 1996). Obviously there is a behavioural advantage to knowing when a stimulus is going to occur, the heightened awareness being evident in improved response times. Use of spatial cues enhances stimulus processing in the absence of eye movements, reflecting the activation of mechanisms to shift attention to the stimulus location before its appearance (Corbetta, 1998). There are two ways in which cues can be said to facilitate stimulus analysis: visual analysis is done more rapidly at the attended location, when the cue proves to be a correct indicator of the target location, as time is needed for attention to reorient itself to a new location when a cue proves false (Corbetta, 1998; Posner, 1980); and attention may directly influence visual processes by enhancing sensitivity to the attended location (Corbetta, 1998).

Covert attention is stimulus induced, tied to sudden changes or novel stimuli in the visual field; there is no conscious thought or cognitive processing involved, it is an involuntary process. Covert attention has rapid engagement and dissipates quickly, being fully activated in about 50ms and dissipating in about 250ms (Posner & Cohen, 1984), although new evidence (see Chapter 6) points to the influence of covert attentional mechanisms extending beyond 300ms. It is linked with early, bottom-up, visual processing. Three stages of processing have to take place before a stimulus in the visual field can be identified and responded to: disengagement of attention from a previous location, moving it to another, and re-engagement to the required location. If a cue is in the correct location then there is nothing for attention to do, and the stimulus can be rapidly reported on. If the cue is in the wrong location then attention must utilise all three processes to report on the stimulus. It could be that covert attention only operates in the periphery, and not in the centre of the visual field. Peripheral cues attract attention automatically whereas central cues require a conscious shift in attention (Egeth & Yantis, 1997). Responses to a peripheral cue are characterised by being fast and transient; they produce a rapid rise and fall in attention and may induce Inhibition of Return (IOR) at later time intervals, generally considered to be around 300ms post cue onset (Egeth & Yantis, 1997), but this may be a somewhat early timeframe, and there is evidence to suggest that the IOR effect is not active until later (see Chapters 5 and 6)., or indeed earlier and rapidly dissipating.

The main question being researched through neuroimaging in visual attention is how early the attentional modulation occurs in the visual pathway. It was thought possible that the initial inputs into V1 were modulated; however, this appears unlikely as there is evidence from EEG (for example see: Clark & Hillyard, 1996; Mangun, et al 1998) and MEG (see Chapter 5) research to suggest that the initial modulation shown in fMRI studies (for example: Roelfsema, et al 1998; Somers, et al 1999; Watanabe et al., 1998) is in fact due to feedback mechanisms acting from higher cortical areas such as the later extrastriate areas and the parietal cortex.

In the occipital cortex there is evidence that the P1, at 80-130ms post stimulus onset, and N2, around 150-200ms post stimulus onset, components of the waveforms have larger amplitudes under attended conditions, but show the same latency as the unattended conditions (Martinez, et al 2001). The source of the P1 is thought be the early extrastriate area V2 or V3, corresponding to Brodmann's areas 18/19. This has been the earliest finding of attentional modulation of visual input. Attentional modulation of the early C1 component (see Chapter 2), which corresponds to V1 at around 50-60ms post stimulus onset, has not been found (Martinez et al, 2001).

The main source of attentional feedback from higher cortical areas, 'top-down' modulation, has been shown to be the parietal cortex (Coull & Nobre, 1998; Posner &

Dehaene, 1994), which has a key role in the selection of information for higher, conscious, integration, leading to an overt response (Posner, et al 1984). The parietal cortices form part of the 'fronto-parietal' attentional network, documented in many imaging experiments (for example: Corbetta, et al, 1993; Coull, et al, 1998). The right parietal cortex is involved with spatial attention (Corbetta et al., 1993), and the left parietal cortex with non-spatial selective responding, and covert orienting in space (Coull et al., 1998), as well as attentional processing which is relevant for motor behaviour (Rushworth, et al., 2001). There is a right hemisphere bias for spatial processing and a left-hemisphere process for temporal processing in the parietal lobes (Macaluso & Frith, 2000). This does not mean that the hemispheres are exclusively processing one kind of visual information; it is likely that both types of information are processed in each hemisphere (Coull & Nobre, 1998). The notion of hemispheric specialisation implies that each hemisphere is organised to deal preferentially with one type of information processing, spatial in the right hemisphere and non-spatial in the left. An important role of the parietal cortex is in processing that sensory information which relates to behaviour, the planning of actions, and how the intention to respond behaviourally, as a result of attentional influences, is carried out (Snyder, et al 2000). The role of the parietal cortex can be thought of as being dominated by visuo-motor components of the task, rather than the explicit visual demands (Walsh, et al 1999). The right parietal cortex is important for attending to both halves of the visual field, but the left parietal cortex is only important for attending to the right visual field (RVF) (Walsh, et al, 1999). This is a somewhat odd laterality, indicating that the right parietal cortex is more involved with the process of attention than is the left parietal cortex. It could also indicate that the right parietal lobe has executive control over the attentional processes, and the left parietal lobe is only involved for certain types of processing in the RVF. However, as we shall see in this study this is not necessarily the case, as is the idea that the right hemisphere is activated for the entire visual field and the left hemisphere only for the RVF.

There are three key areas of the parietal cortex, which are involved with attention, the superior parietal lobe (SPL), the inferior parietal lobe (IPL), and the inferior parietal sulcus (IPS). The superior parietal lobe (SPL) is the location for spatial attention and for spatial processing of external areas (Posner & Peterson, 1990). Activity here is related to the elaboration of somatosensory information (Rizzolatti, et al 1997), which could suggest that it is activated when behavioural goals involve making an overt, non-linguistic, response. The SPL processes peripheral information preferentially (Macaluso & Frith, 2000), being more active when attention is shifted into the periphery, in particular on the basis of cognitive or sensory cues which are independent of the overt response (Corbetta et al., 1993). The inferior parietal lobe (IPL) is part of the visuo-motor network specifically dealing with grasping (Rizzolatti et al., 1997). The inferior parietal sulcus (IPS) is involved in spatial, the right IPS, and temporal, the left IPS, orienting (Coull & Nobre, 1998). It is also involved in sustained, active, covert attention to the peripheral visual fields (Martinez et al., 2001).

This study is based on the 'Cost-Benefit' paradigm of Posner et al (Posner, et al 1978). The neutral trial has been removed, as there is a plethora of evidence showing that it is the midpoint between the two conditions (see Chapter 6 and Vecera & Farah, 1994). We therefore used a 'valid' trial, where the cue and target were co-located, and an 'invalid' trial, where the cue and target were located at different locations. Based on previous research (Chapter 6) we used a 300ms gap between the cue and the target, as the attentional effects of the 'cost' and the 'benefit' are still very clearly shown and there is enough time between cue and target for the neuronal response to the cue to have dissipated. The experiment was divided into two to enable the two visual fields to be studied separately, specifically the early visual areas, the activation of which can be segregated when measuring the visual fields separately and prevents the cancellation of parallel sources. In terms of parietal sources this would appear not to be necessary, based on the results in Chapter 5 that show attentional processing to be lateralised regardless of task, however, for the early visual areas there is likely to be an advantage to splitting the recording of the visual fields. A difficult orientation task was employed for the purpose of engaging early visual areas, these being the subject of interest in this thesis. There is some evidence to suggest that increasing difficulty of task is more successful at engaging the early visual areas than are simple tasks (Motter, 1998). The behavioural data was collected, but with a delay in the response being required. The method of analysis for the imaging data required that there be a period of passive viewing after each experimental trial, so the response from the subject for the behavioural data was delayed by one second.

We expected to find a difference between the visual fields and between the conditions, with a possible interaction between them. It was unknown if the orientation task would provide any significant data. The behavioural data was expected to reveal no difference between the conditions, due to the delay in the response from the subject.

7.2. Methods

7.2.1. Apparatus

Stimuli were produced using a VSG5.021 grating generator (CRS Ltd.). The viewing monitor was an EIZO T562-T 17" colour monitor, calibrated and gamma-corrected using a computer-controlled photometric procedure (Optical, CRS Ltd). Responses were made on a button box with 0.25mm contact switches.

7.2.2. Stimulus Parameters

Stimuli were 2c/deg sinusoidal luminance gratings of 90% contrast and 28.9 Cd/m^2 (Figure 7.3) mean luminance bounded within a square region 1.2 x 1.2 deg. The gratings were presented tilted ± 2 deg off vertical in the lower right (or left) quadrant of the visual field. Participants fixated on a 0.25deg square. Gratings were presented 2.0 deg eccentric to the fixation at 30, 45, 60 degrees. Stimuli were preceded by a brief cue, which was a white outline box matched in size to the stimulus. The cue appeared at 2.0deg eccentric from the fixation in 3 locations along radii in the same positions as the stimuli (see Figure 7.1). The locations denoted the top left hand corner of the cue or grating. Stimuli were presented on a uniform grey background, calculated to be the midpoint between the black and white of the stimuli.

7.2.3. Timing Parameters

A cue appeared 500ms after the onset of the fixation point for 100ms, followed by a target 300ms later, which was onscreen for 100ms after which the screen was blank for 2 seconds or until the participant responded. There were 500 trials per run, taking approximately 30 minutes.

7.2.4. Participants

Participants all had normal, or corrected-to-normal, vision. There were 6 participants, 4 females and 2 males. The mean age was 29.8 years, age range 22-45. All were right-handed. For the psychophysical data collection there were 10 participants, 6 females and 4 males. The mean age was 30.3 years, age range 21-51. All were right-handed.

7.2.5. Procedure

The task was to judge the direction of tilt of the stimuli, signalling their choice with a button press. A right button press indicated a 'right orientation' response and a left button press indicated a 'left orientation' response. There were 2 categories of stimuli: valid (cue and target were co-located), and invalid (cue and target spaced apart) (see Figure 7.2). Trials were randomly generated with an average of 100 trials being produced for each trial type. The experiment was run twice, once in each of the lower visual quadrants (left and right visual fields, LVF and RVF), the fixation point being in located in the upper corner of the stimulus closest to the central meridian. Each participant received 500 randomised trials in each visual field, 40% of trials were invalid and 60% valid. Participants were required to achieve at least 80% accuracy in the identification of target grating orientation. Participants were instructed to attend to the fixation point in the top left-/right-hand corner of the screen and to attend to the target grating rather than the cue. Participants were instructed to respond after the fixation point changed colour (to white rather than black), and not before, with the left button if the target grating appeared to be oriented towards the left, based on the top edge of the grating, and with the right button if the target grating appeared to be oriented to the right, based on the top edge of the box. Participants were instructed to keep their fingers on the buttons and not to move them throughout the experiment, particularly in the blank phases. Post-experimentally participants had the significance of the cue relative to the target explained to them, and what it was hoped their results, in terms of both the psychophysical and imaging data, would show. All participants had their results, in terms of percentage accuracy and how they responded in each condition, given to them. The majority of participants also saw the finished results from the combination of all sets of data across participants. Participants did not report any strategies being used.

7.2.6. MEG

Participants sat 2.1m away from the screen and viewed the screen through a front-silvered mirror in a magnetically shielded room, the monitor being situated outside the room. For more details on the MEG methods see Chapter 4. Participants were positioned in the MEG system and the head localised, to obtain the position of the coils with respect to the dewar, within the dewar. The experiment was run in two sessions, one for the LVF part of the task and one for the RVF. After the experiment had finished the subject was removed from the MEG system and their head digitised using the Polhemus software (see Chapter 4) to localise the coils with respect to the head.

7.2.7. Analysis methods

The data from the Polhemus system was co-registered with the participant's MRI scan using the 'Coregister' program (see Chapter 4). The data were analysed using Synthetic Aperture Magnetometry (SAM) (Vrba & Robinson, 2000). A neutral time window was chosen (1-2 seconds post stimulus onset) and this was compared with the active time window (0-1 seconds post stimulus onset) for both valid and invalid trials. Four different frequency bands were analysed, 0-10/10-20/0-15/5-15/Hz. The SPM99 program (see Chapter 4) was used to average the MRIs to form a template brain. The SAM images were then averaged into a global image and placed on the template brain. The results are based on these averaged group images. Spectrograms and virtual electrodes were also computed for selected areas. Areas for this analysis were chosen on the basis that the early visual areas were the most important in terms of timings. The co-ordinates were obtained from individual subject SAM data viewed in the MRI Viewer program (CTF Ltd). All Spectrogram and Virtual Electrode data was on single participants, it is not possible to average data by this method at this time. The majority of consistent activity was found in the 0-15Hz ranges. This is evident in the Spectrogram output.

7.2.8. Psychophysical data collection

The methods were the same as above except the participants sat in a dimly lit room, rather than the MEG shielded room:

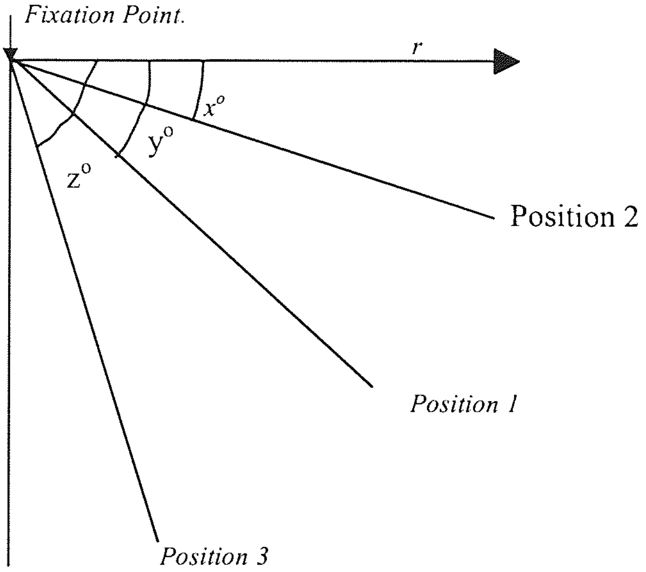
7.2.9. Apparatus

Lighting conditions were limited to one overhead spotlight located posterior to the participants and angled so there was no glare on the viewing monitor.

Figure 7.1: Target and Cue Positions.

The targets and cues were positioned with the top left hand corner touching the end of the line shown.

Target and Cue Positions.



r = E° eccentricity

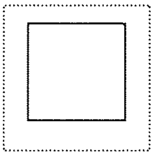
$x^o = 30$
$y^o = 45$
$z^o = 60$

Figure 7.2: Relative Positions of Cues and Targets.

The dashed line represents the cue and the solid line represents the target.

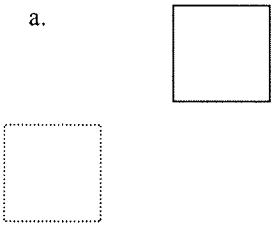
4. When target and cue are in position 1:
Item a represents the valid trial (the cue was no bigger but is drawn so as to be visible.

a.

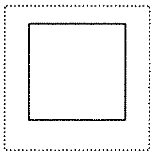


5. When the target is in position 2 and the cue is in position 2 or 3:
Item b represents the valid trial (the cue was no bigger but is drawn so as to be visible). Item a is the invalid trial.

a.

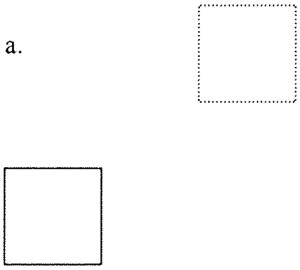


b.



6. When the target is in position 3 and the cue is in position 3 or 2.
Item b represents the valid trial (the cue was no bigger but is drawn so as to be visible). Item a is the invalid trial.

a.



b.

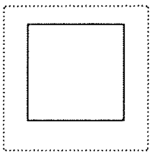


Figure 7.3a: The Stimulus.

The gratings was a sinusoidal luminance grating of 2c/deg at 90% contrast and 28.9 Cd/m^2 mean luminance bounded within a square region 1.2 x 1.2 deg. The gratings were ± 2 deg off vertical in the lower right (or left) quadrant of the visual field. Shown here in position one (see Figure 7.2.). Not drawn to scale.

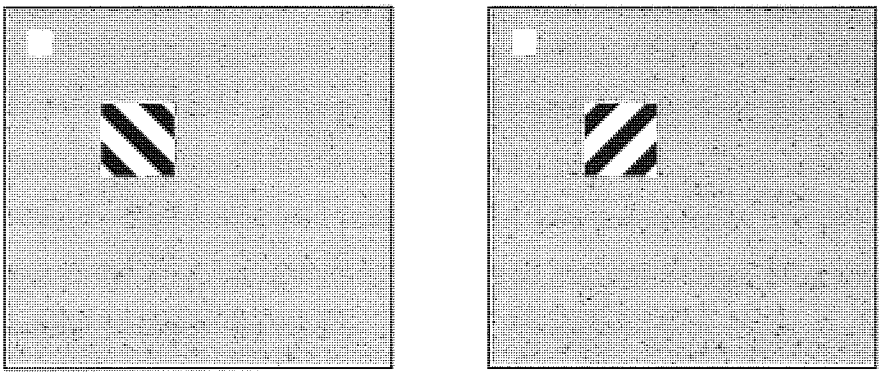
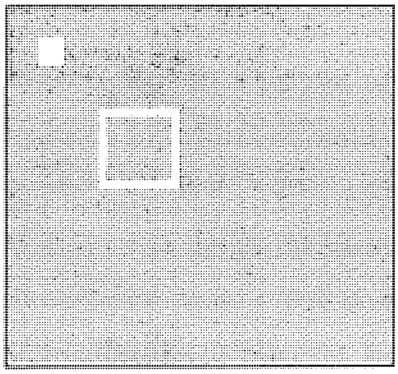


Figure 7.3b: The Cue

The cue was a white outline box the same size as the target. Shown here in position one (see Figure 7.2). Not drawn to scale.



7.3. Results

7.3.1. Imaging Results

For all the imaging results below, please refer to Tables 7.5 – 7.8. These tables show the source of activation in terms of left and right hemispheric dominance for each condition, organised into visual fields and orientation conditions. Each brain region is represented in terms of valid and invalid trial types. A key accompanies the tables. The 0-10Hz range showed the most consistent activation and, for this reason, they will form the basis of the interpretation for the results. This is evidenced by the Spectrogram results (see Figure 7.12) that show a clear concentration of activity around 0-15Hz. For all results only qualitative data was available, no quantitative analysis methods were available at the time of writing.

7.3.2. The Superior Parietal Lobe

The SPL showed a pattern of activation in the 0-10Hz range. For the left-orientation conditions for both RVF and LVF there was bilateral activation with a left dominance (see Figures 7.4B and 7.4D), and for the right-orientation conditions there was bilateral activation with a right dominance (see Figures 7.4A and 7.4C). The RVF conditions were both bilateral with a left dominance (see Figures 7.5B and 7.5D), whereas the LVF conditions showed bilateral activation with a left dominance for 'valid' conditions (see Figure 7.5A), and a right dominance for 'invalid' conditions (see Figure 7.5C), regardless of orientation.

The SPL showed that for same side presentation and orientation conditions (e.g. LVF-left-orientation) the activation is dominant in the ipsilateral hemisphere to presentation (see Figures 7.4B and 7.4C). For the different side and orientation conditions (e.g. LVF-right-orientation) activation was dominant for the contralateral hemisphere to side of presentation (see Figures 7.4A and 7.4D). If the information from the visual field crosses to the contralateral hemisphere to side of presentation this would mean that, for same-side presentation and orientation, the information was processed by the non-dominant hemisphere while the different-side presentation and orientation, the information is processed in the dominant hemisphere.

7.3.3. The Inferior Parietal Lobe

The IPL also showed a pattern of activation in the 0-10Hz range. For the LVF-left-orientation condition there was bilateral activation with a left dominance, and in the RVF-right-orientation condition there was bilateral activation with a right dominance. For the LVF-right-orientation condition there was bilateral activation, with a right dominance for the valid trials, and a left dominance for the invalid trials (see Table 7.3). However, for the RVF-left-orientation condition there was bilateral activation, with left dominance for valid trials and right dominance for invalid trials (see Table 7.4). The LVF-left-orientation condition had, as before, bilateral activation with left dominance, but the right-orientation had bilateral activation with a right dominance. The RVF-left condition showed the same pattern as before, but the RVF-right-orientation condition showed the reverse: the valid trials had bilateral activation with a right dominance, and the invalid trials had bilateral activation with a left dominance.

The IPL showed the same pattern of activation for same-side presentation and orientation conditions as the SPL. For the different-side presentation and orientation conditions there was a somewhat different pattern. For valid trials the information was processed by the ipsilateral hemisphere to the orientation of the stimulus, for example the RVF-left-orientation condition was processed in the left hemisphere). Whereas the invalid trials were processed in the ipsilateral hemisphere to the side of presentation, for example the RVF-right-orientation condition was processed in the right hemisphere.

From Figures 7.6 and 7.7 it is evident that the dissociation of activation between the orientations and fields of presentation is consistent with that described above. In the same side of presentation and orientation conditions (see Figure 7.7) the left hemisphere was activated more strongly. For the different side of presentation and orientation conditions (see Figure 7.6) the right hemisphere was activated more strongly. There was a larger increase in activation for the invalid trials in the same side of presentation and orientation conditions than for the different side of presentation and orientation conditions.

Other areas activated showed no pattern of activation consistent with the demands of the task in the 0-10Hz range. The majority of areas were activated for the majority of the conditions, with the exception of the early visual areas, which showed little activation throughout the experiment. In all conditions there appeared to be an increase in activation for the invalid trials, in the majority of areas, but primarily the SPL and IPL (see Figure 7.5). The pseudo-t-values associated with these increases in activation (see Tables 7.1 and 7.2) give an indication of the strength of increase. It is, at present, not possible to quantify such values using this technique. However, it is possible to see that, for the SPL, larger pseudo-t-values were more consistently elicited by the invalid condition relative to the valid condition, particularly in the right hemisphere. The left hemisphere exhibited more equal levels of activation; this is possibly due to the site of activation for the task, to be discussed later. The IPL did not show any perceivable pattern, except for being activated by the invalid conditions more frequently than the valid conditions, levels of activation being somewhat similar across the hemispheres.

Figures 7.6, 7.7 and 7.8 show that there is a small increase in the amplitude of the first two positive components of the parietal response, also the components P1, N1 and P2 in the occipital response showed increased amplitudes for the invalid responses relative to the valid responses (see Figure 7.9). Currently there is no way of telling of this is significant, but from the pseudo-t-values shown in Table 7.1 it is possible to state that it is possible that there is a significant difference between the amplitudes for the valid and invalid conditions. There is a program designed by I.E.Holliday (2001, at Aston University), based on the General Linear Model (GLM), which is able to use a MANCOVA to determine significance between two data sets or parts of data sets. However, at present there is no way of using multiple markers in this program. Once this is possible, it is expected that there will be a small significant difference between the levels of activation for the valid and invalid conditions, the invalid showing significantly higher levels of activation than the valid conditions.

The occipital activation was bilateral, but dominant in the contralateral hemisphere to the side of presentation (see Figure 7.10). This was expected. In Figure 7.4 it is possible to see activation in the extrastriate cortex contralateral to the visual field.

The psychophysics results were somewhat surprising (see Table 7.3 and Figure 7.11). We had not expected any difference between trials types at all, and none between the two visual fields. There was a significant difference between the RVF and the LVF, with the RVF eliciting significantly faster RTs than the LVF ($p<0.001$) (see Table 7.4). This corresponded with the dominance of the left hemisphere in the imaging data. There was also a significant effect of trial type; the valid trials were significantly slower than the invalid trials ($p<0.005$). There was no significant effect of orientation and there were no significant interactions between the conditions.

Figure 7.4: Differences Between the Hemispheres for the SPL and IPL Relative to the Different Conditions.

This figure is made up of group analysis results using SPM99. For all images there was a Fun Integration Depth of 0.05, and an amplitude cut-off of 1.0. The concentration of colour indicates the strength of the response. The closer through pink to white the colour is, the stronger the response. The closer to blue through purple the response is the weaker the response relative to baseline conditions. Colour in the pink/white-blue range indicates a decrease in activation relative to baseline activation. Hence 'activation' here will indicate a decrease in activation relative to normal baseline activity.

A: Left Visual Field, right orientation. Bilateral activation with stronger activation in the SPL in the left hemisphere, and stronger activation in the IPL in the right hemisphere.
B: Left Visual Field, left orientation. Bilateral activation with stronger activation for both IPL and SPL in the left hemisphere.
C: Right Visual Field, right orientation. Bilateral activation with increased activation in the right hemisphere.
D: Right Visual Field, left orientation. Bilateral activation with increased activation for both IPL and SPL in the left hemisphere.

Here we see activation contralateral the visual field in the extrastriate cortex, as expected, and also in the inferior parietal cortex, alongside the left hemisphere parietal dominance. This dominance may be linked to response selection, known to be lateralised to the left SPL (Rushworth, Krams et al., 2001).

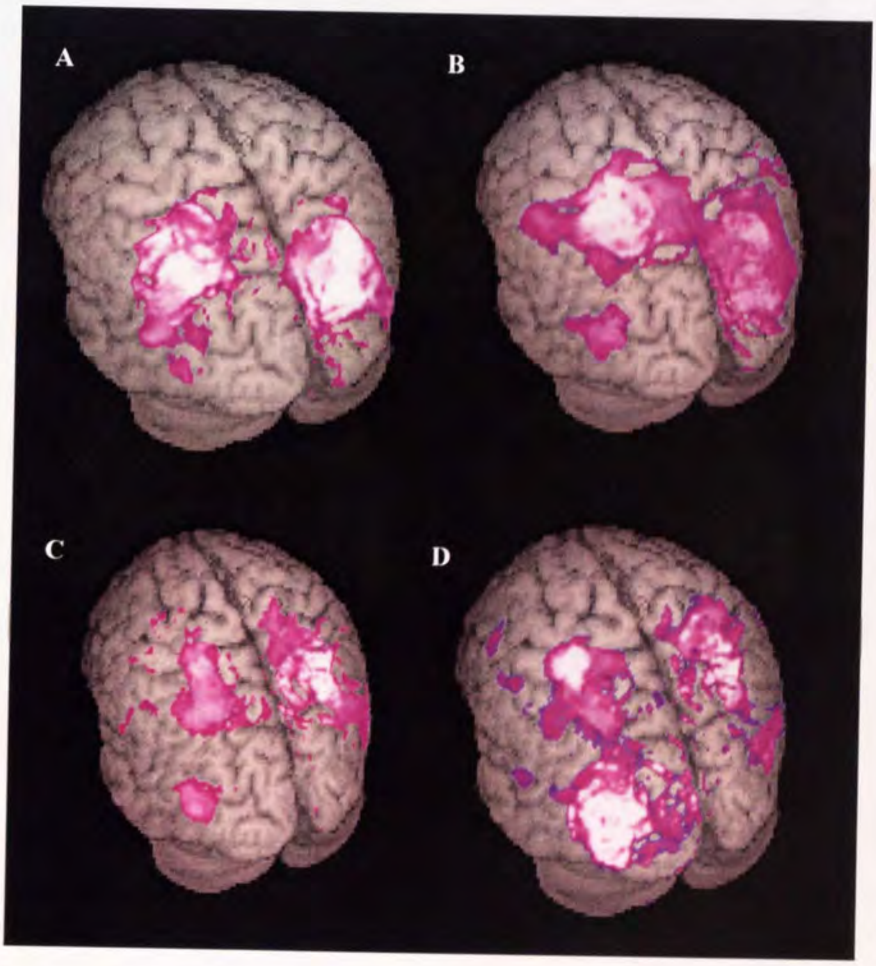


Figure 7.5: Differences Between Levels of Activation for the Valid and Invalid Trials.

This figure is made up of group analysis results using SPM99. For all images there was a Fun Integration Depth of 0.05, and an amplitude cut-off of 0.8. See Figure 7.4 for colour representation information.

A: Left Visual Field, valid condition. There is slightly more activation over the left hemisphere.
B: Right Visual Field, valid condition. There is slightly more activation over the right hemisphere.
C: Left Visual Field, invalid condition. There is considerably more activation in this condition, particularly over the left hemisphere.
D: Right Visual Field, invalid condition. There is more activation over both hemispheres, but less so than the change in activation for the left visual field.

Here we see a definite increase in activation for the invalid trials, in both hemispheres over parietal and extrastriate regions. The extrastriate activation appears to be only evident in the invalid trials, and is stronger contralateral to the field of presentation.

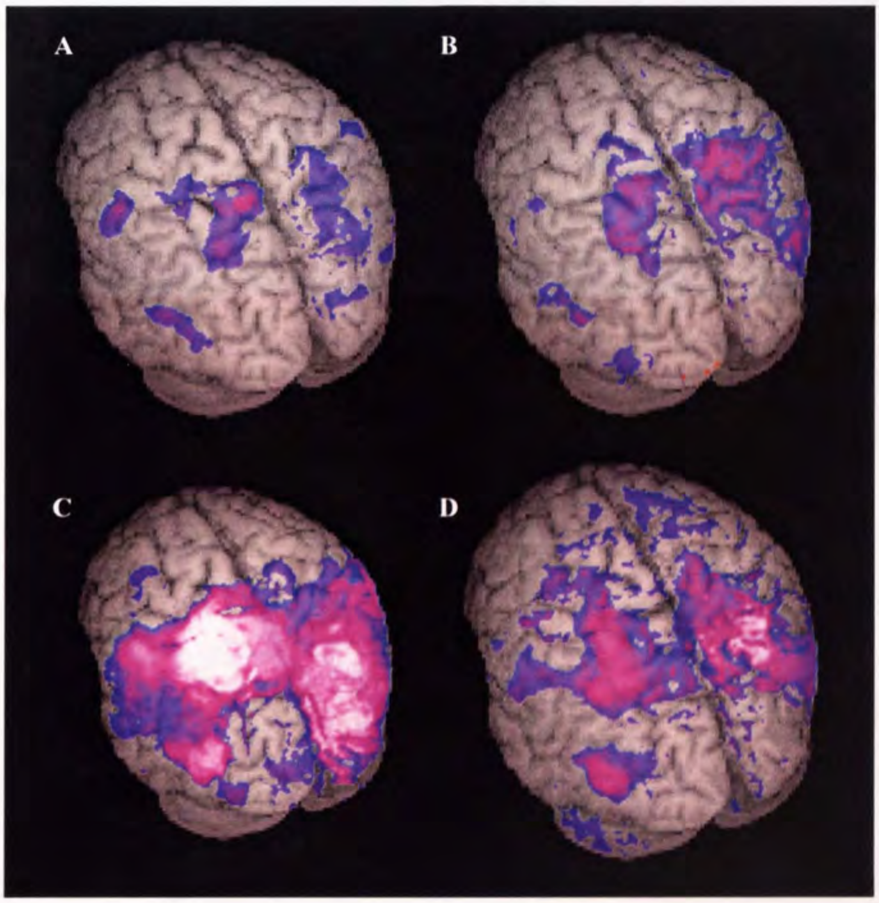


Figure 7.6: Subject BG's Parietal Activation for the RVF-left Condition.

Black lines are the valid trials and the purple lines are the invalid trials. Left hemisphere sensors are on the left side and the right hemisphere sensors are on the right side. This pattern was observed for the LVF-right condition also. Also visible is an increased level of activation for the invalid relative to the valid conditions.

Figure 7.7: Subject IH's Parietal Activation for the LVF-left Condition

Black lines are the valid trials and the purple lines are the invalid trials. Left hemisphere sensors are on the left side and the right hemisphere sensors are on the right side. This pattern was also observed for the RVF-right condition. Also visible is an increased level of activation for the invalid relative to the valid conditions.

Table 7.1: Activation as Measured in Pseudo-t-values for the Superior Parietal Lobe

SPL	Left Hemisphere		Right Hemisphere	
	Pseudo-t-values	Co-ordinates (x,y,z)	Pseudo-t-values	Co-ordinates (x,y,z)
LVF-left invalid	2.398	-34.8/-45.6/62.9	1.836	23.9/-66.9/45.5
LVF-left valid	1.257	-13.9/-54.3/64.2	0.932	26.8/-52.6/59.5
LVF-right invalid	1.254	-37.8/-50.8/55.8	1.701	26.8/-68.0/44.6
LVF-right valid	1.402	-34.8/-44.7/61.9	1.18	27.8/-68.7/50.2
RVF-left invalid	1.868	-30.8/-38.8/61.6	2.029	27.8/-54.9/53.2
RVF-left valid	1.865	-28.8/-51.8/54.9	1.43	18.9/-48.6/61.2
RVF-right invalid	1.255	-29.8/-57.5/57.9	1.799	25.8/-59.9/48.9
RVF-right valid	1.285	-29.8/-58.8/52.5	1.31	24.9/-49.6/61.2

Table 7.2: Activation as Measured in Pseudo-t-values for the Inferior Parietal Lobe

IPL	Left Hemisphere		Right Hemisphere	
	Pseudo-t-values	Co-ordinates (x,y,z)	Pseudo-t-values	Co-ordinates (x,y,z)
LVF-left invalid	1.954	-34.8/-49.9/53.9	1.857	30.8/-67.0/43.7
LVF-left valid	-	-	-	-
LVF-right invalid	1.603	-30.8/-62.2/43.4	1.584	31.8/-69.9/45.7
LVF-right valid	1.32	-28.8/-67.1/42.8	1.517	28.8/-69.9/45.7
RVF-left invalid	1.404	-31.8/-60.0/47.9	-	-
RVF-left valid	-	-	-	-
RVF-right invalid	1.367	-32.8/-59.9/48.9	1.404	32.8/-59.0/47.9
RVF-right valid	-	-	1.165	29.8/-65.1/42.7

Figure 7.8: An Example Parietal Waveform from Subject SW, the RVF-left Condition

Component 1 (first point on both lines), at 107ms post onset, and component 2 (third point on both lines), at 120ms post stimulus onset for the valid (black line with red points) and 158ms post stimulus onset for invalid (purple/grey line with green points), of the parietal response are increased, in channel MRP21, for the invalid condition relative to the valid condition. The other channels on the dominant side of the response were affected in this manner; some channels on the non-dominant side were affected.

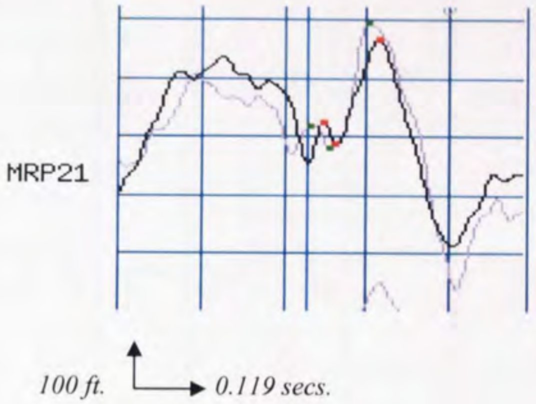


Figure 7.9: An Example Occipital Waveform from Subject VP, the LVF-left Condition.

The purple line with green points is the invalid condition, while the black line with red points is the valid condition. In channel MLO12, the P1 component (first point on both lines) is similar for both conditions. The latency and amplitude of the P2 component (third point on both lines) is increased for the invalid condition.

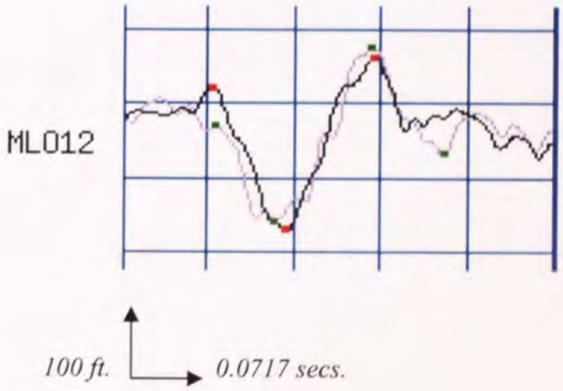
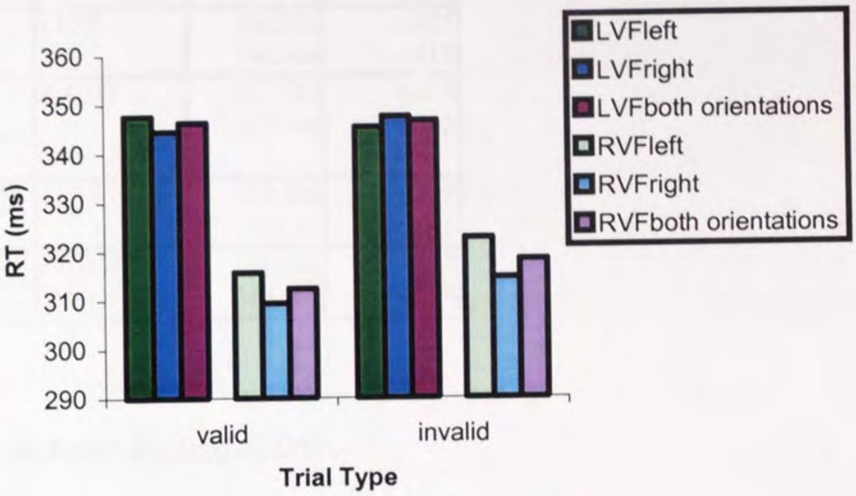


Figure 7.10: Example Channels from Subject VP, the LVF-left Condition

The occipital channels from subject SW, the LVF-left condition, are pictured. They show a dominance of responding on the contralateral side to presentation, in this case the right hemisphere shows the largest responses.

Figure 7.11: Reaction Times Show a Significant Difference Between LVF and RVF.



As can be seen there was a significant difference (see Table 7.4) in the RTs for the RVF and LVF conditions, with the RVF conditions being significantly faster than the LVF. The orientation responses were similar for all conditions. This was the same as the previous experiments in Chapter 6, where there was no delay in responding. To find this result after a delay to the response was unexpected. There was little difference for the valid and invalid conditions.

Table 7.3: Summary of Reaction Times for the Psychophysical Data.

Trial Type	Side	Orientation	Mean	sd
Valid	LVF	LEFT	360.323	5.425
Invalid	LVF		340.544	4.818
Valid	LVF	RIGHT	357.423	4.878
Invalid	LVF		351.503	4.902
Valid	RVF	LEFT	332.696	5.229
Invalid	RVF		323.74	5.045
Valid	RVF	RIGHT	331.803	5.117
Invalid	RVF		312.567	4.796

Table 7.4: Results of the Within-Subjects ANOVA.

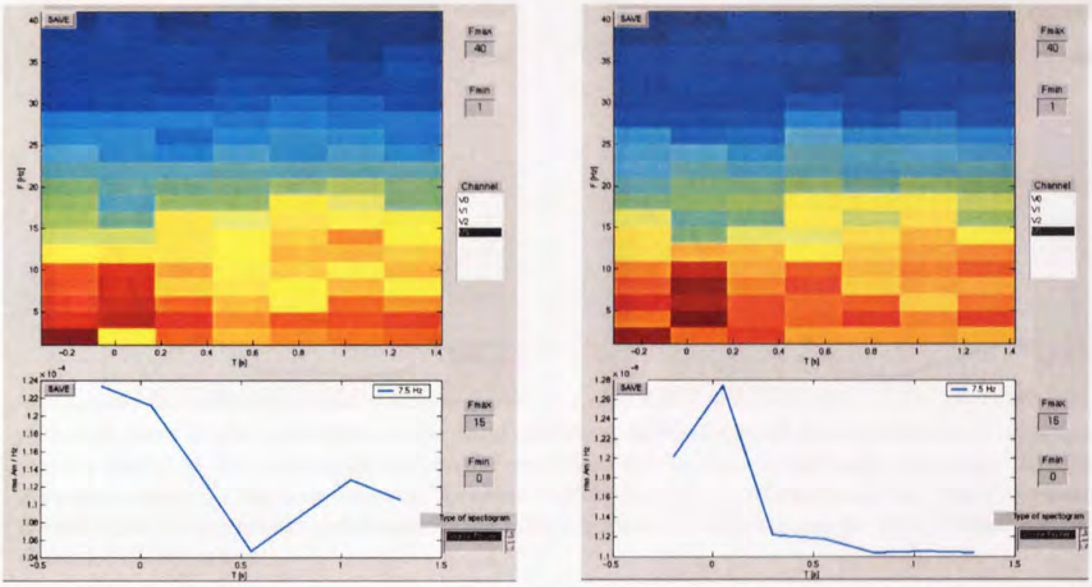
comparison	F-value	df	p-value	
trial type	8.345	1	<0.005	significant
orientation	0.096	1	0.757	non-significant
side of presentation	64.729	1	<0.000	significant
trial types * orientation	0.075	1	0.784	non-significant
side of presentation * trial type	0.034	1	0.853	non-significant
side of presentation * orientation	2.324	1	0.128	non-significant
side of presentation*orientation	3.384	1	0.066	non-significant

Figure 7.12: Spectrogram Output showing Responses in the SPL, IPL and V1.

Red indicates higher levels of activation relative to baseline whereas blue indicates none/lower levels of activation. Data is taken from individual participants, and is compared across participants. In some case the time scales are not the same. This was an unavoidable part of the Spectrogram program at the time of writing.

A: Participant SW, RVF–left condition.
Right Hemisphere SPL, valid condition.

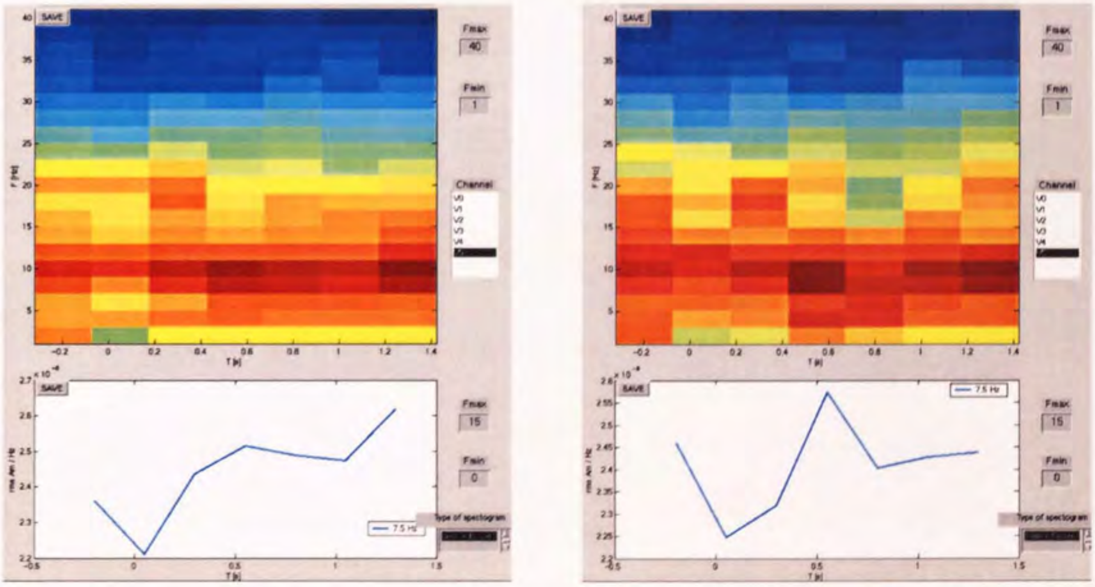
B: Participant SW, RVF–left condition.
Right Hemisphere SPL, invalid condition.



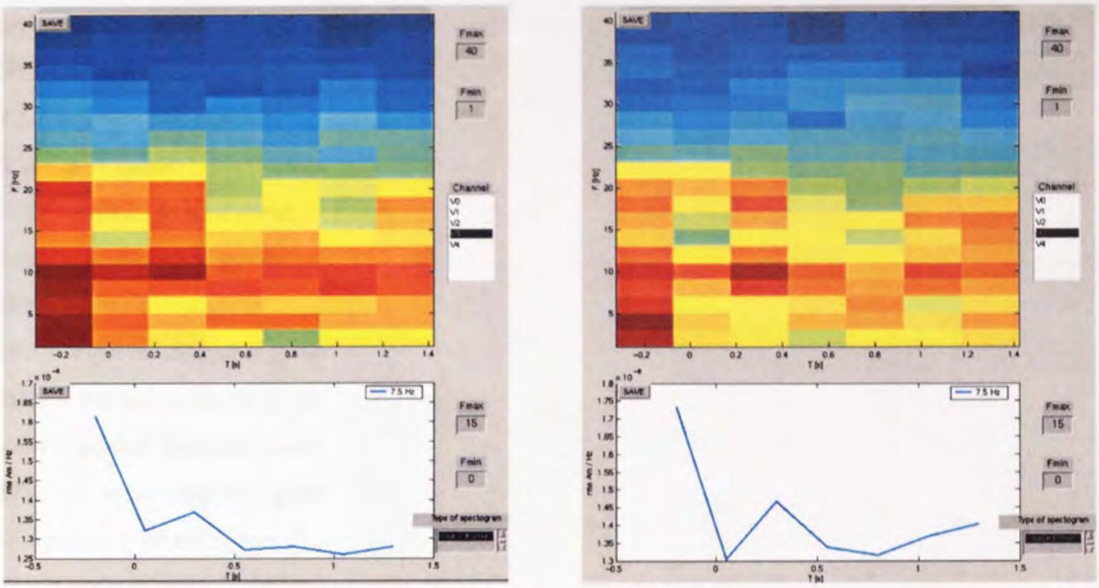
There is a sharper decline in activation for the invalid condition than for the valid condition, with a slighter higher level of activation for the invalid condition. Coordinates for both virtual electrodes are -2.17/-1.96/5.68 (x/y/z).

C: Participant KS, LVF-right condition.
Left Hemisphere IPL, valid condition.

D: Participant KS, LVF-right condition.
Left Hemisphere IPL, invalid condition.



There is a clearer, much more pronounced, response for the invalid condition relative to the valid condition, showing a clear influence of attention. There is also a higher level of activation for the invalid relative to the valid condition. Coordinates for both Virtual electrodes are -4.86/1.97/4.48 (x/y/z).



E: Participant KS, RVF-left condition.
Right Hemisphere V1, valid condition.

F: Participant KS, RVF-left condition.
Right Hemisphere V1, invalid condition.

Although there is more activation in the valid condition, there is a much more pronounced response in the invalid condition. For both valid and invalid conditions the increase in activation following the target onset is in approximately the same temporal location, indicating that it is unlikely that the initial response into V1 is modulated by attentional influences as the later response is. Coordinates for both Virtual Electrodes are -4.06/-0.87/0.98 (x/y/z).

Tables 7.5 –7. 8: The Results of the SAM Analysis: Areas Activated and the Hemispheric Dominance Exhibited.

Key to brain regions

***SPL** – superior parietal lobe*

***IPL** – inferior parietal lobe*

***PCu** – precuneus*

***GFM** – medial frontal gyrus*

***GPoC** – post-central gyrus*

***GPrC** – pre-central gyrus*

***GOS** – superior occipital gyrus*

***GOM** – medial occipital gyrus*

***GTM** – medial temporal gyrus*

***GTS** – superior temporal gyrus*

***V1** – primary visual cortex*

***V2/Cu** – visual area 2/cuneus*

A cross indicates the activation was in that area, so a cross in both left dominant and bilateral boxes indicates there was bilateral activation with left hemisphere dominance. A single cross in any one of the boxes indicated straightforward unilateral activation or equal dominance bilateral activation.

LVF and RVF indicate left visual field and right visual field respectively.
'Left' and 'Right' indicate left orientation and right orientation respectively.

Table 7.5: 0-10Hz, Left Visual Field

Area		LVF					
		left			right		
		left dominant	bilateral	right dominant	left dominant	bilateral	right dominant
SPL	valid	X	X	-	-	X	X
	invalid	X	X	-	-	X	X
IPL	valid	X	X	-	-	X	X
	invalid	X	X	-	X	X	-
PCu	valid	-	-	X	-	-	-
	invalid	X	X	-	-	X	X
GFM	valid	X	X	-	-	-	-
	invalid	X	X	-	X	-	-
GPoC	valid	X	X	-	-	X	X
	invalid	X	X	-	-	X	X
GPrC	valid	-	-	-	-	-	-
	invalid	X	X	-	-	-	-
GOS	valid	-	-	-	-	-	-
	invalid	-	X	X	-	X	X
GOM	valid	X	-	-	-	X	X
	invalid	-	X	X	X	X	-
GTM	valid	-	X	X	-	X	X
	invalid	-	-	X	-	X	X
GTS	valid	-	-	-	-	-	-
	invalid	X	X	-	X	X	-
V1	valid	-	-	X	-	-	-
	invalid	-	-	X	-	-	-
V2/Cu	valid	X	-	-	-	-	-
	invalid	-	X	X	-	-	-

Table 7.6: 0-10Hz, Right Visual Field

Area		RVF					
		left			right		
		left dominant	bilateral	right dominant	left dominant	bilateral	right dominant
SPL	valid	X	X	-	-	X	X
	invalid	X	X	-	-	X	X
IPL	valid	X	X	-	-	-	X
	invalid	-	X	X	-	X	X
PCu	valid	X	-	-	-	-	X
	invalid	X	-	-	-	-	-
GFM	valid	-	-	-	-	-	-
	invalid	-	-	-	-	-	-
GPoC	valid	X	X	-	-	-	-
	invalid	X	X	-	-	-	-
GPrC	valid	-	X	X	-	-	-
	invalid	-	-	-	X	X	-
GOS	valid	-	-	-	-	-	-
	invalid	-	X	X	-	-	-
GOM	valid	X	-	-	-	X	X
	invalid	-	-	-	X	- -	-
GTM	valid	X	-	-	-	X	X
	invalid	X	X	-	-	X	X
GTS	valid	X	X	-	-	X	X
	invalid	-	X	-	-	-	X
V1	valid	-	-	-	-	-	-
	invalid	X	-	-	-	-	-
V2/Cu	valid	-	-	-	X	-	-
	invalid	X	-	-	-	-	-

Table 7.7: 10-20Hz, Left Visual Field

Area		LVF					
		left			right		
		left dominant	bilateral	right dominant	left dominant	bilateral	right dominant
SPL	valid	X	X	-	X	X	-
	invalid	-	X	X	-	X	X
IPL	valid	X	-	-	-	X	X
	invalid	X	X	-	-	X	X
PCu	valid	-	-	-	-	X	-
	invalid	-	-	-	-	-	X
GFM	valid	X	X	-	-	-	-
	invalid	X	X	-	X	-	-
GPoC	valid	X	X	-	X	X	-
	invalid	X	-	-	X	X	-
GPrC	valid	X	X	-	-	-	-
	invalid	X	X	-	X	X	-
GOS	valid	-	-	-	-	-	-
	invalid	-	-	-	-	-	-
GOM	valid	-	-	-	-	-	-
	invalid	-	-	-	-	-	-
GTM	valid	-	-	-	-	-	-
	invalid	-	-	-	-	-	X
GTS	valid	-	-	-	-	-	-
	invalid	X	-	-	-	-	-
V1	valid	-	-	-	-	-	-
	invalid	-	-	-	-	-	-
V2/Cu	valid	X	X	-	-	-	-
	invalid	X	X	-	X	X	-

Table 7.8: 10-20Hz, Right Visual Field

Area		RVF					
		left			right		
		left dominant	bilateral	right dominant	left dominant	bilateral	right dominant
SPL	valid	X	X	-	X	X	-
	invalid	X	X	-	X	X	-
IPL	valid	X	X	-	-	X	X
	invalid	-	X	X	X	X	-
PCu	valid	X	-	-	-	-	X
	invalid	-	-	-	-	-	-
GFM	valid	-	-	-	-	-	-
	invalid	-	-	-	X	X	-
GPoC	valid	X	-	-	X	X	-
	invalid	-	X	X	X	X	-
GPrC	valid	-	-	-	-	-	-
	invalid	-	-	-	-	-	-
GOS	valid	-	-	-	-	-	-
	invalid	-	X	-	X	-	-
GOM	valid	X	-	-	X	-	-
	invalid	-	-	-	X	- -	-
GTM	valid	-	-	X	-	-	-
	invalid	-	X	X	X	-	-
GTS	valid	X	-	-	-	-	-
	invalid	-	-	-	X	-	-
V1	valid	-	-	-	-	-	-
	invalid	-	-	-	-	-	-
V2/Cu	valid	-	-	-	-	-	-
	invalid	-	-	-	-	-	-

7.4. Discussion.

The patterns of activation for the SPL and IPL suggest that there is a link between the field of presentation and the orientation of the stimulus, and the unexpected lateralized dominance of the response contradicts traditional theories of lateralization of the attentional response in the parietal lobes. There was also increased activation for invalid trials over valid trials in both parietal and occipital lobes, suggesting there is a neurological correlate of visual selective attention in both areas. The psychophysical data show an unexpected but highly significant effect of side of presentation and trial type.

The lateralization of activation was a surprise. We had been expecting to find dominance of activation in the hemisphere contralateral to the visual field. The pattern of activation appears to be far more complicated than was anticipated. Firstly there was the interaction between orientation and side of presentation. It appears that, in the SPL, when the orientation of the stimulus was directed towards the fixation point (same side of presentation and orientation condition) the activation was dominant in the hemisphere ipsilateral to the visual field, whereas when the orientation of the stimulus was directed away from the fixation point (different side of presentation and orientation condition) the activation was dominant in the contralateral hemisphere to the visual field. This suggests that the orientation of the stimulus has more of an effect on hemispheric dominance than does the visual field. It could be that the object is the primary source of focus, as was the case with behavioural goals, and that the side of presentation had little bearing on the response required, thus removing it from the 'processing equation'. This was the case with the behavioural goals, and the processing reflected this.

The two visual fields were presented in separate runs of the experiment, this could account for the visual field playing little or no part in the dominance of processing relating to behavioural goals. This explanation favours object-based theories of visual attention (see Chapter 1). The object is clearly the focus of attention here, and attentional resources are directed to the object, rather than the location, as location of the stimuli is irrelevant to the task. Behavioural goals dictate the focus of attentional resources. However, the task is based on one that classically favours location-based theories of visual attention (see Chapter 1). A previous experiment (see Chapter 6) found that the cue seriously impaired the speed of response to the stimulus when in a different location, 'invalid' trials. This indicates that attention was focused on the location and not the object involved, attention was drawn to a location by the cue, only to have to move to another location once the stimulus appeared. This indicates that this task can induce both object-based and location-based attentional resources, the behavioural task of responding to the stimulus promotes object-based attention, but this is activated after the location-based resources, which have the advantage of initiating after the cue has appeared, rather than when the stimulus appears. The results from psychophysical experiments (see Chapter 6, and Posner et al., 1978) show that the location-based attentional resources dictate the speed of the response made, but the object-based resources dictate the level of brain activation in specific areas of the brain, namely the SPL, in the manner highlighted above.

This picture gets more complicated when the responses from the IPL are considered. Here there was an interaction with trial type, orientation and side of presentation. The valid trials produced activation ipsilateral to the orientation, whereas the invalid trials produced activation that was ipsilateral to the side of presentation. The validity of the cue clearly has an impact on the neurological response. This may indicate that the response to the object is dominant in the valid trials, whereas for the invalid trials the side of presentation is the overriding factor in processing.

Macaluso et al (Macaluso & Frith, 2000) used a dual task paradigm, using orientation and varied timings, looking at the influence of task on selective spatial attention. They found that the left visual field (LVF) gave stronger responses overall than did the right visual field (RVF). Activation in the temporal task was stronger overall than activation in the orientation task. They found that the left hemisphere produced stronger modulations in activity in response to the temporal task, and the right hemisphere showed stronger modulations during the orientation task. It has also been found that the right hemisphere is involved with mediating attention in both halves of the visual field, whereas the left hemisphere is involved only in mediating attention in the RVF (Walsh et al., 1999).

Secondly there was increased activation in the left parietal lobe relative to the right parietal lobe. This could be down to task demands. The task involved spatially selective attention, using cues to direct attention to the location of an object in space. There is plenty of evidence to suggest spatial specialisation in the right hemisphere, but this does not necessarily preclude the left hemisphere being involved, even to the point of dominance, in certain aspects of spatial attention. In this case, the task of orienting attention to an object in space, which requires a behavioural response, may involve the left parietal lobe more than the right parietal lobe. It could also be due to the idea that covert attention, as a whole, is lateralized to the left hemisphere and overt attention is lateralized to the right hemisphere. This is the opposite of that hypothesised by Gainotti (Gainotti, 1996), that the right hemisphere is dominant for automatic orienting mechanisms, while the left hemisphere was dominant for conscious, volitional mechanisms, this research would also seem to be contradicted by the wealth of fMRI evidence that shows the right hemisphere to be dominant for attentional processing (for example: Corbetta et al., 1998; Somers et al, 1999). Given that fMRI has time resolution of around 2 seconds (Haxby et al., 1998), it seems unlikely that the automatic, covert attentional processes were being measured these fMRI experiments. Another possibility that may contribute to the left-hemisphere dominance could be response selection (Rushworth, et al., 2001). The left parietal cortex; specifically the SPL, dominant in mediating visuomotor associations, and the anterior portion of the IPL, concerned with motor attentional factors (Rushworth, et al., 2001), has been shown to be specifically activated for response selection rather than single detection responses, which activate the right parietal cortex (Rushworth, et al., 2001). If this is the case then there may be a case for a further study including detection responses in the same task, looking at whether the attentional paradigm would produce the same results without the response selection. The orientating mechanism involved in the left hemisphere may be involved in the task in this experiment, the orientation of the stimulus. It could be that the orientation of the stimulus triggered the orienting mechanisms to automatically orientate our awareness in the direction of the orientation. In terms of the lateralization in the orientation response, see above, this may not hold up, unless an explanation can be found to account for the difference in hemispheric activation for orientation towards or away from the point of focus.

It could be the case that the differences in activation may not be related to factors intrinsic with the grating itself. Rather, the differences could be due to hand movements made during the response. Even though the actual response was not analysed, the processing leading up to this response was. When the orientation was the same as the side of presentation, the activation dominance in the parietal lobe was ipsilateral to the orientation. When the orientation was different to the side of presentation the activation dominance in the parietal lobe was split between the valid and invalid trials. For valid trials the activation was ipsilateral to the orientation and for invalid trials the activation was contralateral to the orientation of the stimulus. It could be that the hemisphere contralateral to the hand dominating the response is only dominance under the most difficult task conditions, and in all other situations the hemisphere ipsilateral to the hand of response is activated. However, it could be that in this case, response selection if determining the response, along with the attentional influences, and hand of response is not involved at this level at all.

There was increased activation in the parietal and occipital lobes for the invalid task relative to the valid task. There is increased processing load due to the increasing task demands from the invalid trials in the SPL, IPL (see Tables 7.1 and 7.2) and visual pathway. The trace data from the MEG recording (see Figure 7.10) shows that, in the occipital pathway, the earliest component to be modulated by attention is the P1, at around 110ms post stimulus onset. This indicates that V2, or possibly V3, given that these are associated with the P1 component (Hillyard & Anllo-Vento, 1998), is the earliest visual area to be modulated by attentional demands, at least in this type of task. The increase in activation in the parietal lobes was due to increasing task demands. Posner (Posner & Cohen, 1984) identified three stages for the movement of visual attention, disengagement from the previous area of fixation, be it an object or a specific location, movement to the new location or object, and engagement of attention on that new location or target. The reason invalid trials produce longer reaction times (RTs) and larger neuronal responses, is that all three process are required before the appropriate behavioural response can be decided and executed. The valid trials are faster with less neuronal activity as attention has already been correctly cued to the appropriate location or object, and the only processing left is to execute the behavioural response.

As the imaging data produced was qualitative rather than quantitative, and used the active-passive comparisons instead of the active-active comparisons favoured is MRI and PET experiments it is not possible to conclusively explain this data. However, the indications are that there is a reproducible left hemisphere parietal dominance in both the SPL and IPL generated by this task, and also a reproducible activation contralateral to the field of presentation in the occipital lobe.

The lateralization of the activation indicates that the left hemisphere is more involved with the processing of movement of attention than is the right hemisphere. It can be postulated that the function of moving attention from one location to another is a function of the right parietal lobe, specifically the SPL and IPL. It is difficult to examine the exact role of these two areas in the execution of attention. The IPL is said to be the location of visuo-motor coordination, specifically grasping (Rizzolatti et al., 1997). This could indicate that, while the SPL is involved with the movement of attention from one location another, the IPL is involved with transforming this new information into motor coordinates and thus into a plan for the behavioural response.

The fronto-parietal network is well documented (for example see Corbetta, 1998; Coull et al., 1998; Posner & Dehaene, 1994) in the literature, and there is generally frontal activity as well as parietal activity in many attentional tasks (see Figures 5.3 and 5.4 in Chapter 5 and Nobre, et al 2000)). There was no frontal activity observable in the imaging data for this experiment. The activation of the superior frontal gyrus, the supplementary motor area that is involved in manual and voluntary movement, was expected. However, the lack of activation may be due to the fact that the response was not produced until later, and after the analysis window chosen, encompassing the trial up to the cue for the response, but not afterwards, when the response was made. The processing for the response could possibly have been carried out previous to the cue to respond, however, the RTs were in the region of 200-300ms and thus too long for the response to have been fully programmed. Initial processing will have taken place, but the motor activity, which would have activated the frontal lobes, was probably not done until after the cue to respond.

The results from the psychophysical data were a surprise. We were expecting no difference between conditions or hemispheres. Instead we found that there was a significant effect of side of presentation ($p<0.001$) and trial type ($p<0.005$). The RVF produced significantly faster responses than did the LVF. This was unexpected but it does correlate with the dominance of the left parietal lobe in the imaging data. This dominant hemisphere for the task, the left, produced the quickest RTs, whereas the non-dominant hemisphere, the right, produced the slowest RTs. The effect of trial type was that the valid trials were slower than the invalid trials. This is the reverse of that seen in previous experiments (see Chapter 6 and Posner, 1980), which show that the invalid trials are slower, by some margin, than valid trials. This could be due to the phenomenon of Inhibition of Return (IOR) (see Chapter 1).

7.5. Conclusions

This experiment highlights the idea of lateralization of attentional processes, challenging conventional views of lateralization and proposing new ones. The SPL and IPL are clearly involved with spatial selective attention, with object-based and location-based mechanisms also being activated. The validity of the trials had an impact on lateralization of activation in the IPL, but it had more of an impact on the strength of the response, in both occipital and parietal lobes. However, there is no evidence, as yet, for V1 being modulated, the earliest modulation of the response appearing in the P1 component at around 110ms, presumably corresponding to area V2 or V3 (Hillyard & Anllo-Vento, 1998); indicating that is unlikely for V1 to be modulated on a feedforward basis, but rather through feedback mechanisms working from V2/V3 and above.

Summary

In this thesis several experiments were presented, which were designed to measure spatially selective covert attention. Attention was defined, at the start of the thesis, as a process "which defines our mental ability to select and respond to stimuli, internal or external, on the basis of behavioural goals in the presence of competing, behaviourally irrelevant, stimuli" (pp10). The experiments in this thesis were designed in order to test this definition in relation to the underlying neural events accompanying covert attentional mechanisms, in particular the parietal cortex and the visual system. These experiments covered dual task and cue-based paradigms, and utilised both psychophysical and brain-imaging techniques. Attentional mechanisms are considered to be specifically located in the parietal lobes and to be part of the fronto-parietal network. The fronto-parietal network has long been known to be involved in attentional processing (Corbetta et al., 1993; Posner et al., 1984). The left parietal cortex is seen as the site for temporal, non-spatial, selective attentional processing, along with covert spatial orienting, (Coull & Frith, 1998; Macaluso & Frith, 2000), whereas the right parietal cortex is seen as the site of spatial attentional processing, along with overt spatial orienting (Corbetta et al., 1993; Posner et al., 1984). The information from the neglect literature (see Chapter 2) has also shown that the right hemisphere appears to mediate attentional resources for the whole of the visual field, whereas the left hemisphere appears to mediate attentional resources for just the right visual field. The posterior parietal cortex (PPC) was found to be the main site of activation during these attentional experiments, containing the superior parietal lobe (SPL), the inferior parietal lobe (IPL) and the inferior parietal sulcus (IPS). A common theme was found in the MEG experiments, the left parietal lobe being activated more strongly than the right, throughout this series of experiments, and also being modulated in accordance with attentional demands. Reference to the experiment by Corbetta et al (1993) and the results produced (see Figure 1.2, pp 25) will show that although the results presented in this thesis are qualitative, the quantitative results, analysed in the typical manner used in MEG experiments, produced by Corbetta et al (1993) are in line with the results here; indicating that, had quantitative analysis methods been available, a statistically significant correlation between the areas activated and the attentional demands of the tasks could have been found.

These experiments support the view that attentional processes are lateralised. However the conventional views of lateralization are questioned and new ones are proposed. The left parietal cortices have been seen as primarily concerned with temporal processing, while the right parietal cortices are concerned with spatial processing. The SPL and IPL are bilaterally involved with spatial selective attention in these experiments, the left hemispheric response being stronger. The evidence presented in this thesis show that it can no longer be claimed that left parietal cortices are temporally dominant and the right parietal cortices are spatially dominant. The possibility must be entertained that the lateralization in the parietal cortices is more complicated that has been thought, and that there may be much more bilateral modulation of temporal and spatial attentional processing that has been previously believed. However, further, quantitative, research is needed to pursue this idea any further.

Spatially selective covert visual attention was the focus of this thesis, and it was thought that the cued attentional paradigm was the best way to go about investigating this form of attentional processing. The valid-invalid cued attentional design was drawn from the Cost-Benefit paradigm put forward by Posner (1980). Posner (1980) proposed that where a cue is co-located with the target there would be an advantage in responding, a benefit, whereas when the cue and target were located in different positions, there would be a disadvantage, a cost. The experiments in Chapters 6 and 7 have shown this to be the case, supporting the work of Posner (1978, 1980). The effect of valid and invalid cues in the experiments in Chapter 7 also had an impact on lateralization of activation in both the SPL and the IPL, as well as an impact on the strength of the response, in both occipital and parietal lobes. For invalid trials there was a significant increase in the level of activation. This indicates that increased attentional demands cause a greater level of activation than attentionally undemanding trials. There is very little imaging evidence of a difference in levels of activation as a result of cued-attentional paradigms of this nature, and further quantitative analysis would be needed to discover how significant this difference between valid an invalid levels of activation is. Although, based on the differences in visible activation it is thought that there would be a highly significant difference between these conditions.

In Chapter 6 it was shown that the two hemispheres of the brain are remarkably different, and some of these asymmetries have been linked with handedness. For example a difference in the length of the of the left occipital horn of the ventricles has been found between hemispheres and the handedness of the individuals (McRae et al, 1968 - in Galaburda et al., 1978). A fundamental problem in researching handedness is the basic determination of the handedness of the participants. Self-reporting is fraught with problems, although it remains remarkably accurate as a basic handedness test (Hochberg & LeMay, 1975 - in Galaburda et al., 1978). Handedness is based along a continuum, and individuals fall at a point along this (Annet, 1970 – in, Geschwind & Galaburda, 1987); this is true anatomically as well as behaviourally (LeMay & Geschwind, 1975 - in Galaburda et al., 1978).

The experiments in Chapter 6 followed the pattern originally found by Posner et al (1978). It was considered exclusionist to restrict testing to right-handed participants alone, it was thought that left-handed participants may or may not provide different responding patterns. A small pilot study was conducted to investigate this. Hand of choice for writing was the only categorisation of participants, no handedness inventories were used, a further study would need to use handedness inventories to see if there is any gradation of the response. A significant difference was found nevertheless, contrary to expectations. From this data two different kinds of lateralization were proposed, sensory-perceptual lateralization, and motor-processing lateralization. The view was advanced that only motor-processing lateralization was different between left- and right-handed populations, sensory-perceptual lateralization being processed identically with no regard for hemispheric dominance in other forms of processing, such as handedness. It was further proposed that motor-processing lateralization was reversed in left-handers with respect to right-handers, but that the sensory-perceptual lateralization was not, being a universal lateralization, indicating that the left dominance of the left hemisphere with respect to spatially selective covert attentional tasks would be found in all participants, regardless of handedness.

This research indicates that the mechanisms for spatially selective covert attention may be located in the left hemisphere, ostensibly the left parietal lobe regardless of processing for motor responses. If this is the case, then the results in Chapter 6 show an advantage, in terms of handedness, when the left hemisphere is the non-dominant hemisphere. Right-handers, on the other hand, having their dominant hemisphere as the left-hemisphere, have a disadvantage with regards to covert attention, but an advantage with regards to the motor-processing lateralization, their right-hand being dominated by the hemisphere which is dominant for the attentional task. This indicates that dominance of a hemisphere may restrict attentional processing in some way.

In Chapter 5 it was suggested that there were common processes at work serving two disparate perceptual and cognitive systems. The two tasks produced the same pattern of responses although the first contained letters and the second a rotating grating. It is suggested that there may be a common process serving both the language and spatial domains, and that divergence of this process for specialised processing occurs after the parietal lobe and after any attentional processing. The location of this common process ostensibly appears to be within the parietal lobes, in particular the SPL and IPL, given that there was the most variation of activation in these areas, however, further quantitative analysis is required before any formal conclusions can be drawn.

Attention is driven by stimulus change and behavioural goals; and we are unable to interact with the external visual environment without first knowing with what we are to interact. Without preattentive processing, we would be attending to all things all the time, which is in direct contradiction to the widely accepted concept of a limited capacity attentional system. The concept of a limited capacity of attention indicates that we are unable to attend to all items in the visual world at all times, this being perceptually and behaviourally impossible, there is a limit to the amount of visual information filtering through for further processing. However, we still have to know what is in the external visual environment before we can filter out the unwanted, behaviourally irrelevant information. This leads to the idea of preattentive processing, how can we attend to what we do not know is there? There has to be an early level of processing that includes all the visual information from the external environment that precedes attentional processing. This information is then subject to feedback connections, through which attention operates, from higher visual areas and parietal areas and attention thus selects that information which is behaviourally relevant, though feedback mechanisms, for further processing.

The concept of pre-attentive processing indicates that the initial inputs into V1 are not modulated by attention, thus any modulations found in experimental data are the result of feedback mechanisms from higher cortical areas, namely the parietal cortex and extrastriate areas. The results from Chapter 5 appear to suggest that the modulation of V1 and V2 is indeed in the form of feedback from higher areas, the extrastriate and parietal areas, at a time later than the initial feedforward sweep of information processing. Figures 7.9 and 7.10 (Chapter 7) show that, in the occipital pathway, the earliest component to be modulated by attention is the P1, at around 110ms post stimulus onset. This indicates that V2, or possibly V3 are the earliest visual areas to be modulated by attentional demands, at least in this type of task. Thus the initial modulation of the visual pathway is V2, or possibly V3, at the earliest, V1 being modulated by feedback projections from extrastriate visual areas and the parietal cortex.

Further research in these areas would take the form of several studies. Firstly there would be an extension of the handedness investigation in Chapter 6 involving a larger group of participants as well as full handedness inventories. An extension of this study would involve looking at these same participants using MEG, to see if there were any differences in activation levels and lateralization of responses in left-handed participants. In other words, the experiment would be a repeat of the experiment from Chapter 7 but with left-handed participants in order to directly compare them. Another avenue of further research is cross-modal studies, ostensibly audition vs. vision. A full imaging study is planned to encompass a dual-cued attentional design using the valid-invalid conditions simultaneously in both the visual and auditory domains. The purpose of this experiment would be to investigate whether the attentional modulation found between valid and invalid conditions in the parietal cortex is a result of a purely visual attentional mechanism, or whether it is a result of a global attentional mechanism. For all studies presented ad proposed the newer, quantitative, analysis techniques would be used, including the GLM program (see Chapter 4) and SnPM (for details please contact Dr K Singh at http://www.aston.ac.uk), a non-parametric version of SPM 99 which provides actual t-values as opposed to pseudo-t-values, giving an opportunity for direct, quantitative, comparison of the data.

This research opens the way for more work into attentional influences and where they first have an effect, alongside more work into whether the left or right parietal lobe is modulated initially in attentional processing, and whether the modulation of each hemisphere is subject to specific attentional processing. It could also be that this lateralization is itself subject to the influence of handedness. This work challenges the accepted ideas of laterality in relation to both handedness and attentional processing in the parietal cortex. There is a new possibility for the lateralization of attentional processing in the parietal lobes. The left hemisphere may be dominant for covert spatially selective attentional processing, though bilateral activation is seen throughout. A new, dual system of attentional processing is proposed: sensory-perceptual processing, which is always left lateralized within the parietal lobe, and processing linked with motor responses, which is dependent on the handedness of the individual, reversed for left-handers relative to right-handers. This research has also concluded that V1 is most likely modulated by feedback mechanisms, and not in the initial feedforward sweep of information processing, although more detailed research using MEG is required to confirm this hypothesis.

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Appendix A

Experiment 1 – Centre

Right hemisphere V1/V2: There was a steady decrease in activation to 250ms, more so for the 'same' condition, with a peak at ~500ms, greater in the different' condition. There was a dip in activation until ~1250ms in the 'same' condition and 1500ms in the 'different' condition. Both then exhibited a steady increase in activation.

Left Hemisphere V1/V2: There was a high level of activation for both conditions. There was a steady decrease for both to 250ms the activation was flat to ~800ms with an increase to 1500ms for the 'different' condition when the activation dipped. The 'same' condition was fairly flat with a slight decline in activation.

Experiment 1 – Periphery

Right Hemisphere V1: Both conditions had a steady decrease in activation until ~500ms. The 'different' condition had a peak at ~750ms which was much smaller and flatter than the one for the 'same' condition. There was a smaller peak at 1250ms, with slightly larger activation in the 'same' condition.

Left Hemisphere V1: Only the 'same ' condition had the decrease in activation until 250ms. The 'different' condition had a fairly flat level of activation until a slight peak at 250ms. These were followed by dips at ~500-750ms and a peak at 750ms, the 'different' condition had a much bigger level of activation for this peak. These were followed by a dip at ~1000ms and a peak at 1250ms for both conditions, smaller for 'different' and larger for 'same'.

Experiment 2 – Centre

Left Hemisphere V1: There was a steady drop in activation to 250ms followed by an increase in activation in the 'different' condition. There was an increased level of activation up to ~750ms, peaking in 2/3 participants, followed by another peak at ~1250-

1500ms for both 'same' and 'different' conditions in 2/3 participants. This last peak was preceded by a dip ~1000ms.

Right Hemisphere V1: A steady drop in activation was shown in the 'same' condition until ~250ms, whereas for the 'different' condition the activation was fairly consistent until ~100ms when there was a slow decrease. For ½ Participants there was a peak ~1000ms, bigger and more pronounced in the 'different' condition. For ½ Participants there was a dip at ~1000ms, flatter and showing less of a decrease in activation for the 'different' condition. This was followed by a peak ~1500ms with a higher level of activation for the 'different' than the 'same' condition.

Left Hemisphere V2: The steady decrease in activation for 250ms was followed by a dip at 500ms, flatter in the 'different' condition. There was a negative peak ~1500ms in the 'different' condition only, corresponding to a positive peak in the left hemisphere V1.

Experiment 2 – Periphery:

Left Hemisphere V1/V2: A fairly steady decrease in activation was exhibited to 250-500ms followed by an increase to a peak at 1000ms. There was a second peak at 1500ms, though this was smaller than the first peak.

Left Hemisphere V1: Activation deceased to 250ms and was followed by an increase to 500 or 750ms, which then flattened out. The peak at 750ms was followed by a dip at 1000ms and another peak at 1250ms. The peak at 500ms was followed by a peak at 1000ms and a dip at 1500ms, followed by another peak at 1750ms.

Right Hemisphere V1/V2: There was a steady decrease in activation to 250ms. In one case there was a dip ~750ms for the 'same' condition and at 1000ms for the 'different' condition, followed by an increase in activation up to 1250ms for the 'same' condition and ~1500ms for the 'different' condition. This peak for 'different' coincided with a dip at 1500ms for the 'same' condition. For another case there was a dip at 500ms for the 'same' condition and at 1750ms for the 'different' condition. For this case there was very little change in activation for the 'different' condition. The 'same' condition had peaks at ~1200ms and 1750ms and dips at 500ms and 1500ms.