THE EFFECTS OF INTERNALLY VERSUS EXTERNALLY DIRECTED ATTENTION ON THE HUMAN ELECTROENCEPHALOGRAM

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ABSTRACT

This study was carried out in order to test the intake-rejection hypothesis and examine the functional significance of the associated EEG bands. This model argues that the nervous system reacts differently according to the locus of attention, traditionally interpreted as a differentiation between externally and internally directed attention, but work in this field remains fragmented and often contradictory.

Experiment 1 was an exploratory study examining differences between internal and external attention using a mental arithmetic versus auditory signal detection protocol. Contrary to expectations, effects were observed in the fast EEG bands, where power was greater during internal attention than during external attention. Experiment 2 employed a multi-modal mental imagery (auditory, haptic and visual) versus sensory-intake protocol. Effects in all modalities in the alpha band were noted showing greater power during internally directed attention. Other less ubiquitous effects were also observed, including differences according to task difficulty in the theta band. Experiment 3 was a constructive replication of the second experiment. Improvements were made to the protocol enabling both increased confidence in the experimental findings and a more detailed topographical analysis of the data. Again, consistent experimental effects were observed in the alpha band. Experiment 4 sought to answer several questions arising from experiments 2 & 3, in particular whether the findings resulted from an evoked component in the EEG deriving from the externally directed attentional stimuli. Results indicated that changes in the alpha band reflect a

modulation of the induced component of the EEG caused by attention to mental imagery. These findings suggest that changes in the alpha bandwidth (and other components) of the human EEG maybe seen as an index of attention to mental imagery possibly reflecting top-down executive cortical control mechanisms.

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FORWARD

Since Berger first reported the discovery of the electroencephalogram (EEG) in humans in 1924, much scientific effort has been spent in an attempt to understand its functional significance. Despite this, there is still little or no consensus. Consequently, the primary concern of this thesis is to investigate the functional significance of the human electroencephalogram (EEG). The secondary topic and the avenue through which the primary concern can be addressed, is that of the study of attention. Specifically, it is an exploration of the notion that one can get a more thorough idea of the mechanisms underlying attentional processing by examining the direction of expression of that attention. Namely, whether attention is directed outwards towards the external environment or inwards towards the thoughts and images of one's own mind, referred to as externally directed attention and internally directed attention respectively throughout the course of this document. Additionally, it is argued that by adopting such a perspective, one can take a step towards making more sense of many of the seemingly contradictory findings regarding attention within the field of cognitive neuroscience.

The medium of this investigation was quantitative electroencephalography (qEEG). This field has been given a new lease of life in recent years thanks to two main reasons. Firstly, there has been something of a paradigm shift away from strict information processing / computer analogies of cognition and towards an interpretation of the brain as a more dynamic and complex system. Secondly, huge increases in computer processing power and speed have

facilitated the previously only dreamed of exploration of vast amounts of experimental data. However, such benefits rarely come without costs and in the case of EEG work they have been two-fold: First, there is the greater possibility of finding significant experimental effects by chance due to the number of comparisons being made. Second, there is the challenge and the responsibility to discuss and further explore those effects that have been reliably validated that were beyond the scope of the original hypothesis. In this spirit, this study will report findings from all the traditional bandwidths of the EEG and where appropriate, investigate more recent methods of subdividing and individually adjusting band parameters.

The layout of this thesis is as follows. The first half presents the background to the main topics of concern. Chapter one describes the common sense (folk psychology) and psychological approaches to the concept of attention and introduces various theories pertaining to it. Chapter two outlines the current understanding of the basic mechanisms underlying the EEG and describes many of the traditional ways of describing the functional significance of the various components of the EEG spectrum. Chapter three introduces the concepts and reviews the literature regarding the work relating to internally and externally directed attention.

The second half of the thesis presents the experimental work carried out in the course of this study and the conclusion and proposals derived there from. Chapter four presents the first experiment that compared the differences in EEG activity during mental arithmetic versus an auditory continuous performance

task. Chapter five is concerned with a multi-modal experiment contrasting auditory, haptic and visual tasks with their mental imagery equivalents (experiment 2). Chapter six describes the third experiment that is in essence a constructive replication of experiment two. Chapter seven presents the last experiment in this study that sought to answer various interpretational possibilities arising from the previous experiment. The last chapter serves as a discussion forum for the results, interpretations and implications of all the experiments carried out during this project. Finally, proposals are made, shortcomings addressed and ideas for future research are advanced.

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Now I guess I'll have to tell 'em

That I've got no cerebellum,

Gonna get my PhD

I'm a teenage lobotomy

Dedicated to the memory of Joey Ramone

(1951 - 2001)

1 ATTENTION

1.1 INTRODUCTION

Attention is a chimeric concept; it is at once part folk psychology, part neuroscientific. The naïve understanding of the notion of attention afforded by folk psychology is itself both obvious and yet useful. As William James famously wrote,

> "Everybody knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out what seem several simultaneously possible objects or trains of thought" (James, 1890).

Unfortunately, the common sense view of attention is also problematic. It is intimately associated with notions of free will and volition. To quote James again, "My experience is what I agree to attend to". However numerous studies, for instance those investigating unconscious processing (Stoerig & Cowey, 1997; Weiskrantz, 1996) or intent (Libet, 1993; Libet, 2002) have thrown doubt upon such a stance. Nevertheless, neuroscience and psychology have adopted attention as a working hypothesis and so doing have sought to limit the scope of its meaning to some kind of perceptual selection and processing capacity mechanism (Pashler, 1999). Even then however, the meaning is not clear. Such selection may be conscious, unconscious, endogenous, exogenous, externally focused, internally focused, sustained, covert, immediate or derived. Despite the semantic ambiguities, attention does appear fundamental to how the brain

functions and interacts with the environment. Cohen (Cohen, 1993) describes it as "the interface between current stimulus input and the encoding process". Arguably, if one could understand attention, one would have made a major step to understanding how the brain processes information and perhaps how consciousness arises.

Consequently, attempts to understand the mechanisms of attention underpin virtually every field in modern cognitive psychology and neuroscience. Whether for example, it be exploring the attentional influences on time perception (Zakay, 1989) or investigating the problems with attention exhibited by schizophrenic patients (e.g. Gruzelier, 2000), an in-depth understanding of the neuronal processes involved in attention is crucial.

In recent years, researchers in this area have returned to investigate a (once optimistically touted) proposal that to gain a more complete understanding of these mechanisms, notice has to be taken of where attention is directed. In particular, psychophysiological differences have been observed between attention directed outwards to the external environment and attention directed inwards to the contents of one's own mind. These findings have been explained in terms of the 'intake-rejection hypothesis' (Lacey, 1967; Lacey, Kagan, Lacey, & Moss, 1963; Lacey & Lacey, 1970) and are described in chapter three. Before examining the intake-rejection model in more depth it may perhaps prove useful to introduce some more general theories of attention (section 1.2) and provide an overview of traditional descriptions of the EEG spectrum (chapter 2).

1.2 A BRIEF INTRODUCTION TO THEORIES OF ATTENTION

Over the years, many theories of attention have described it as being a kind of processing bottleneck (e.g. Broadbent, 1958; Deutsch & Deutsch, 1963; Deutsch & Deutsch, 1967; Treisman, 1964). They disagree however, as to when in the perceptual process this filtering occurs. Is it in early selection of sensory information (Broadbent, 1958), is it in late selection (Deutsch et al., 1963)? Or is it a much more dynamic process entirely, with the brain continuously re-mapping the environment as automatically and as unconsciously as possible? In such a scenario, attention becomes the preserve of that which stands out, because it is unexpected or salient (McCrone, 1999). What then are the mechanisms that 'decide' what stands out or what can be processed without the extra burden of conscious attention?

Rather than one simple attentional bottleneck, much of the recent work suggests that there are a whole host of sub-cortical bottlenecks, which have the effect of organising perception. Different investigators tend to emphasise different bottlenecks. For instance, It has been proposed that the thalamus may act as one major processing bottleneck (e.g. Crick, 1984; LaBerge, 1995; LaBerge, 1997). The majority of connections in the thalamus are feedback loops from the cortex ; indeed there exists a ratio of at least 10:1 of cortico-thalamic as opposed to thalamo-cortical connections (Sherman & Koch, 1990). Additionally, it appears that the thalamus is topographically organised to mirror the cortex (e.g. the relationship between the pulvinar and the sensorimotor regions of cortex; the lateral geniculate nucleus and the visual cortex or the medial geniculate nucleus

and the auditory cotex). A signal passing along one such connection has to travel through the reticular nucleus (wrapped around the thalamus) and this causes inhibition in neighbouring thalamo-cortical connections (e.g. Crick, 1984). LaBerge (LaBerge, 1995; LaBerge, 1997; LaBerge, 1998; LaBerge, 2001) has suggested a triangular circuit of attention, involving (in sensory perception at least) the thalamus, the prefrontal cortex and the appropriate sensory regions of the cortex. In this model, planning areas in the prefrontal cortex can influence activity in for instance, sensory cortex via the appropriate region of the thalamus: the 'volume' can be turned up on incoming signals of note and turned down on the rest. In this sense, attention would be modulated by selective suppression or enhancement of the thalamo-cortical feedback loops. Interestingly, LaBerge and colleagues (Liotti, Fox, & LaBerge, 1994) found that the greater the thalamic activation (as revealed by PET recordings), the greater the subjective difficulty of the attentive task reported by his subjects. The role of the thalamus has also been incorporated into a model of attention by Posner and colleagues (Posner, 1995; Posner & Raichle, 1997). The next section begins with a description of this and compatible theories and seques into an overview of dynamist approaches to attention and relations to working-memory.

1.2.1 On the Posner Model of Attention

Posner's model is similar to LaBerge's in that it emphasises the anatomical discreteness of the sources of attention and the sites of attentional expression. The sources of attention are viewed as those neural networks involved specifically with attention and primarily concerned with attentional switching

and control. The sites of attentional expression are those cortical and sub-cortical areas wherein activity is affected by the sources of attention but are also involved in the passive registration of information without attentional control (Posner, 1995).

Posner has also stressed the importance of three separate attentional processes: arousal, orienting and executive functions such as control and target detection. They can be described in the following ways:

1) Arousal: This aspect of attention refers to those mechanisms that are concerned with the maintenance of an alert state. The brain areas thought to be involved are in right frontal and parietal areas and are especially important during sustained attention tasks and during the period between a warning signal and its target stimulus. The neurotransmitter thought to be particularly associated with arousal is noradrenalin (NA). NA can serve to modulate activity in large areas of the brain including frontal and parietal areas due to widespread projections arising from the noradrenergic nuclei in the locus ceruleus.

2) Orienting: The most obvious way that one can shift or orientate one's attention is by directing one's gaze in the direction of the object to be attended. Thus the study of eye movement has proven a worthwhile subject for investigating attention and associated pathologies (e.g. Kennard, 2002). However, it is also possible to attend to something without shifting one's gaze to it. This form of attention is known as 'covert' attention and studying

it permits the examination of attention without the extra processing of ocular motor requirements. Posner (Posner, 1995) has proposed that there are three sub-components to the process of covert attention. Firstly, disengagement from the present focus of attention is required. It has been proposed that the posterior parietal lobe is the area concerned with this function. This theory is mainly based on work investigating patients with hemispheric neglect due to damage to the parietal lobe (particularly so in the right hemisphere). The second sub-component needed is the process whereby attention is shifted to the new focus of attention. The superior colliculus and nearby areas in the midbrain are thought to be important for carrying out this operation. Finally, one needs to restrict information input to the cortex from possibly competing stimuli. This brings us back to the theories regarding the importance of the thalamus as a gating mechanism, particularly in this instance, the pulvinar.

Another region thought to be important with regard to orienting is the nucleus accumbens (e.g. Gray, 2003). This forms part of the so-called *interrupt pathway*, which is the pathway thought to underlie the Orientation Response (OR). This is related to, and yet different from Posner's approach to covert orientation as it is primarily an exogenous response to unexpected stimuli. In this sense the OR can be described as the "what is it" reaction to a surprise (McCrone, 1999). Early work on the OR, by researchers such as Sokolov (e.g. Sokolov, 1963; Sokolov, 1990) found that it was a whole body reaction; everything gets re-tuned ready for what may happen next. Interestingly, this response seemed to be tuned to the characteristics of the stimulus. Thus, a frightening stimulus would elicit one set of physiological responses, whereas

an interesting stimulus may provoke a different set entirely. Or perhaps, for instance, a sudden movement near the face may evoke a string of defensive reflexes. The point is, all of these reactions are pre-conscious, fast and yet appropriate.

The interrupt pathway also involves the brainstem (early-warning links to thalamus and cortex) and the amygdala (links with hypothalamus) adding emotional salience. The role of the nucleus accumbens can be to either allow the basal ganglia to carry out its intended motor program or it can act to stop what had been planned (by releasing a flood of the neurotransmitter dopamine) and allow new actions to be programmed. The emotional centres can also engage at this point triggering appropriate survival-based responses (McCrone, 1999).

3) Executive Control: It is widely believed that perception and indeed conscious awareness requires an optimal balance of both bottom-up (environmental input) and top-down (goal-orientated, internally driven) processes (e.g. von Stein & Sarnthein, 2000b). See box 6.1). A normally functioning attentional system facilitates this balance. The aspect of attention behind this balance has been referred to as an executive control mechanism. Posner and others have proposed that frontal and prefrontal cortical areas are central to such control especially the anterior portion of the cingulate cortex (ACC).

The ACC has been observed to be activated during many processes in which executive control has been deemed necessary. The full extent of these

activities is beyond the scope of the present study but a few examples may provide the reader with a hint of their importance: The ACC is active during the conscious effortful learning of a new task and this activity *subsides* as automaticity develops (McCrone, 1999 pg. 231). It has been found to associated with the subjective experience of pain (Croft, Williams, Haenschel, & Gruzelier, 2002), and of hypnosis (Rainville, Hofbauer, Bushnell, Duncan, & Price, 2002). The ACC has also been found to be active during the incongruent phase of the stroop task[1] (Gruber, Rogowska, Holcomb, Soraci, & Yurgelun-Todd, 2002). This task is thought to engage executive control mechanisms involved in conflict resolution and maintaining the attentional set (MacLeod & MacDonald, 2000).

Posner (Posner & Dehaene, 1994; Posner et al., 1997) has stressed that the anterior cingulate can act with frontal areas to create intent or anticipation for the next moment. Connections between the cingulate and the hippocampus allow the hippocampus to be primed by these intentions. The hippocampus also receives information about what actually happened and relays this back to the cingulate via the fornix. In a sense the hippocampus is making a comparison between what was anticipated and what occurred. Gray (Gray, 2003) argues that the hippocampal-theta rhythm (4-8Hz oscillations in the EEG, see sections 2.2.2 and 3.1.3) may be a psychophysiological index of this comparison process taking place.

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[1] The task typically involves naming the colour of the ink of a word. The incongruent aspect occurs when the word represents a different colour to that of the ink (e.g RED).

1.2.2 Attention and Working Memory

It has been proposed by at least one commentator in the field (McCrone, 1999) that attention and working memory are two subsets of a larger and perhaps more integrated process than is often portrayed. Namely, that they are both anticipatory mechanisms in the sense of making 'information' available and priming the brain in order facilitate appropriate behaviour based on a constant stream of up-dated information. This is based on ideas arising from both psychology (Gregory, 1970; Gregory, 1980; Gregory, 1997) and philosophy (Dennett, 1997) that state that in effect the brain is a hypothesis-making machine. Knowledge in the sense of experience built up both over an individual lifetime (ontogenesis) and during the course of evolution (phylogenesis) allows predictions to be made about the nature of the current environment and also of likely outcomes of behaviour. Working memory and attention are the two main mechanisms that facilitate this process and allow it to be constantly up-dated. Perhaps a more convenient umbrella term for this process would be 'working attention' (Baddeley, 1993).

1.3 SUMMARY AND COMMENTS

The work summarised in this chapter suggests the following:

- The brain processes described by the term 'attention' are multi-faceted and involve many different cortical and sub-cortical areas.
- It is useful to make the distinction between sources of attention (i.e. those networks purely involved with attention and its control) and sites of

attentional expression (those networks enhanced by attention but also involved with primary perceptual processes regardless of the focus of attention).

- The thalamus is regarded as being particularly important as a means of the gating and regulating information flow to and between the cortex.
- Posner and others (Posner, 1995; Posner et al., 1994; Posner et al., 1997) have emphasised the importance of three processes underlying attention: *arousal*, involving the maintenance of an alert state; *orienting*, comprising of three further sub-processes – disengagement, attentional shift - filtering input; and *executive control* of the immediate behavioural and adaptive needs of the organism involving a balance of the specific bottom-up and top-down processing requirements at hand. Frontal and pre-frontal cortices as well as the anterior cingulate are thought to be intimately involved with executive control.
- Orienting has also been described in terms of the Orientation Response. This process underlies the automatic, fast and appropriate response to unexpected or salient stimuli. Brain areas of note include the brainstem, the nucleus accumbens, and emotional centres such as the amygdala.
- The distinction between working memory and attention is often a blurred one. It has been suggested that the brain is in one sense a 'prediction making mechanism' and that such prediction is based on the experience built up both over an individual lifetime and during the course of evolution. In this sense, working memory and attention are both types of anticipatory processes, the former being more precise in its priming capabilities than the latter

(McCrone, 1999). It has been suggested that perhaps a more convenient umbrella term may be 'working attention' (Baddeley, 1993).

The above evidence suggests then, that attention is not a simple, one-site mechanism. Additionally, there is increasing evidence that suggests a continuous, reiterative, multi-faceted process. Indeed, many researchers are now exploring not only the intrinsic complexity of the brain's mechanisms, but also its apparent dynamic properties (e.g. Edelman & Tononi, 2000; Friston, 1995; Kelso, 1995). Such approaches tend to stress the non-linear, self-organising characteristics of the brain itself. With this point of view, the brain is constantly evolving and re-evolving its next state and the mechanisms underlying attention play a large part in shaping this evolution. The system is in a state of continuous reciprocal causation, where each part of the system is continuously affecting and being affected by the other parts (Wheeler, 1998). It is proposed that this is facilitated by the vast array of feedback loops within the brain e.g. thalamo-cortical, cortico-thalamic, cortico-cortical, hippocampo-cortical et cetera. Several researchers have proposed that resonance of the firing patterns of the neurons involved in these feed-forward and feedback loops may be the sources of the oscillations in the electrical potentials that can be recorded at the scalp as the electroencephalogram (EEG. See section 2.1 on EEG mechanisms). It is these oscillations and their relationship to the processes of attention and whether that relationship changes as a function of the direction of attention that this study aims to address. The following chapter outlines the electro-chemical processes thought to underlie such oscillatory activity and introduces proposals relating to its functional significance.

2 THE EEG

2.1 AN INTRODUCTION TO EEG MECHANISMS

The human electroencephalogram is a measure of the differences in electrical potential between two positions on the head - the recording (or active) site and a reference electrode (Coles & Rugg, 1995). The EEG is regarded as reflecting the summed activity of a large population of cortical pyramidal neurons underlying the active electrode (Martin, 1991). Use of multiple electrode arrays allows a picture to be built up of dynamic brain activity. This activity is thought to be a measure of post-synaptic dentritic potentials (not action potentials) in neuronal populations in parallel orientations to each other and perpendicular to the scalp electrode (Martin, 1991). Thus, EEG activity is generally thought to reflect the activity of neurons in cortical gyri rather than those in the sulci, which because of their orientations are immeasurable at the scalp (see figure 2.1).

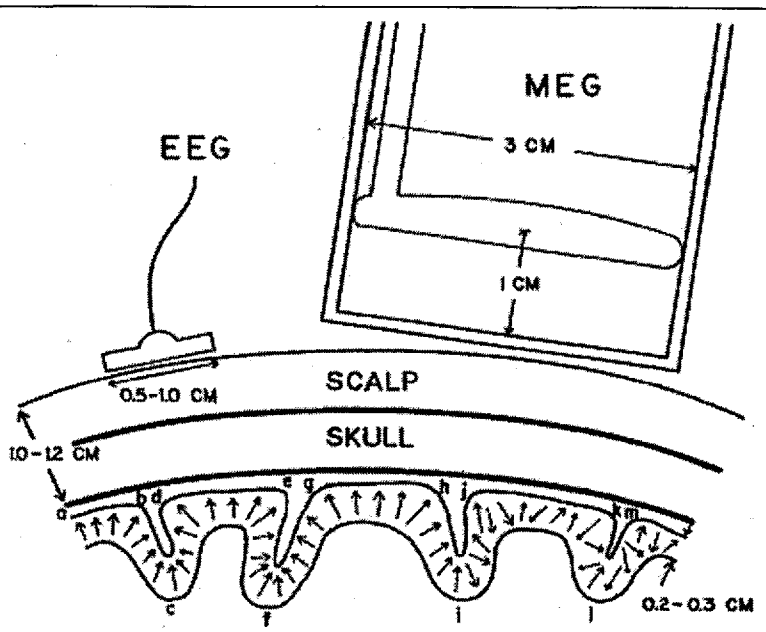


Figure 2.1: Schematic showing orientation of dipoles in cortical sulci and gyri (from Nunez, 1995)

In order to understand this summation of activity it is useful to reflect upon the mechanisms of post-synaptic potentials at the level of a single pyramidal neuron. In effect, ionic flow in and around the neuron creates what can be regarded as an electrical dipole. In the case of excitatory post–synaptic potentials (EPSP's), current flows in (known as the sink) through the post-synaptic ion channels on the dendrites and out (known as the source), at or near the cell body, creating a battery-like circuit (see figure 2.2).

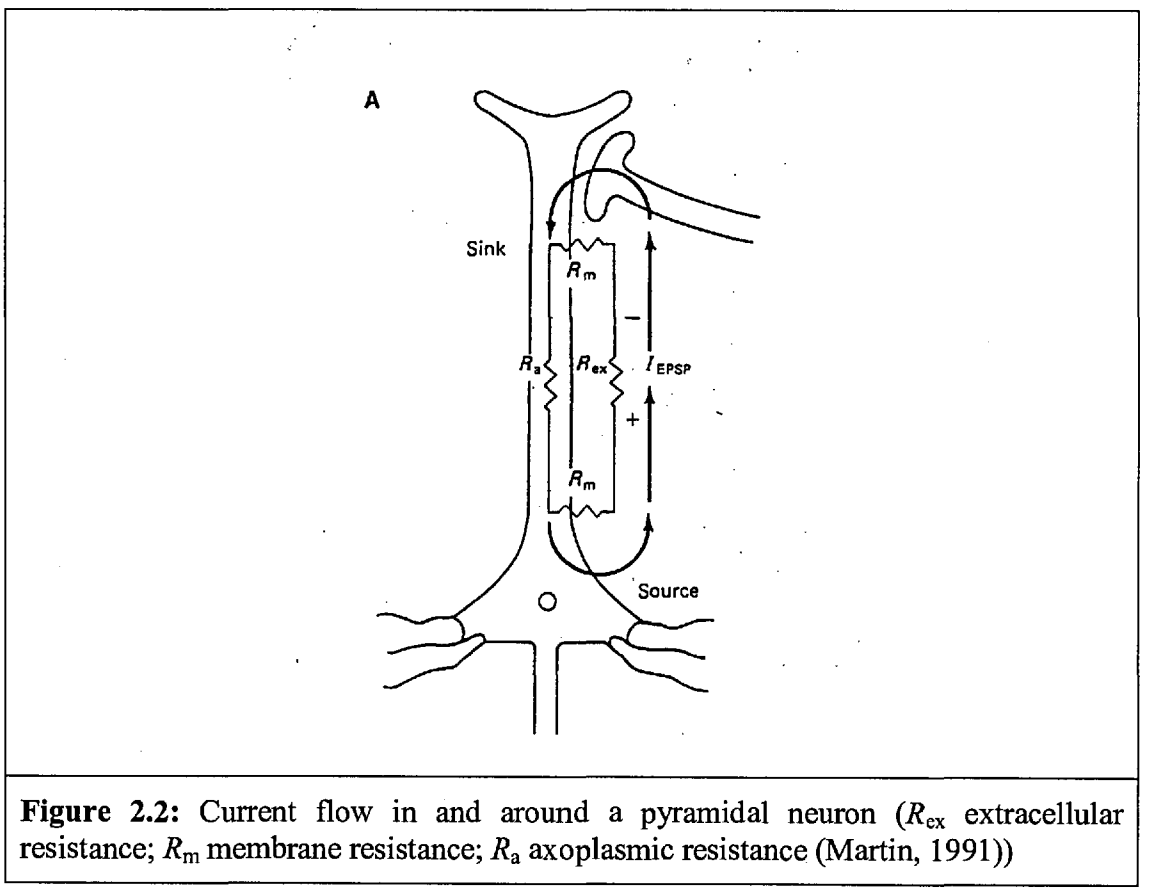


Figure 2.2: Current flow in and around a pyramidal neuron (R_{ex} extracellular resistance; R_m membrane resistance; R_a axoplasmic resistance (Martin, 1991))

In the case of inhibitory post-synaptic potentials (IPSP's) the current flow is opposite, i.e. current flows out at the post-synaptic ion channels on the dentrites and in at the 'trigger zone' - so called because this is where the action potential is

initiated. However, the general scenario is not straight forward and often a combination of excitatory and inhibitory forces will be acting upon a neuron (see figure 2.3). The neuron's output, in terms of action potentials, will result from a summation of these influences. One example of excitatory input is the neurotransmitter acetylcholine (ACh). Release of ACh from the pre-synaptic neuron causes post-synaptic ACh-gated ion channels to open allowing sodium ions to flow through the cell membrane causing it to depolarise (and therefore more likely for summation of potential activity to result in an action potential). An example of inhibitory input is the neurotransmitter gamma-amino butyric acid (GABA). Release of this amino acid opens post-synaptic GABA-gated ion channels making the membrane permeable to chloride ions which act to either keep the membrane polarised (at its resting potential of approximately –70mV) or repolarise it if depolarisation has begun (Bear, Connors, & Paradiso, 1996a).

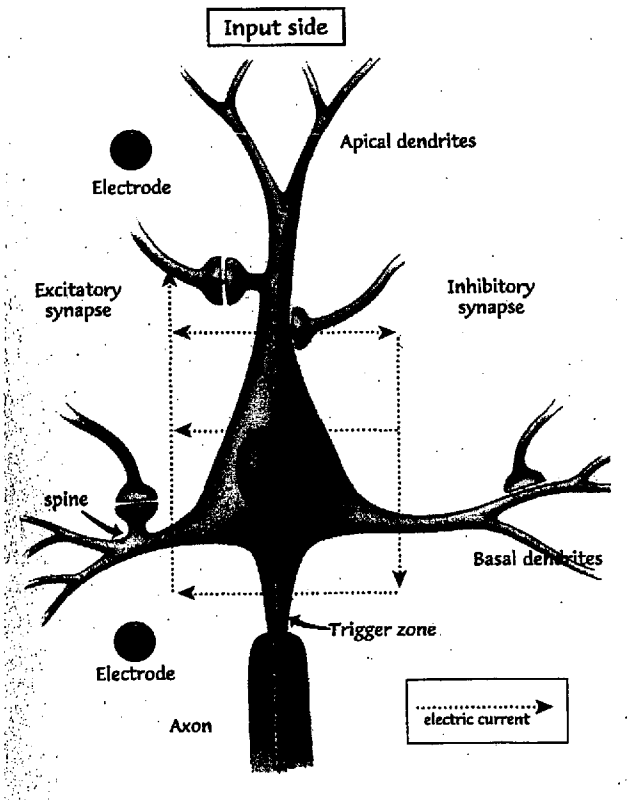


Figure 2.3: Current flows inward at excitatory synapses and outward at inhibitory synapses and vice versa at the 'trigger zone'. The summation of these currents from local populations of neurons emerges as the changes in electrical potential measured at the scalp by EEG (figure from (Freeman, 1999), page 45).

2.1.1 On the Generation of Oscillations

There are two main approaches to understanding the generation of oscillations in the brain. The first, and until recently, the most widely accepted was the notion of 'pacemaker' cells. These are neurons with an intrinsic 'ability' to oscillate at a specific frequency. That is to say, the generation of the current in and around the cell (described above) displays a rhythmicity that is independent of any synaptic transmission. For instance, Jahnsen & Llinas (Jahnsen & Llinas, 1984b; Jahnsen & Llinas, 1984a) found thalamic neurons that oscillate at theta / alpha

frequencies (6-10 Hz) in vitro. The idea is that such cells function to regulate other cells and populations of cells to oscillate in a similar manner – hence the term 'pacemakers'. The analogy has been made that pacemaker neurons act in a way similar to a conductor in an orchestra (Bear, Connors, & Paradiso, 1996b).

The second main approach to understanding oscillatory activity tends to emphasise the connectivity of the neuronal population involved. It has grown out of findings such as those of Steriade and colleagues (Steriade, Deschenes, Domich, & Mulle, 1985) and Freeman (Freeman, 1992) that in vivo, the oscillatory activity of pacemaker cells appears to be dependent on many factors including neuromodulation and input from other local neurons and interneurons (Lopes da Silva & Pfurtscheller, 1999). One simple way in which oscillations may arise is via the interplay between populations of excitatory and inhibitory neurons within a neural group with a background 'propensity' for neural excitation (Freeman, 1999). The model can be pictured as simple circuit, wherein excitatory cells excite the population of inhibitory neurons, who in turn inhibit the excitatory cells. When the excitation to the inhibitory cells 'dies down' (due to the inhibition), the drive to the inhibitory cells to fire is removed and hence the inhibition of the excitatory cells stops. Consequently, given a background propensity for neural excitation (e.g. background noise), the excitatory cells rebound, and the whole process can begin again. As can be seen, the important aspect here is the inter-connectivity, the existence of not only feed-forward links but feed-backward connections too. A schematic representation of the above description using a two-neuron model can be seen in figure 2.4.

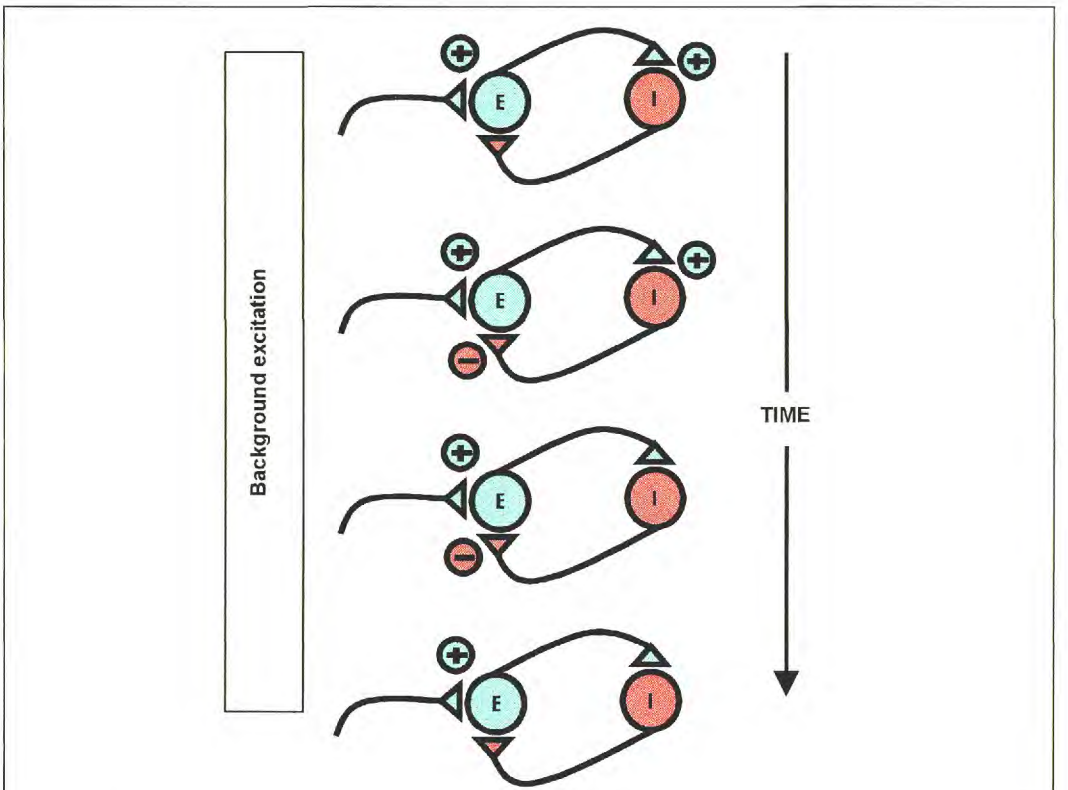


Figure 2.4: A model of a two-neuron oscillator. E = excitatory neuron. I = inhibitory neuron. Excitatory neuron received constant excitatory drive (after Bear et al., 1996b).

The general 'working' consensus is that oscillatory activity results from a combination of both pacemaker and connective, collective activity (Steriade, Gloor, Llinas, Lopes da Silva, & Mesulam, 1990). One important sub-cortical area thought to be particularly important in generating or regulating rhythmic activity is the thalamus (Bear et al., 1996b). As mentioned above, many neurons in the thalamus display intrinsic oscillatory behaviour. In particular the reticular nucleus of the thalamus can generate synchronised activity in the absence of external input (Steriade & Llinas, 1988) and these cells can entrain thalamic relay cells (Sherman et al., 1990). This activity can in turn be relayed to the cortex via various thalamo-cortical connections. The important factor to bear in

mind, whether considering models based upon pacemaker cells driving the system, or the more dynamic approaches, is the connectivity of the system. In order for oscillatory activity to spread, the neural networks involved require reciprocal connections. Such reciprocity facilitates interaction and resonance[2] within the system and in so doing perhaps allows information transfer and interareal communication (see box 2.3 on binding).

2.2 TRADITIONAL APPROACHES TO EEG COMPONENTS

The EEG has traditionally been sub-divided by filtering the raw data by methods such as the fast Fourier transform (FFT – see Box 1) into five main bandwidths: delta, theta, alpha, beta and gamma. These divisions are based on the number of oscillations per second (the frequency, measured in hertz - Hz) that can be recorded by EEG methods on the scalp. The original reason for such categorisation was that electrical oscillations at such frequencies in certain portions of raw EEG traces were apparent to the naked eye during clinical observation. A general rule of thumb regarding the EEG is that (during eyes-open) the lower the frequency of the component the greater the amplitude (or power).

[2] The "effect of oscillating in phase so that scattered elements may work together as one in an amplified fashion" (Llinas, 2001).

Box 2.1: ***The Fourier Transform***

J.B. Fourier (1768-1830) was a French mathematician who discovered that functions of variables – for instance, a periodic waveform, can be analysed as a series of sine and cosine waves which sum to the original waveform (Brigham, 1988; Lynn, 1989). The Fourier transform facilitates the identification of the various frequencies of a particular waveform and their respective amplitudes. Thus, with regard to the EEG, it allows the complex waveform measured at the various scalp electrodes to be decomposed into various 'component' wavebands and their amplitude or power values. The fast Fourier transform is a modification of a discrete Fourier transform that allows the analysis of discrete digital data while at the same time reducing the number of computations necessary (Cooley & Tukey, 1965; Hoffman, 2002).

It should be noted however, that not all scholars of the brain and behaviour are convinced as to the significance of the EEG. It is of course possible that the electroencephalogram as measured at the scalp is at best, a mere epiphenomenon and at worst, noise to be ignored. Or to take a less extreme but perhaps more disheartening view, the EEG may be a real and functional aspect of brain activity but it is far too complex, complicated and intricate for us to understand, given the tools available at present. Nevertheless, much investigation of the EEG has been carried out and findings have proven helpful in the formation of subsequent hypotheses of brain processes and mechanisms. The understanding surrounding the EEG and brain function is constantly evolving, but it may prove useful to this thesis to reflect on traditional views. There now follows an introduction to the proposed role of oscillations (box 2) and an overview of many of the traditional

approaches to understanding the functional significance of the various EEG wavebands.

Box 2.2: ***On the proposed role of oscillations***

Since the early days of EEG recording there has been debate as to whether the fluctuations in electrical potentials that can be measured at the scalp are at best, genuine and useful reflections of cortical activity or at worst, mere epiphenomena. A somewhat more cautious approach has been to endorse study of the EEG by simply allowing the possibility that changes in electrical potentials may be regarded as an index of changes in cortical activation sub-serving various aspects of sensori-motor, cognitive and emotional processing.

However, since the renewed interest in EEG following proposals that 40Hz (gamma) oscillations may serve as a binding mechanism facilitating the formation of percepts from various discrete sensory and memory-related cortical networks or modules (e.g. Basar-Eroglu, Struber, Schurmann, Stadler, & Basar, 1996; Bertrand & Tallon-Baudry, 2000; Engel & Singer, 2001; Freeman & Barrie, 2000; Tallon-Baudry, Bertrand, Delpuech, & Permier, 1997) see Box 2.3 on binding) , a stronger, more direct hypothesis about the nature of EEG is emerging. It is suggested that groups or networks of neurons oscillating at similar frequencies or with common phase characteristics are the basis for functional processing units and for information sharing and transfer between such clusters. The manner in which it is proposed that such processing occurs follows classic Hebbian principles like (Hebb, 1949) – 'cells that fire together, wire together'. This approach can be encapsulated in the following

remark,

"[EEG] oscillatory activity is not an index, it is a mechanism that shapes the selectivity of the system through time-dependent synaptic plasticity" (Tallon-Baudry, 2002).

2.2.1 Delta (0.1 ~ 4Hz)

Slow wave activity in the delta (δ) band is normally only seen in the raw EEG during deep sleep or coma. If present in awake, adult subjects it is often taken to indicate cortical dysfunction or pathology (Walter, 1936). However, its presence in normal healthy awake individuals is revealed by a Fourier transform of the EEG and several possible cognitive functions for δ-waves have been proposed, including attention to internal processes such as mental arithmetic (see section 3.1.2). It should be noted that artefact in the EEG due to contamination by eye movements (as measured by the electrooculargram or EOG) is maximal at delta frequencies and hence, great care should be taken when analysing and interpreting data.

2.2.2 Theta (4 ~ 8Hz)

This frequency band is typically associated with states of drowsiness and low arousal in human adults. It is however, the dominant occipital pattern of activation in children, replaced gradually by alpha activity during brain maturation (Alvarez, Valdez, & Pascual, 1987; John et al., 1980). It is also noted

that theta (θ) activity is dominant during highly relaxed, blissful experience and during meditation for experienced meditators (Aftanas & Golocheikine, 2001). Another, and seemingly contradictory line of thought regarding theta is that of the so-called frontal-midline theta (Fmθ). In various experiments, Fmθ has been observed to be positively associated with memory processing and increased task-difficulty factors (Burgess & Gruzelier, 1997b; John et al., 1980; McEvoy, Pellouchoud, Smith, & Gevins, 2001). The apparent contradiction was originally explained in terms of different classes of cortical inhibition: class 1 (widespread) inhibition related to low psychophysiological arousal and class 2 (local) inhibition serving to 'direct' or focus response systems (Vogel, Broverman, & Klaiber, 1967), see section 3.1.3). More recently, theta activity is becoming increasingly interpreted as an active phenomenon, associated with septo-hippocampal and cingulate mechanisms governing memory and executive functions (Gevins, Smith, McEvoy, & Yu, 1997; Ishii et al., 1999; Kubota et al., 2001).

2.2.3 Alpha (8 ~ 12Hz)

Alpha waves were the first oscillations in electrical potential to be detected at the scalp in humans (hence their name) by Hans Berger (Berger, 1929; Berger, 1930). They are the most easily seen component in the raw EEG, maximal at occipital sites with eyes closed. Traditionally, this posterior activity that desynchronises (or is 'blocked') with eyes opening has been viewed as reflecting the brain in a calm and relaxed state, often referred to as 'cortical idling' (Pfurtscheller, Stancak, Jr., & Neuper, 1996a). It is now increasingly accepted

that there are a whole host of different and discrete alpha oscillations expressed in different parts of the cortex, including the 'mu' rhythm in sensorimotor areas and the 'tau' rhythm in the auditory cortex. It has also been proposed that the traditional broadband definition of alpha (i.e. 8-12Hz) obscures many possible findings by grouping together frequencies that are possibly functionally independent. For instance, Klimesch and colleagues have argued that activity at the lower end of the alpha bandwidth may be associated with attentional factors, whereas those at the upper end may reflect memory processes (Klimesch, 1997; Klimesch, 1999; Klimesch, Doppelmayr, Pachinger, & Ripper, 1997). In an attempt to clarify matters Basar (Basar, Basar-Eroglu, Karakas, & Schurmann, 2000; Basar, Basar-Eroglu, Karakas, & Schurmann, 2001; Basar, Schurmann, Basar-Eroglu, & Karakas, 1997) has introduced the term 'alphas' to emphasise the plurality of activity centred around 10Hz in various cortical regions relating to differing brain functions. The more recent proposals and hypotheses relating to alpha waves will be discussed in greater depth in sections 7.1.1 and 8.3.

2.2.4 Beta (12 ~ 30Hz)

Beta is often subdivided into lower (12-20Hz) and upper (20-30Hz) components. There are many seemingly contradictory proposals regarding the functional significance of the beta band. These range from notions of cortical arousal and engaged attentional mechanisms (Andreassi, 2000) to the near functional equivalence of beta and alpha over central sensorimotor areas, i.e. alpha and beta desynchronisation over contralateral motor areas coincident with movements reflecting activation of those areas (e.g. Berger, 1929; Berger, 1930;

Pfurtscheller, Stancak, Jr., & Neuper, 1996b). Other recent work has found beta activity to be associated with the encoding of novel stimuli, attenuating with habituation (Haenschel, Baldeweg, Croft, Whittington, & Gruzelier, 2000) and with a possible role in medium range interareal cortical communication requisite for certain top-down processes (von Stein et al., 2000b). Latterly, a handful of studies have also hinted at a relationship between beta activity and the semantic aspect of certain working memory processes (Haarmann, Cameron, & Ruchkin, 2003; Vernon et al., 2003).

Mullholland has proposed (Mullholland, 1995) that one reason for some of the conflicting findings regarding beta is due to a problem with terminology. Namely that while many researchers use the term 'beta' to refer to synchronous activity in a specific bandwidth (e.g. 12 – 30Hz) others (particularly in less recent times) have applied it to a more general wide-band desynchronisation in the EEG. The latter is particularly true of clinical EEG with its traditional reliance on visual inspection of the data. The use of the term 'beta' in the four experiments reported in this thesis will only be used to refer to activity relating to the first of these definitions, i.e. oscillations in the 12-30 Hz bandwidth.

2.2.5 Gamma (30 ~ 80Hz)

Gamma is a term generally used to refer to EEG activity around 40Hz, but can be extended to include fast oscillations up to 80Hz or more. It is commonly measured in response to sensory stimuli. It is the bandwidth regarded by many as being responsible for the renaissance in the study of electroencephalographic

measures that occurred throughout the 1990s. This was due, in no small part, to a set of papers many of which were published in the late 1980s proposing that gamma activity may serve to fulfil the (long sought after) role of a binding mechanism for perceptual processing (e.g. Basar-Eroglu et al., 1996; Bertrand et al., 2000; Engel et al., 2001; Freeman et al., 2000; Tallon-Baudry et al., 1997). See Box 2.3 – The Binding Problem). The interest in gamma was further enhanced by Crick & Koch's proposal that gamma should be investigated as a possible contender as a neural correlate of consciousness (NCC - Crick & Koch, 1992). More recently, the excitement surrounding gamma as a NCC has subsided somewhat. This has been due to various reasons including findings of gamma activity during almost all types of cognitive and sensory processes (e.g. Basar, 1999) and also in no small degree to the problems associated with making inferences of functional significance and operational necessity from correlational relationships. However, the study of gamma oscillations is a vibrant field and the part played by gamma in sensory and cognitive processing, particularly in the formation of percepts is increasingly being investigated.

Box 2.3: ***The Binding Problem***

At one level, the binding problem relates to the question of how is it possible for the brain to 'build' percepts out of the sensory information it receives given that this information is thought to be processed initially in modular form. For instance, with regard to vision, it is widely accepted that there are "four parallel systems concerned with different attributes of vision – one for motion, one for colour and two for form" (Zeki, 1993, page 47). Thus, how does the activity of these discrete modules become integrated in the brain in order to construct the coherent experience of seeing an object rather than a collection of constituent properties?

There is also a higher order version of the binding problem that refers to how a conscious, first-person, subjective experience is generated out of all the information available to the brain. How for instance, an adaptive balance is achieved between immediate factors such as visual, acoustic, haptic, olfactory, gustatory and proprioceptive information and the experience-related biases of memory and emotion.

2.3 SUMMARY

The EEG as measured by scalp electrodes is a reflection of post-synaptic activity from large populations of cortical pyramidal cells. Despite suggestions that such activity is an epiphenomenon, and that the EEG may be just noise, much work has been carried out that appears to ascribe a functionally significant role to its sub-components in various cognitive processes. However, there is as yet no

consistent consensus of opinion as to the specific functional significance of the various oscillatory activities observable in the EEG. Misunderstandings arise thanks to differences in the methodologies employed. In particular, the clinical division of the EEG, based on visual inspection of the raw data is not always readily compatible with qEEG analysis derived from fast Fourier transforms. Also, different hypothetical starting points can led researchers to interpret EEG activity in differing ways. One such hypothesis that involves a different interpretation of various components to traditional views, especially those surrounding the alpha band, is the intake-rejection hypothesis. It is this approach that is examined in the following chapter.

3 THE INTAKE-REJECTION HYPOTHESIS

3.1 BACKGROUND

The intake-rejection (I-R) hypothesis was originally championed by Lacey and colleagues (Lacey, 1967; Lacey et al., 1970). It emphasises the need to differentiate between sensory "intake" processes, such as those evoked during exogenous visual attention tasks, and non-sensory "rejection" processes, such as those elicited during pure mathematical calculation, mental imagery, working memory tasks and ideation in general. It was argued that in order to successfully carry out such internal tasks, one would need to filter out incoming sensory information, to inhibit the processing of external, environmental stimuli. Hence the rejection aspect of the model – the rejection of sensory information. The intake aspect being the taking in of sensory stimuli.

It has been proposed that the physiological mechanisms behind the I-R model influences and is influenced by cardiovascular activity. Studies have shown that sensory intake tasks are associated with a decrease in heart rate (HR), whereas, rejection tasks (e.g. mental arithmetic) are accompanied by an increase in HR (Cole & Ray, 1985; McCarthy, Ray, & Foa, 1995b). Lacey (Lacey, 1967; Lacey et al., 1963) proposed that a decrease in HR enhances sensory processing. Conversely, an increase in HR will serve to inhibit such processing, resulting in reduced sensory information intake. It is proposed that such a mechanism is mediated by baroreceptor activity (the baroreflex) in the carotid sinus (Andreassi,

2000). The means by which such mediation takes place is briefly outlined in Box 3.1.

Box 3.1: ***The Baroreflex***

Baroreceptors in the carotid artery form part of a feedback mechanism that influences heart rate and blood pressure in the following way: increases in blood pressure distend the baroreceptor initiating an increase in firing rate. These nerve impulses travel to the nucleus of the tractus solitarius (NTS) in the medulla via the sinus and glossopharyngeal nerves. This inhibits sympathetic nerve impulses to the peripheral blood vessels causing vasodilation and a lowering of blood pressure (Berne & Levy, 1998). It has also been observed in animal models that distension of the carotid baroreceptors elicits a progressive reduction in fast cortical activity and an increase in slow wave activity (Bonvallet, 1954). Furthermore, with regard to the intake-rejection hypothesis, it has been proposed that baroreceptor activity stimulates thalamocortical resonance activity in the alpha range which interferes with the processing of sensory information, hence inhibiting sensory-intake tasks (Wolk & Velden, 1987).

Other theoretical works pertaining to notions of intake-rejection have sporadically surfaced. Karl Pribram (Pribram, 1981) introduced the idea of internal and external controls of behaviour and information processing. In his hypothesis, anterior cortex is associated with internal control and inhibition of

distracting environmental stimuli (in other words "rejection"). Conversely, posterior cortical areas are associated with maximising informational input from the external environment (i.e. "intake"). These ideas, in keeping with basic physiology, have been expounded upon more recently by Kok (Kok, 1990). Using his battery of findings from event-related potential research (ERP), Kok suggests that changes in amplitude in various ERP components to some degree reflect differences between these two different controls (or modes) of information processing. External control factors are associated with general thalamic disinhibition facilitating sensory input to posterior cortical areas, with the orienting response and with increased positivity of such ERP components as the P300 (the positive deflection in the averaged electrical potential occurring around 300ms after a stimlulus) at posterior sites. Internal control is associated with discrete inhibition of the thalamic nuclei resulting in selective suppression of 'distracting' environmental events/stimuli and with increased negativity of ERP components at frontal and central electrodes. Kok postulates that both systems act together to control thalamic gating and that multiple cortical networks are involved in their regulation.

In order to examine the findings pertaining to intake-rejection studies in a systematic manner, there now follows a breakdown of the literature according to EEG band.

3.1.2 The Intake-Rejection Hypothesis & Delta

Harmony *et al* (Harmony et al., 1996b; Harmony et al., 1999) proposed that delta activity might index inhibitory mechanisms underlying internal attention. In two experiments they found that delta power was positively related to internally directed attention and task difficulty. The internal versus external attention effects (experiment 1) were elicited using a mathematical task e.g. (24+39)/9 versus a visually balanced control stimulus, e.g. (&&+&&)/&. The difficulty effects (experiment 2) were observed during a version of the Sternberg short-term memory paradigm (Sternberg, 1966) – easy (3 digit memory set) versus hard (5 digit memory set).

Harmony and colleagues based their rationale on ideas put forward by Vogel *et al* (Vogel et al., 1967) that the brain expresses (in the form of slow waves in the EEG) two kinds of behavioural inhibition:

Class I: "Gross inactivation of an entire excitatory process, resulting in a relaxed, less active state, as in sleep"

Class II: Selective suppression of "inappropriate or non-relevant neural activity during the performance of a mental task" (page 161).

This led them to propose the possibility that internal tasks activate the corticofugal pathway leading to inhibition of thalamocortical networks resulting in "functional disconnection of the cortex from environmental stimuli" (Harmony et al., 1996b, page 169). However, it should be noted that all the

experimental tasks described above involve to some extent externally directed attention in the form of visual processing. It is possible that the increases in delta in experiment 1 reflect either semantic differences in task, i.e. mathematically meaningful versus non-sense characters or even more fundamentally, "do something" versus "do nothing" in the cognitive sense apart from initial visual processing.

3.1.3 The Intake-Rejection Hypothesis & Theta

Although not directly related to the intake-rejection hypothesis of the Laceys it is useful to explore more the work of Vogel *et al* regarding class I and II inhibition mentioned above (Vogel et al., 1967). This is because it was contemporary with much of the work concerning I-R and came from a similar theoretical background (e.g. Darrow, 1947; Darrow, 1957). Vogel *et al*'s findings pertain to both slow waves (less than 7 Hz) and alpha waves, but for utilitarian reasons will be included in the theta section as it has been with theta activity that these ideas have subsequently been commonly associated (e.g. Graffin, Ray, & Lundy, 1995; Sabourin, Cutcomb, Crawford, & Pribram, 1990).

The aim of the 1967 study was to investigate links between the EEG and one particular facet of IQ – the Automatization Cognitive Style. This style was defined as the ability (strong or weak) to perform simple repetitive tasks in relation to their general IQ level. In two experiments, three conditions were measured: rest, simple subtractions and difficult subtractions. In experiment 1, automatization was related to increased performance on the difficult task and

inversely related to beta power and frequency. Efficient performance on simple subtractions was related to slow alpha frequencies. In experiment 2, automatization was related to increased performance on the difficult task and slow wave activity (< 7Hz), and contrary to the first experiment, beta frequency. It was inversely associated with alpha frequency and beta power during difficult tasks. Efficient performance on difficult subtractions was related to slow wave activity and slow alpha frequencies.

As a consequence of these findings, Vogel at al introduced the notion of class I and II inhibition as an attempt to explain their findings (see I-R & Delta above). They argue that class II (or selective) inhibition can be regarded as accompanying automatic and well rehearsed behaviours and are indicative of increased mental efficiency. This they argue allows them to explain not only their own findings but also those of Mundy-Castle (Mundy-Castle, 1951) and Arellano & Schwabb (Arellano & Schwab, 1950) who published findings of associations between 'mental effort' and slow wave activity. This paper has spawned many citations over the years, however, certain caveats should be taken into account: Firstly, the robustness of the relationship between automatization and slow waves is questionable given that it was only directly observed in the second experiment. Secondly, implicit, naïve inferences between efficient performance on tasks (especially difficult ones) and overall intelligence should not be made. Indeed, it was found that those with the highest IQ were the worst automatizers and vice versa. Given that Vogel and colleagues equate automatization with mental efficiency one needs to bear in mind the specificity

with which they intended this term to be understood (i.e. in the context of habituation and non-conscious processing).

Theta oscillations have also been implicated in internally focused attentional states such as meditation. For instance, Aftanas and Golocheikine (Aftanas et al., 2001) report not only increases in frontal and midline theta power during meditation but also increases in coherences between prefrontal and posterior association cortex (thought to index communication between these areas) in the theta bandwidth. These findings are compatible with many studies that relate specific theta activity at frontal midline sites to various effortful cognitive activities. This activity has been dubbed 'frontal mid-line theta (Fmθ); see box 3.2 below.

Box 3.2: ***Frontal midline Theta (fM θ)***

Frontal midline Theta is the term given to EEG activity in approximately the 4 – 8 Hz range and located over midline, anterior sites (i.e. centred around electrode Fz). The first major study in this area was carried out in 1950 by Arellano & Schwab (Arellano et al., 1950). They found an increase in activity in the theta at midline sites just anterior to Cz during problem solving tasks. Further studies later that decade reported similar findings (e.g. Mundy-Castle, 1951) but it was not until the early 1970s that the expression 'frontal midline theta' was coined (Ishihara & Yoshi, 1972). It has been proposed that Fmθ may reflect medial pre-frontal attention and working memory networks, particularly involving the anterior cingulate cortex (e.g. Gevins et al., 1997;

Ishii et al., 1999; Kubota et al., 2001; Rippon, Burgess, Singh, & Barnes, 2002). The findings of theta generation in the hippocampus and this area's proposed role in memory encoding and retrieval (e.g. Treves & Rolls, 1994) has led to the intriguing possibility that medial temporal activity may also be related in some way with the role of Fmθ in memory processes (Burgess & Gruzelier, 2000). Fmθ has also been observed during REM sleep and has been associated with the mental activity associated with dreaming (see Inanaga for a review - Inanaga, 1998).

3.1.4 The Intake-Rejection Hypothesis & Alpha

In the mid-1980s, Ray & Cole (Cole et al., 1985; Ray & Cole, 1985a; Ray & Cole, 1985b) set out to test the intake-rejection hypothesis using EEG techniques and thus to test the proposal that alpha power might index inhibition necessary for successful internal processing. In two studies they used the following tasks:

a) External attention – counting verbs in a text, finding errors in arithmetical problems; picking the correct 3D object embodying a 2D plan, mooney faces, looking at emotionally valient pictures (e.g. landscapes, happy or sad faces, accident scenes).

b) Internal attention – mental arithmetic, creating phrases beginning with a certain letter, mental rotation, visualisation, imagining or recalling pleasant and unpleasant events from the subject's past or future.

Results revealed that alpha power was greater during internally directed attention. It was observed that this effect was greater at temporal and posterior sites in the right hemisphere. It should be noted that only four electrodes (F3, F4, P3, P4) were used in one experiment and six (F3, F4, T3, T4, P3, P4) in the other, thus a full topographical analysis was not available to the researchers. As far as heart rate measures are concerned, they too were consistent with the intake-rejection hypothesis, being that HR was faster for internal attention than for external attention tasks.

Ray and colleagues further replicated both the EEG alpha and HR findings in normal low anxiety subjects but not in high anxiety subjects or patients with obsessive compulsive disorder (OCD) (McCarthy, Ray, & Foa, 1995a). This was contrary to their hypothesis regarding OCD where they expected intake-rejection differences to be enhanced for patients due to a proposal that OC'c attentional style is biased in favour of environmental rejection. However, such a bias was observed by Grillon & Buchsbaum working with patients with generalised anxiety disorder (GAD. Grillon & Buchsbaum, 1987). They observed less alpha desynchronisation and indeed some alpha synchronisation in response to photic stimulation in GAD patients compared to normals. They interpret this as revealing that people with GAD attend less to external stimuli due to competition from internal interference.

Many researchers have reported similar findings to Ray & Cole. Schupp *et al* (Schupp, Lutzenberger, Birbaumer, Miltner, & Braun, 1994) investigated both a visual (watching versus imagining watching a swinging pendulum) and a tactile

task (feeling versus imagining feeling a rubber 'coshball'). They found alpha power to be greater during mental imagery as opposed to sensory tasks and that this effect was greater at parietal sites. Electrodes over occipital areas were not employed during this experiment and so potential imagery effects at these sites were not observable. Klinger *et al* (Klinger, Gregoire, & Barta, 1973), also observed that imagination was associated with increased alpha. And working in the early 1970s Bremner and colleagues found in a series of EEG biofeedback experiments that subjects could produce alpha waves 'to order' using various mental imagery techniques (Bremner & Moritz, 1972a; Bremner, Moritz, & Benignus, 1972b).

An association has also been observed between higher average alpha amplitude for high scorers in a mental rotation test compared with low scorers (Williams, Rippon, Stone, & Annett, 1995). In the same article but from a different experiment, Williams and colleagues also observed differences between good and poor imagers (i.e. those who procured high or low scores on a vividness of movement-imagery questionnaire). Good imagers had higher alpha amplitudes than poor imagers at various electrode sites (F3, Fz, F4, F7, F8, PO1, Pz & O2). They also reported a decrease in alpha amplitudes during the act of mental rotation compared to baseline levels. Given that mental rotation is traditionally regarded as a mental imagery task, this finding would appear to be contrary to intake-rejection expectations. However, mental rotation tasks involve a variety of mental processes including (external) attention to the stimulus to be transformed. Thus one would expect results to vary according to the individual cognitive bias of the subject and the level of complexity of the tasks employed.

It is perhaps for these reasons that conflicting findings for mental rotation and alpha have been reported over the years.

More recent support for an up-dated version of the I-R hypothesis has emerged from Russia. These studies have emphasised the proposed inhibitory nature of alpha oscillations and their role in internal attention. One investigation by Aftanas & Golocheikine involved the study of long-term and short-term meditators in and out of a meditative state (Aftanas et al., 2001). They found that frequencies at the low end of the alpha band increased at frontal sites for long-term meditators during meditation and that this alpha synchronisation correlated positively with subjective reports of quiet, internally focused attention. It is interesting to note that they also found measures of EEG complexity (thought to reflect the number of neural assemblies involved in a task) to be negatively correlated with alpha (Aftanas & Golocheikine, 2002). These results led Aftanas & Golocheikine to conclude that alpha activity is involved in the 'switching off' of external attention mechanisms facilitating the internal focus of attention necessary during meditation.

A study by Stroganova *et al* (Stroganova, Orekhova, & Posikera, 1998), carried out on infants (8-12 months) presents a slightly different perspective of internal and external attention in that it emphasises the differences between external control of attention (ECA) and internal control of attention (ICA). ECA is exogenous attention by another name, in that it is related to attentional capture by external environmental stimuli. ICA is governed by task demands and 'internal cognitive schemata' and is therefore an endogenous process. Another way of

viewing these different cognitive states is to think of them in terms of the amount of bottom-up (i.e. stimulus driven – see Gibson - Gibson, 1950; Gibson, 1966; Gibson, 1979 for a prime example of bottom-up theories of cognition) or top-down processing involved (i.e. under the control of some form of supervisory attention system – e.g. Baddeley, 1990. See Gregory, 1970; Gregory, 1997 for an account of top-down hypotheses). This notion of the balance of top-down versus bottom-up processing requirements will be examined in more depth in box 6.1.

The tasks employed in the Stroganova study were as follows: ECA was metered when the infant was watching an adult blowing soap bubbles; ICA was measured during anticipatory phase of a 'peek-a-boo' game (i.e. during that period when the adult was hiding from the infant and the child was 'awaiting' her return. Orekhova and colleagues observed that infants with longer 'anticipatory attention spans' had greater alpha synchronisation than those with short attention spans. As a result, they proposed that alpha synchronisation reflects inhibition of irrelevant visual stimuli while awaiting the return of the adult in the peek-a-boo game.

From these points of view, it can be argued that alpha activity is not indexing an idling brain; rather it is a measure of the active processing necessary for internally directed or controlled mental operations. A different but somewhat compatible theory regarding alpha and other slow components of the EEG (in this instance, theta and low beta) has been proposed by Mullholland (Mullholland, 1995). Mullholland sees the EEG as measure of cortical work and

that most of this work is related to cortical control of movement, balance, posture et cetera. In what appears at first to being an analogue of the alpha-as-idling hypothesis, Mullholland argues that alpha, theta and low beta reflect a lack of such work – what he terms 'behavioural stillness'. However, in terms that are of more accordance with Ray & Cole (Cole et al., 1985; Ray et al., 1985a; Ray et al., 1985b) he goes on to say,

> "Behavioural stillness can then be associated with an increased awareness of thoughts, feelings and memories. Conversely, active, complex behaviours which are not well-practiced, not routine, do not favour reverie, meditation, relaxed wakefulness, quiet thinking, imagery, remembering or other complex, intelligent cognitions".

Mullholland's ideas introduce the idea of alpha activity being associated with memory mechanisms. Much work has been carried out in this area. For example, Klimesch *et al* (Klimesch, Schimke, Ladurner, & Pfurtscheller, 1990) found that participants who did well in memory tests had higher average alpha frequencies than those who did poorly. The association between alpha activity and memory mechanisms will be explored more thoroughly in sections 7.1 and 8.3.

3.1.4.1 Contradictory Alpha Findings

Not all studies that have investigated the intake-rejection hypothesis have produced findings that are compatible with those of Ray & Cole (Cole et al.,

1985; Ray et al., 1985a; Ray et al., 1985b) (See section 3.1.4). Valentino & Dufresne (Valentino & Dufresne, 1991) sought to examine the intake-rejection hypothesis in the auditory modality. They employed three tasks: 1) Rest; 2) Intake – an auditory continuous performance task (CPT). Letters of the alphabet were acoustically presented. The task was to lightly tap one's finger if there were two the same in a row; 3) Rejection – recite the alphabet backwards. The findings were that alpha was greater in the intake than in the rejection tasks, in direct opposition to the Ray & Cole results. However, it must be noted that not only were the tasks not balanced in terms of stimlui but also there was a major inconsistency with regard to response requirements. Namely, that the intake task required a motor response and the rejection task involved linguistic processes including speech production. It is possible that it is these differences that were reflected in the results rather than the experimental factors themselves.

Another more recent study that did not find a positive relationship between alpha power and internally directed attention was Harmony *et al* (Harmony et al., 1996a) (see section 3.1.2). Harmony reported a lowering of alpha power in both internal and external experimental conditions. There may be some question however, regarding the mixing-up of the intake and rejectional aspects of the tasks, i.e. there was still externally directed, visual processing during the mental calculation tasks. This could therefore account for the alpha findings without detracting from the delta findings which it is argued is also related to task complexity, not just direction of attention.

3.1.5 The Intake-Rejection Hypothesis & Beta

Although frequencies in the beta band have been included in studies addressing the I-R hypothesis, there appears little evidence to suggest their involvement in the differentiation of direction of attention. Instead, Ray & Cole (Ray et al., 1985b) have argued that changes in beta power reflect both cognitive and emotional demands of the task. During spatial-synthetic versus verbal-analytic tasks they found greater differences in beta activity between the hemispheres during verbal tasks. With regard to emotion they observed increased beta activity during positive as opposed to negative tasks and that this effect was greater over right temporal areas.

3.1.6 The Intake-Rejection Hypothesis & Gamma

There have been no reports of a relation between gamma oscillations and the intake-rejection hypothesis. Despite this, for reasons of completeness, the measurement of gamma oscillations has been included in the experiments reported in this study.

3.2 Rationale for Experiment 1

The findings reviewed in the previous sections constitute an interesting avenue of research that has been neglected by the main stream of EEG research despite, or perhaps because of, its implications for traditional approaches. It is important therefore, that this omission be addressed. A fuller, more accurate understanding

of the functional significance of the various EEG frequency components is warranted not just for theoretical reasons but also because of its practical and clinical implications.

Similarly, a more holistic understanding of the factors influencing and controlling attention will be of use not only to those interested in understanding brain mechanisms per se but also to those attempting to treat conditions that are characterised by disturbances in attentional processing, such as schizophrenia and attention deficit disorder.

With these factors in mind, a protocol was devised that sought to differentiate between brain states characterised by attention to external stimuli and those characterised by attention to internally generated stimuli. This protocol and the results pertaining to it are described in the following chapter.

4 EXPERIMENT 1

4.1 INTRODUCTION

This experiment was carried out in order to investigate findings reported in chapter three, that various EEG measures appear to index a differentiation of attention in terms of its directional focus. Specifically, that slow components of the EEG reflect attention to internally directed processes. In order to facilitate this aim, a comparative protocol was developed contrasting an auditory continuous performance task (externally directed attention) against mental arithmetic (internally directed attention).

The work of Harmony et al (Harmony et al., 1996b) proposing a relation between delta, internal processing and task difficulty and the various observations of frontal theta (see sections 3.1.2/3) led to hypotheses 1 and 2:

1. Delta and theta power will be greater during mathematical internal attention tasks as opposed to auditory external attention.
2. Delta and theta power will increase as a function of task difficulty.

The third hypothesis was derived from the work of Ray & Cole (Ray et al., 1985b; Ray et al., 1985a) and others, who found an increase in alpha activity coincident with rejection of sensory input:

3. Alpha power will be greater during mathematical internal attention tasks as opposed to auditory external attention.

4.2 METHOD

4.2.1 Subjects

12 participants (6 male & 6 female) were tested, ages ranged from 27 to 48 years (mean: 34.4). All participants reported normal hearing, normal or corrected to normal vision and no known psychiatric or neurological problems. Participants gave written informed consent and were paid GB£15 for taking part. Ethics Committee approval was granted for this study.

4.2.2 EEG Recording

The participants were fitted with an electrode-cap containing 28 electrodes, arranged according to the international 10-20 system plus eight additional electrodes: FTC1, FTC2, TCP1, TCP2, CP1, CP2, PO1 and PO2 (see figure 4.1 for electrode configuration). Four facial electrodes were employed to measure eye movements from which horizontal, vertical and radial electrooculographs (EOG's) were derived. These were positioned at the left (E5) and right (E6) outer canthi and approximately 2cm above and below the left eye (E1 and E3 respectively).

EEG was recorded relative to the left ear and re-referenced off-line to linked ears (see box 4.1 on the reference issue). Data were digitised at 500Hz with a bandpass of 0.1 – 200Hz (24dB/octave roll-off). All data were recorded and processed using a SynAmps amplifier and Neuroscan 4.1.1 software.

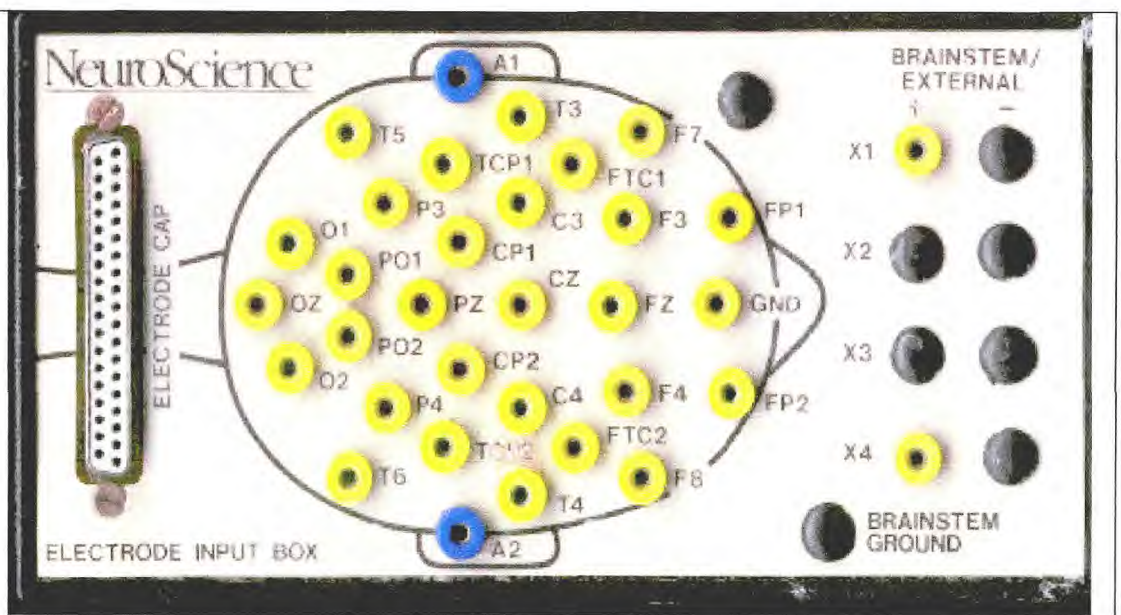


Figure 4.1: Impedance meter showing schematic lay-out of electrode placements

Box 4.1: ***The Reference Issue***

A major problem when interpreting EEG activity is that the measure one is examining is the difference in electrical potential between two points (e.g. an 'active' and an reference electrode) and not just the activity of interest at the target electrode (Nunez, 1981). Thus it is impossible to infer whether the measure one is observing is the result of activity underlying the target electrode, or reflects some combination of measures from both electrodes. It follows then, that moving one's reference site will

result in different values being recorded. Optimally, one requires a reference electrode with as little EEG activity at that site as possible or whose activity can be taken into account and subtracted from the active measure. Various sites have been tested including the nose, ear lobes (both singular and linked), mastoids, vertex, common average reference (the average activity at all electrode sites) etc. However there is little consensus as to the best solution.

Measuring from a single lateralised site (e.g. left ear lobe) has the problematic effect of biasing the measure towards the activity in one hemisphere. However, recording from linked ears or mastoids creates a short circuit across the head due to leakage and so despite its popularity is also problematic (Nunez, 1981). Using a *central vertex reference* appears a solution to hemispheric imbalance however, when phase differences between sites are taken into account, distortions of power asymmetry still occur (Hagemann, Naumann, & Thayer, 2001). The *common average reference* (i.e. the potential difference between the target electrode and the average of the total electrodes) has some advantages but is has two main reported limitations (Hagemann et al., 2001): firstly it drawn from models that assume that the head is a concentric spherical structure (Bertrand, Perrin, & Pernier, 1985). Secondly, in this model, an 'ideal' reference would be the average of the entire integrated surface area of the scalp, but in practice this is not feasible as one would need large numbers of electrodes. However, this model does appear to work well when using a 10-20 (or adapted) set-up and been widely used. Nevertheless, there is another problem associated with this approach; this method appears to 'exaggerate' alpha activity at frontal sites (Hagemann et al., 2001). Therefore, as the present study is interested in alpha activity at all locations, in both hemispheres and given a 28-electrode set-up, the

afore mentioned methods were not employed for this analysis.

Another method that has been suggested as a feasible solution to the reference problem is the *current source density* approach (CSD). In short, this method aims to calculate the current flow into and out of the scalp at electrode sites using a weighted average of potential differences between the target electrode and a selection of its neighbouring electrodes. It has been found to be a robust method (Hagemann et al., 2001) but with some limitations. The most problematic being the possible inaccuracy of estimates of electrode potentials at peripheral sites (i.e. those not surrounded by other electrodes) and also CSD produces very small power measures, leading to potential difficulties with small signal-to-noise ratios. Obviously, the smaller the signal-to-noise ratio, the less chance there is of 'noticing' task-related electrical activity.

The reference method chosen for this study was that of re-referencing off-line (i.e. after recording) to the average of the two ears – *the computational linked-ear reference* ((A1 + A2) / 2). It has been argued that this method provides an idealistic "virtual reference site in the middle of the head" (Miller, Lutzenberger, & Elbert, 1991) without the problems of distortion associated with recording with a linked-ears reference. This distortion is often due to asymmetric impedances at A1 and A2. The computational linked-ear reference is the current standard model particularly in use in research centred on hemispheric asymmetries which are specifically affected by problems associated with the reference issue.

4.2.3 Protocols

4.2.3.1 Eye movement calibration

Prior to testing the participants carried out an electro-oculogram (EOG) calibration paradigm. This was to facilitate the off-line removal of eye-movement artefact in the EEG. The paradigm required the participant to sit in front of a 12" computer monitor at a distance of approximately 40cm. They were presented with written instructions on the screen to follow a rectangular shape (2.5cm x 1.5cm) as it moved around the screen. This allowed the measurement of vertical, horizontal and radial eye-movements (VEOG, HEOG and REOG respectively). The rectangle moved from the middle of the top of the screen to the bottom (and vice versa) and from the middle of the left of the screen to the right (and vice versa). Stimulus presentation lasted 0.8s with an inter-stimulus interval (ISI) of 0.2s. Each apparent movement of the shape constituted one trial. There were 50 up-down, 50 down-up, 50 left-right and 50 right-left trials. Following this, participants were instructed to blink every time that a rectangle (2.5cm x 1.5cm), positioned at the centre of the screen changed colour. Colours alternated between dark red and royal blue. Presentation time was 0.8s and ISI was 0.2s. There were 50 blink trials (25 blue and 25 red) facilitating the subsequent removal of blink artefact from the data.

4.2.3.2 Intake-Rejection Protocol

After EOG calibration, the participants were assisted to sit back in a comfortable chair and the headrest was adjusted. They were asked to relax, close their eyes and follow the instructions that would be verbally given to them throughout the course of the experiment. There now follows a description of the intake-rejection protocol, preceded by a schematic representation providing an 'overview' of the experimental tasks.

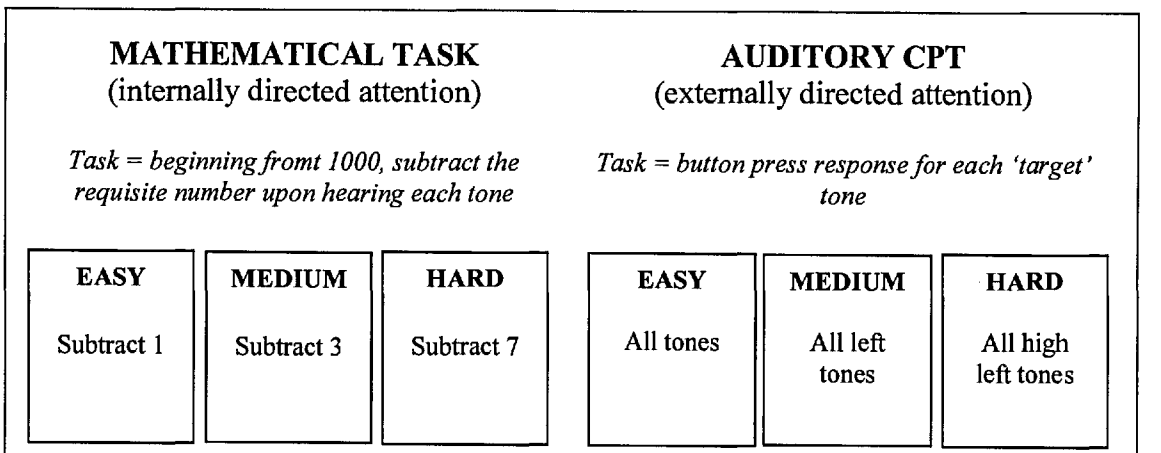


Figure 4.2: Schematic representing experimental protocol. 100 tones were presented in each condition. Order of internal and external blocks were balanced between subjects.

Participants were presented with 6 blocks of 100 hundred trials of STIM generated pure acoustic tones (Neuroscan, El Paso USA). The six blocks can be divided into 3 blocks of the mental arithmetic task (internally directed attention) and 3 blocks of the auditory continuous performance task - aCPT (externally directed attention). Each block of 100 trials comprised of a pseudo-randomly generated sequence of 4 different tones: left-ear high frequency (2000Hz), left-ear low frequency (1000Hz), right-ear high frequency (2000Hz) and right-ear

low frequency (1000Hz). Tones were 50mS in length, with a phase angle of 180° and a D-to-A rate of 20 000. The inter-stimulus interval was 3 seconds and in order to control for expectation, an inter-stimulus range of 0.5 seconds was employed, giving real ISI values of between 2.5 and 3.5 seconds. Each tone had an equal probability rate of occurrence (25%). A different random seed generator was used for each block.

Order of presentation of aCPT and mental arithmetic tasks were balanced between subjects. Different levels of complexity (i.e. blocks 1 –3) were introduced in both tasks in order to attempt to manipulate task difficulty. Prior to each block the participants were verbally instructed to respond in the followings ways:

4.2.3.2.1 Auditory Continuous Performance Task

- Block 1 (external) - respond with a button-press for every tone heard.
- Block 2 (external) - respond with a button-press for every left-ear tone heard.
- Block 3 (external) - respond with a button-press for every left-ear high tone heard.

4.2.3.2.2 Mental Arithmetic Task

- Block 1 (internal) - beginning at 1000 subtract 1 for each tone heard.
- Block 2 (internal) - beginning at 1000 subtract 3 for each tone heard.

- Block 3 (internal) - beginning at 1000 subtract 7 for each tone heard.

4.2.4 Data Preparation

4.2.4.1 Ocular artefact rejection

The type of ocular artefact rejection method used throughout this study was a type of *EOG correction* developed by Croft & Barry (Croft & Barry, 2000a; Croft & Barry, 2000b). It is beyond the scope of the present study to examine in great detail the EOG correction methodology but it is hoped that the following may serve as a useful introduction or reminder to the reader.

In essence, the Croft & Barry method estimates the amount of activity caused by eye-movements to be contaminating the EEG and subtracts it. It is not a straightforward linear problem however, as some EEG activity is recorded by the facial electrodes and this has to be taken into account when it comes to calculating the coefficients for subtraction. Thus it is not a simple subtraction of EOG from EEG (Croft & Barry, 2002).

In this paradigm, it is understood that the EOG is made up of horizontal (HEOG) and vertical (VEOG) eye movements and blinks and that blinks and VEOG consist of both eyelid movement and globe rotation. Consequently a further measure is calculated – radial eye-movement (REOG). HEOG, VEOG and REOG are calculated from the potentials measured at the facial electrodes in the following ways: VEOG = E1 – E3; HEOG = E5 – E6; REOG = (E1 + E3) / 2.

The specific correction algorithm used to remove eye-movement artefact from the EEG was that of Croft & Barry (Croft et al., 2000a).

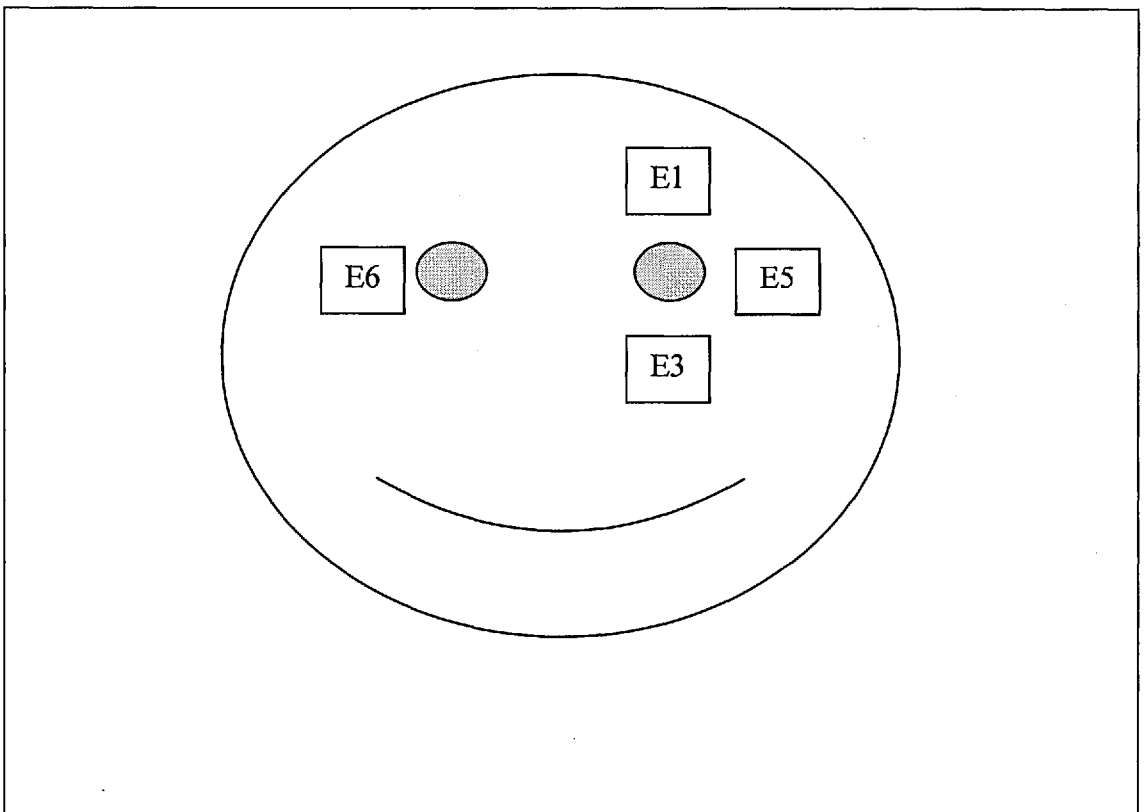


Figure 4.3: Schematic representation of the facial electrode configuration.

4.2.4.2 Epoching, Filtering and Averaging

Following the rejection of EOG artefacts the data were epoched from 2000mS prior to 2000 ms post-stimulus presentation. Data could then be trimmed to leave one second epochs of 0 – 1000mS (0 = stimulus onset). Such large trimming of the epoch is necessary as the filtering methods used tend to cause 'ringing' at the beginning and end of the epoch (i.e. at the introduction and termination of the filter).

Epochs with obvious movement artefact or with amplitude values greater than 75μV were then rejected. An average of 96.78 % of trials were accepted. . The data from electrodes T3/5, F7 and TCP1 from participant number 5 and TCP2, T4 and CP1 from participant 7 were omitted due to excess noise.

The data were filtered (roll-off of 48dB) into the following bandwidths: Delta (δ) = 2 - 4 Hz; Theta (θ) = 4 - 8 Hz; Alpha (α) = 8 - 12 Hz; Lower Beta (β1) = 12 - 20 Hz, Upper Beta (β2) = 20 – 30 Hz, Lower Gamma (γ1) = 30 – 48 Hz and Upper Gamma (γ2) = 42 – 80 Hz. Frequencies in the 48 – 52 Hz range were excluded due to possible contamination from mains electricity supply operating within this waveband.

As this experiment involved an event-related paradigm (i.e. all the tasks involved reaction to multiple stimuli, in this instance, auditory tones) it afforded the opportunity to investigate the data using methods that distinguished between evoked and induced components of the band-pass filtered EEG (see Box 4.2).

Box 4.2: ***Evoked and Induced Oscillatory Activity***

The terms evoked and induced activity have been coined in order to differentiate between two facets of the same EEG data set. The term 'evoked' refers to those components of EEG activity that are phase-locked to the stimulus. Following filtering, they can be calculated using relatively simple averaging techniques:

$$\text{Evoked (j)} = \frac{1}{N}\sum_{i=1}^{i=n} x(i,j)$$

Where N = total number of trials, and x(i,j) = j^{th} sample of the i^{th} trial of the data.

However, using this technique alone disregards a large amount of information. Estimates have it that evoked activity comprises about 1/100 of the total EEG signal.

Thus a technique is needed that enables investigation of the rest of the data set, namely the non-phase locked or 'induced' activity. The means of doing this is by calculating the inter-trial variance using the following equation:

$$IV_{(j)} = \frac{1}{N-1}\sum_{i=1}^{i=N}\{x_{f(i,j)} - \bar{x}_{f(j)}\}^2 .$$

IV = inter-trial variance, N = total number of trials, $x_{f(i,j)}$ = j^{th} sample of the i^{th} trial of the band-pass filtered data and $\bar{x}_{f(j)}$ = the mean of the data at the j^{th} sample, averaged over all band-pass filtered trials (Kalcher & Pfurtscheller, 1995).

4.2.5 Data Analysis

In order to control for motor activity requirements between comparisons, only epochs relating to stimuli whose responses required no button-press responses (i.e. low right tones) were included for analysis.

The mean evoked and induced power values derived from the averaged and filtered epochs served as the dependent variables for the various randomisation t-tests, the results of which are presented in section 4.3. Prior to that, the reasons for and the methods involved in randomisation t-tests are presented.

4.2.5.1 Randomisation t-tests

The randomisation method for the use of t-tests in multiple comparison situations is a robust and assumption-free approach. The major advantage of it that is allows multiple comparisons to be made while both controlling for type I error and without creating an overly conservative *p*- value (throughout this thesis the term *p*-value will be used instead of 'alpha' in order to avoid possible confusions will alpha EEG activity) (Burgess & Gruzelier, 1997a). It is based upon the idea that if the null hypothesis is true (i.e. that there is no experimental effect), then it should make no difference whether a measure was recorded under one condition or another (Burgess et al., 2000). Consequently, randomly swapping dependent variable values between conditions should also have no effect, if the null hypothesis is true. Repeating this procedure many times allows one to calculate the parameters of the distribution of the test statistic (Burgess & Gruzelier,

1999). This procedure is carried out on all electrodes in one's array simultaneously and the largest values for the test statistic for all electrodes for every 'swap' is determined. This allows statistical significance judgements to be made (see below) relating to the whole map rather than just individual electrodes. What then are the values to be substituted in an EEG experiment such as those described in this study?

These measures are the power values (μV^2) of the conditions to be contrasted (e.g. aCPT versus mental arithmetic) in respect to the different subjects. The total number of potential swaps or substitutions that can be made is 2^N (where N = the total number of subjects). Even in a relatively modest sample size of N = 12, the total number of substitutions that are possible is 8,192, rising to 524, 288 for 18 subjects. Clearly this has historically proven to be a time-consuming and computationally expensive problem. Consequently, the randomisation method was developed (Burgess et al., 1997a; Edgington, 1987) that takes a random subset of samples from the total potential set of substitutions. In this study 5000 substitutions were employed. Following the randomised substitutions it is a relatively easy tasks of calculating the *p*-value. Significance is calculated by how many scores (in this case *z*-scores) greater than the comparison being tested are generated using the randomised substitution procedure. Thus with a traditional significance level of 95%, for a *z*-score to be significant following 5000 substitutions, less than 250 greater *z*-scores should be generated. In this experiment, the randomisation procedure resulted in a *z*-value of 2.7-2.9 at the 95-percentile level, compared to 1.96 uncorrected.

4.3 RESULTS

Results are presented according to the frequency band in which they occurred. For all figures, the upper maps indicate *z*-values reflecting the difference between the two comparisons. Brighter colours reflect increased power during internal or hard conditions. The lower (smaller) maps show the randomisation *p*-values for the differences. P-values above and beyond the 95 percentile are accepted as significant. Those between 0.05 and 0.1 are reported as trend findings. For these comparisons, internally directed attentional factor (mental arithmetic) is the average power of blocks 2 & 3, similarly so for external or aCPT measures. The easy and hard factors are the average power of stages 2 and 3 respectively from both of the attentional tasks.

The t-tests for the slower frequencies (delta, theta and alpha) are 1-tailed due to the specific hypotheses being tested. Those for the faster frequencies (in beta and gamma) are 2-tailed due to the more exploratory nature of the comparison.

4.3.1 Delta (2 – 4 Hz)

The results pertaining to the delta bandwidth are displayed in figure 4.4.

Attention: Contrary to our first hypothesis[3], no effect for locus of attention was found in either induced or evoked components.

Difficulty: No effect of task difficulty was observed for induced activity. However, in direct opposition to the second hypothesis[4], a significant effect was found in evoked activity, such that delta power was greater for easy than for hard tasks at the following electrode sites: FP1, F3, F4, C3, C4, P3, F7, Fz, Cz, Pz, FTC1, FTC2, CP1, CP2 and PO1. The same effect was also noted at trend levels at P4, TCP1, TCP2 and PO2. See figure 4.3.

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[3] Delta and theta power will be greater during internal attention tasks than during external attention.

[4] Delta and theta power will increase as a function of task difficulty.

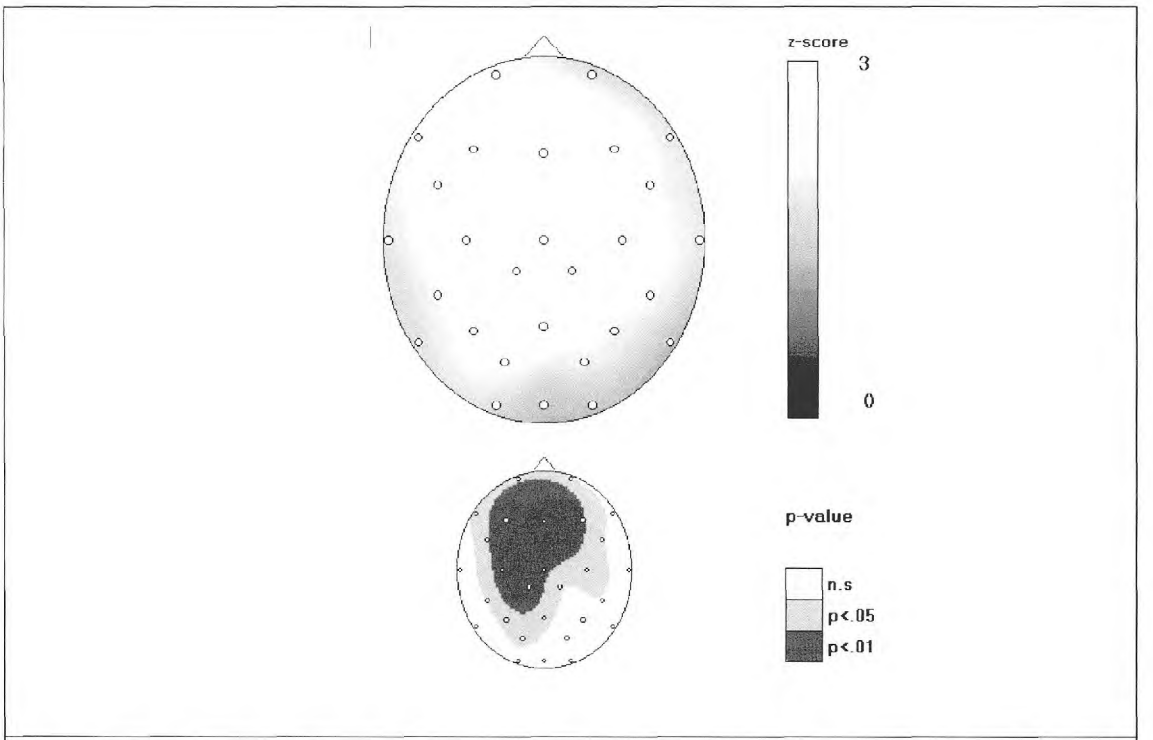


Figure 4.4: EEG amplitudes in the delta bandwidth (evoked) measured during hard and easy task conditions. The upper map indicates *z* values and reveals the differences between the two conditions. Lighter shades reflect increased evoked delta activity during easy tasks. The *p* values (lower map) are the randomisation probabilities for those differences.

4.3.2 Theta (4 – 8 Hz)

The results pertaining to the theta bandwidth are displayed in figure 4.5. No significant effects were observed in relation to hypotheses one or two.

Attention: No effect of attention was found for induced activity. A trend was noted in evoked activity at Fz such that theta power was greater during aCPT than for arithmetic. See figure 4.5.

Difficulty: No effect for difficulty was found for either evoked or induced activity.

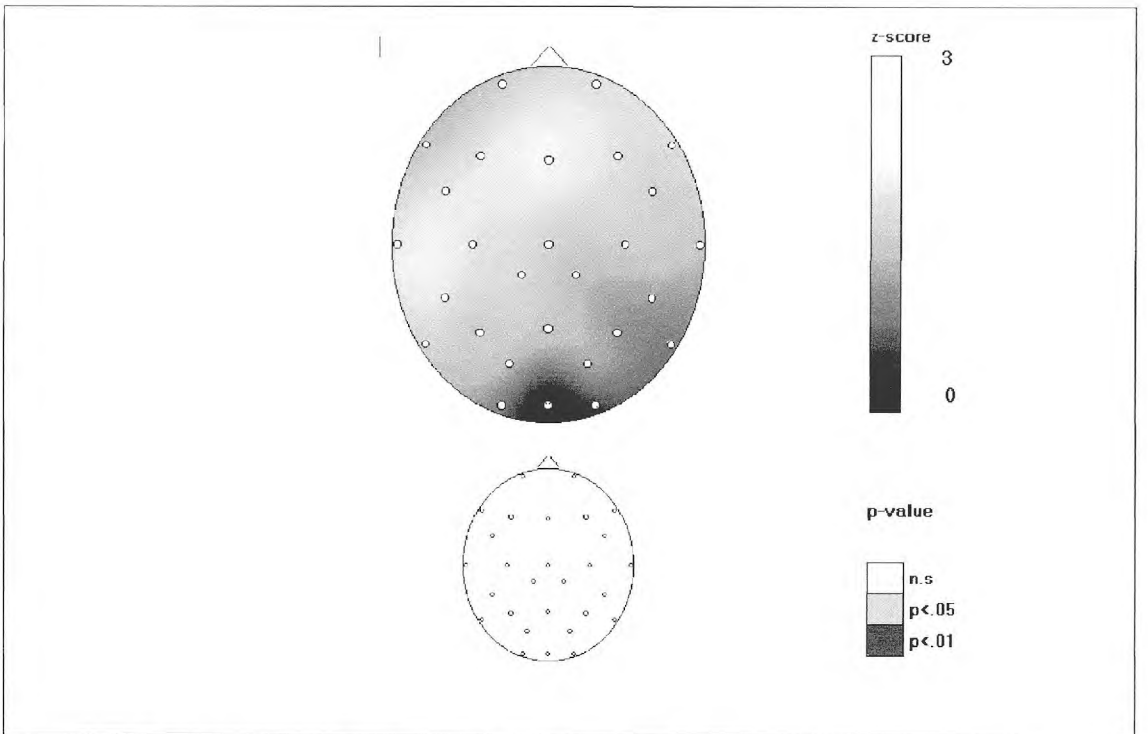


Figure 4.5: EEG amplitudes in the theta bandwidth (evoked) measured during internal and external attention. The upper map indicates *z* values and reveals the differences between the two conditions. Lighter shades reflect increased evoked theta activity during external tasks. The *p* values (lower map) are the randomisation probabilities for those differences.

4.3.3 Alpha (8 – 12 Hz)

The significant results pertaining to the alpha bandwidth are displayed in figure 4.6.

Attention: Contrary to the third hypothesis,[5] no significant differences were observed in either evoked or induced components.

Difficulty: An effect was observed in evoked but not induced activity, such that power was greater during hard tasks at frontal sites. This difference was significant at FP1 and FP2 and at trend levels at F4 and F8. This finding had not been predicted.

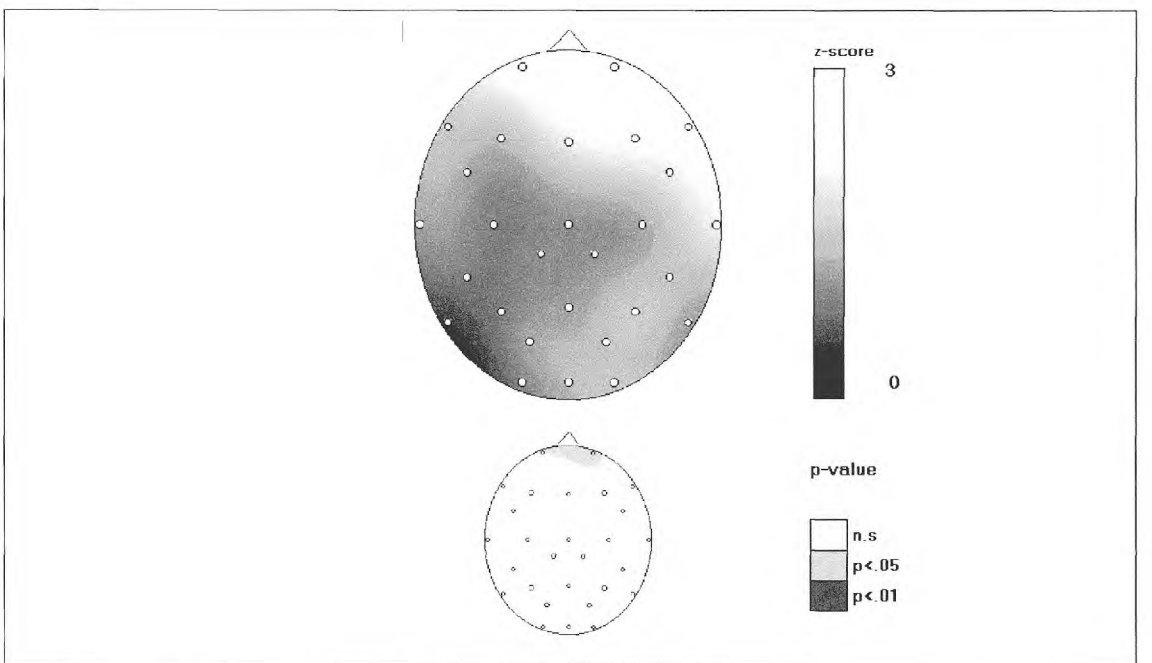


Figure 4.6: EEG amplitudes in the alpha bandwidth (evoked) measured during easy and hard tasks. The upper map indicates *z* values and reveals the differences between the two conditions. Lighter shades reflect increased evoked alpha activity during hard tasks. The *p* values (lower map) are the randomisation probabilities for those differences.

The remaining findings were not intrinsic to our hypotheses. They are reported for reasons of completeness and due to the exploratory nature of this experiment.

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[5] Alpha power will be greater during mathematical internal attention than during external attention.

4.3.4 Beta 1 (12 – 20 Hz)

Attention: No effects of attention were found in either induced or evoked activity.

Difficulty: No effects of difficulty were found in either induced or evoked activity.

4.3.5 Beta 2 (20 – 30 Hz)

The results pertaining to the upper beta bandwidth are displayed in figures 4.7 & 4.8.

Attention: Beta 2 power was greater during the mental arithmetic task than for auditory CPT at numerous sites. For induced activity this finding was significant at F4, C4, P3, P4, T5, T6, Pz, PO1 and PO2 and at trend levels at FP1, C3, O1, O2, F7, Fz, Cz, Oz, TCP2, CP1 and CP2 ($z = 2.448$; $p = 0.053$) (see figure 4.6).

For evoked activity, beta 2 power was significantly greater during arithmetic at F4, C3, C4, P3, O1, F7, T5, Pz, FTC1, FTC2, TCP1, and PO1. This effect was at trend levels at F3, P4, T6, Fz, Oz, TCP2, CP1, CP2 and PO2 (see figure 4.7).

Difficulty: No effects were found for either induced or evoked activity.

4.3.6 Gamma 1 (30 – 48 Hz)

The results pertaining to the lower gamma bandwidth are displayed in figures w & x.

Attention: For induced activity, gamma 1 power was found to be greater during mental arithmetic than aCPT. This was significantly so at F3, F4, C4, P3, P4, T5, T6, Fz, Cz, Pz, CP1, CP2, PO1 and PO2. This effect was at trend at FP1, FP2 =, C3, F7, Oz and TCP2 (see figure 4.7).

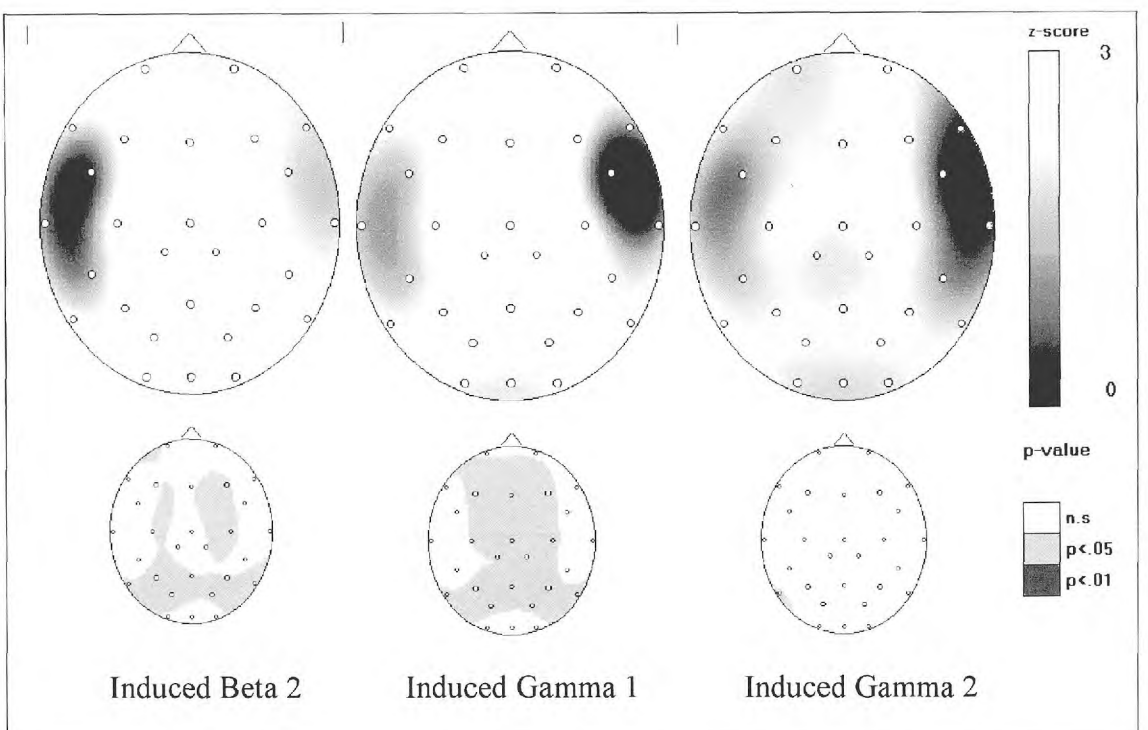


Figure 4.7: EEG amplitudes in the beta 2, gamma 1 & 2 bandwidths (induced) measured during external and internal attention. The upper map indicates *z* values and reveals the differences between the two conditions. Lighter shades reflect increased induced alpha activity during internal attention. The *p* values (lower map) are the randomisation probabilities for those differences.

Evoked gamma 1 power was significantly greater during arithmetic at frontal sites F3, F4 and Fz, and at trend levels at the following sites: FP1, C4, T6, Cz, Pz, FTC1, CP1 and CP2 (see figure 4.8).

Difficulty: No effects of task difficulty were observed in either evoked or induced gamma 1.

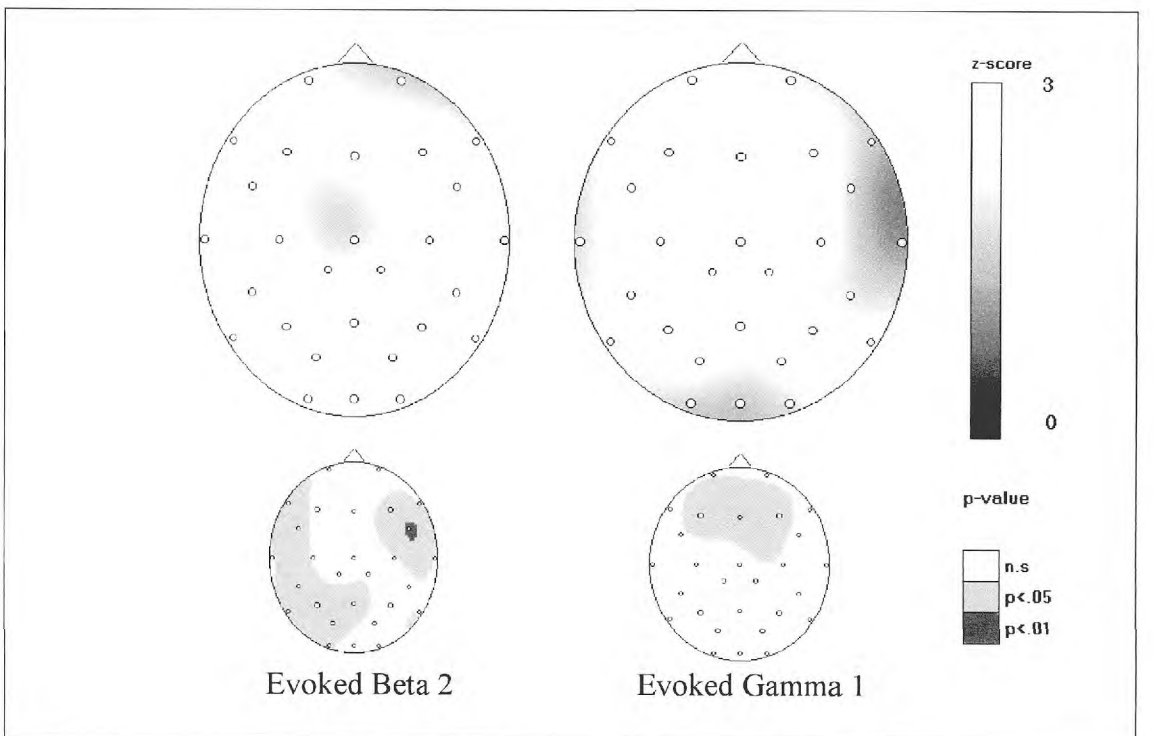


Figure 4.8: EEG amplitudes in the beta 2 & gamma 1 bandwidths (evoked) measured during external and internal attention. The upper map indicates *z* values and reveals the differences between the two conditions. Lighter shades reflect increased evoked alpha activity during internal attention. The *p* values (lower map) are the randomisation probabilities for those differences.

4.3.7 Gamma 2 (52 – 80 Hz)

The results pertaining to the upper gamma bandwidth are displayed in figure 4.7.

Attention: Power in induced gamma 2 was significantly greater during mental arithmetic as opposed to aCPT at electrode site T5. This effect was also at trend levels at FP2 and Fz. No significant effect of attention was found in the evoked activity, but trend level findings of increased gamma 2 power during arithmetic were observed at T5 and TCP1.

Difficulty: No effect of task difficulty was found in either evoked or induced gamma 2 activity.

4.4 DISCUSSION

The main findings as they relate to our hypotheses are as follows:

- Contrary to our second hypothesis, evoked delta power was actually greater during easy as opposed to hard conditions. No other experimental effects were observed in the delta band. Delta has previously been shown to be positively associated with both internal attentional states and task difficulty (Harmony et al., 1996b; Harmony et al., 1999). This had been hypothesised to reflect class II inhibitory processes akin to suggestions by Vogel *et al* (Vogel et al., 1967). Given that the present study used similar tasks (i.e. mathematical) to Harmony *et al*, the notion must be entertained that delta cannot be regarded as an index of the selective inhibition necessary for internally directed attentional tasks. Indeed, the fact that delta power was greatest during easy tasks suggests that delta may in fact occupy a more

passive niche. It is arguable given that the findings are due to evoked activity that they are solely related to the processing of the auditory tones – a process that would be somewhat disrupted during difficult subtraction tasks. This explanation may also hold for the trend level findings of greater evoked theta activity during aCPT.

- Again, contrary to the second hypothesis, no effects of task difficulty were found in the theta band. This study cannot therefore add to the substantial evidence that theta, in particular at frontal midline sites, is positively associated with the difficulty of a task (e.g. John et al., 1980; McEvoy et al., 2001) and increased working memory requirements (e.g. Burgess et al., 1997b). One possible reason for this failure to replicate is that perhaps the differences between the tasks as far as difficulty is concerned are not great enough to elicit significant differences in EEG activity. However, given that differences were observed in both the delta and alpha bands, this explanation remains questionable. An alternative suggestion is that perhaps the link in previous studies between task difficulty and working memory was closer than realised, and that the theta effects were more related to the memory requirements. The working memory requirements in the present study were minimal for all tasks and could therefore account for the scarcity of findings.

- We also have to accept the null hypothesis for hypothesis 3 regarding alpha and attention. No significant differences were observed between mental arithmetic and aCPT tasks. However, there was a small unexpected effect related to task difficulty, wherein evoked alpha power was significantly

greater during hard tasks at FP2. It remains to be seen whether this effect is robust and will be the subject of further investigation in the following experiments.

The failure to find differences between attentional states in the alpha band potentially undermines a basic tenet of this study. Given that the primary EEG evidence for the differentiation between internal and external attentional states was found within alpha parameters (Ray et al., 1985b; Ray et al., 1985a), failure to find such discrimination calls into question the intake-rejection hypothesis. This possibility requires serious consideration and will be returned to in chapter 5. However, there is also the possibility that the scarcity of alpha findings in this experiment is the result of a more immediate problem due to the nature of the protocol used. This problem is the potential mismatch of comparative stimuli and will be addressed in section 4.4.5.

- The most unexpected and widespread findings were in the fast oscillatory activity of upper beta, lower and upper gamma. In all of these bands induced power was greater during mental arithmetic than aCPT. Similarly, evoked power was significantly greater at widespread sites during arithmetic in upper beta and lower gamma and was at trend levels but less prevalent in upper gamma. Clearly these unpredicted findings warrant further investigation. For instance, the question needs to be asked, are these findings particular to the type of mathematical task used in this study or are they a more generalised effect that is related to internally directed attention? However, as mentioned above, there is a further more generalised issue regarding the

protocol used in this experiment that may account for unexpected findings. This is the issue of experimental balance and it will be addressed as it relates to this experiment in the following section.

4.4.1 Experimental Balance

It is a distinct possibility that the difference in terms of cognitive activity between the external attention task (aCPT) and internal attention task (mental arithmetic) was not sufficiently balanced to allow one to draw clear or strong inferences as to the planned experimental comparison. Thus the findings may not reflect the actual experimental effect that the protocol had been designed to test. It is not clear therefore if differences in certain band-power measures between externally and internally directed attention tasks are due to differences in attentional mechanisms or to other unrelated cognitive or pre-motor processes. For instance, despite the fact that motor responses were controlled for (in that only tones in the aCPT that did not warrant a button-press response were used in the analysis) there is still the possibility of sub-vocalisation or even more explicit counting 'under one's breath' during the mathematical tasks. The reader is reminded that these mathematical tasks employed the subtraction of either 3 or 7 beginning from a starting point of 1000. Vocalising the running total (in some manner) would have made the task easier and thus may well have been a strategy employed by the participants. Additionally, post-experiment reports from a small number of subjects suggest that other more success-driven strategies were employed in an attempt to achieve the correct answer with less effort, e.g. counting the number of tones presented, multiplying this number by the number

to be subtracted and subtracting this sub-total from the original starting point of 1000.

4.4.2 Summary

To summarise, no further evidence was found for the involvement of slow-wave EEG activity in internally directed attention. Neither was there found as hypothesised, any increase of delta or theta components in line with task difficulty. On the contrary, evoked delta activity was found to be greater during easy as opposed to hard tasks. These findings were supplemented by unexpected results indicating an association between internal attention and fast-wave EEG activity. Specifically, induced beta 2, gamma 1 and gamma 2 and evoked beta 2 and gamma 1 amplitudes were greater during internally directed attention.

However, it is unclear whether these findings are the direct result of the experimental effect being tested or whether they are due to other confounding variables. Given the above uncertainties arising from both experimental balance and subjects' strategies it would appear unwise to draw too many direct inferences from the results in this first experiment. However, the unexpected nature of the fast EEG findings alone merits interest and will be the subject of further investigation in the following experiments. In order to control for the problems arising from the procedure in experiment one, a new protocol was devised that employed a much greater balance between externally and internally directed attentional tasks. This experiment and the accompanying results will be the subject of the following chapter.

5 EXPERIMENT 2

5.1 RATIONALE

The rationale for the second experiment was as follows. Firstly, we sought to test and replicate the preliminary findings from the previous experiment that showed a relationship between internally directed attention (as exemplified by mental arithmetic) and fast EEG components (beta 2, gamma 1 & 2). Secondly, in order to do this, we required to develop a new methodology that enabled a more balanced and exacting contrast between internally and externally directed attention to be made. Additionally, this would make possible the re-testing of the original intake-rejection hypotheses from the first experiment in such a way as to either render them redundant or to allow a more confident appraisal of their value.

5.2 INTRODUCTION

In order to examine the issue of internally and externally directed attention in as balanced a way as possible it was decided to design a paradigm employing mental imagery methodology. In a very straight forward way, this would allow the direct comparison between, for instance, seeing a stimulus (external attention) and imagining the same stimulus in one's mind's eye (internal attention). Additionally, in order that inferences could be made relating to attention per se, rather than just modality specific conclusions, a multi-modal

protocol was devised that included visual, auditory and haptic (touch) stimuli and their ideational counterparts. Before describing the details of this protocol, it may prove useful to describe mental imagery and outlining the key issues of the debate surrounding it.

5.2.1 Mental Imagery

Mental imagery has been defined as a "process where a 'mental' sensory experience is produced not by an external stimulus but by internal processes" (von Stein et al., 2000b, pg. 310). Typically references to mental imagery are concerned with visual imagery; however, the term can have a broader scope and may be taken to refer to ideation related to any sensory or emotional process, including proprioception. For instance, the Betts QMI (questionnaire of mental imagery) Vividness of Imagery Scale (see Richardson, 1969) covers seven varieties of imagery: visual, auditory, haptic (touch), motor, gustatory, olfactory and proprioceptive. This multi-modal nature of imagery provided further rationale for designing the protocol used in this experiment to test a variety of sensory modalities, thus providing the possibility for a wider, more holistic understanding of imagery per se. The following two sections serve as an introduction to the theories of mental imagery and the debate surrounding them and also to examine various EEG findings as they relate to imagery. Given that most of the literature in the area focuses on visual imagery this will be reflected in these sections.

5.2.1.1 On the Imagery Debate

Since the resurrection of interest in mental imagery in the 1970s, views about the processes and mechanisms involved have polarised into two main camps. These two positions are directly related to the more general perceptual problem of how reality (whatever that may be) can be 'represented' in our minds. In essence, these two approaches can be encapsulated in the following question: are our mental representations analogical or propositional? (Eysenck & Keane, 1995). By analogical, it is meant that the nature of the representation is similar in certain critical ways to that which is being represented, for instance a pictorial representation would fit into this category, as would other topographical representations. On the other hand, a propositional representation is a much more abstract process. Consider the following unlikely scenario: the examiner is enjoying the thesis. This can be represented analogically by a drawing of an obviously learned person reading a weighty tome with an expression of joy and happiness attached to their face. Or, the same scenario can be encapsulated in the following propositional manner: ENJOY(EXAMINER, THESIS). It is important to note that although propositional representations are described using linguistic terminology, it is not argued that representation in the brain is linguistic in nature (at least not at the surface level).

Evidence for the more pictorial, analogical perspective has come from the study of mental rotation. Many researchers have found that when a figure is rotated about an axis, the greater the angle of rotation, the longer it takes to answer a question as to whether the test stimulus is the same or a mirror-image of the

original figure (e.g. Cooper & Shepard, 1973; Cooper, Sheri, Egner, Vernon, & Gruzelier, 2002; Shepard, 1978). This has been used to imply that the mental image occupies a kind of mental space akin to that taken by the 'real' object in the 'real world and hence rotation of the image requires time and manipulation similar to rotating a real object (Eysenck et al., 1995). Additional evidence has also been found by examining the manner in which subjects 'inspect' mental maps of charts they have previously memorised. It has been observed that imaginal scanning times between locations on the map take longer the greater the actual cartographic distances involved (Kosslyn, Ball, & Reiser, 1978).

One of the main protagonists in the pro-propositional camp is the cognitive scientist, Zenon Pylyshyn. One of his central arguments against what he refers to as "picture theory" (Pylyshyn, 2002) comes in the form of a criticism of the protocols used by Kosslyn and others. Pylyshyn argues that the very nature of the tasks involved "invites people to simulate what they believe would happen if they were looking at the actual situation being visualized" (Pylyshyn, 2002). In other words, he argues that during a mental imagery task, we are not actually inspecting our own internal states but what they are 'about' – what philosophers refer to as 'intentionality'. Therefore, according to Pylyshyn, such experiments tell us nothing about the mechanisms of imagery or of representation themselves. Rather they serve to illustrate our own self-delusion with regard to our internal mental lives. Indeed, Pylyshyn argues that Kosslyn and others who espouse analogical theories of mental imagery have fallen into the classic philosophical trap of the 'cartesian theatre' (Dennett & Kinsbourne, 1992). This is the materialist argument against the supposed dualist fallacy of the homunculus – the

little man inside our head watching the movie of our experiences – or what Gilbert Ryle referred to as the "ghost in the machine" (Ryle, 1949). In summary, Pylyshyn argues that analogous or 'depictive' theories of mental imagery are mistaking the phenomenology for the explanation (Pylyshyn, 2002).

As in many debates of this kind, a dialectical approach may prove useful, from which a perfectly feasible synthesis of the two positions may emerge. For instance, it may be the case that analogous representation underlies earlier stages of perceptual processing, with propositional-type encoding occurring at a higher order level – the more information is processed, the more abstract it becomes. In mental imagery, people may use a mixture of imaging skills depending on the task or their dispositions (e.g. children appear to be more image-based). Some people may use higher order methods, others may 'wish' or 'need' or be able to 'go all the way back' to V1 (primary visual cortex) in their imagery. Furthermore, whether or not activation in primary sensory cortex is observed during imagery appears to depend on the sensory modality of the imagery task. For instance, whereas the majority of fMRI studies to address the issue have reported V1 activation during visual imagery (see below), no evidence of primary auditory cortex (A1) activation have been reported during auditory imagery (Kosslyn, Ganis, & Thompson, 2001). Such a task / dispositional explanation of imagery is compatible with more dynamic, connectionist-type theories of mind, wherein perception is a much more distributed process, involving parallel streams of neural networks, some of which may be more depictive, others may be more propositional. However, such speculation requires empirical investigation beyond the scope of the present study. Indeed, with

regard to this study it is unnecessary to answer these questions for the following reason: Our question is not, what are the perceptual mechanisms, but what are the attentional differences? As such, it is sufficient to understand that there is a debate concerning the nature of imagery and that the debate continues. Indeed, despite claims to the contrary, the debate looks set to continue for some years to come. Not the least because it is intimately bound up with understanding the nature of consciousness and notions of epistemology, both areas that are far from resolution at present. However, as with the study of consciousness, this does not mean that useful work can not be carried out, for instance, looking at various psychophysiological correlates of imagery.

In recent years, Kosslyn and colleagues using various imaging and interventional methods, have sought to establish that the same brain areas sub-serving vision, are also active during visual imagery tasks. For instance, Klein *et al* (Klein, Paradis, Poline, Kosslyn, & Le Bihan, 2000) using event-related functional magnetic resonance imaging techniques (ER-fMRI) found that activity along the calcarine sulcus (the site of the primary visual cortex) increased when participants were required to form a visual image of an animal. Additionally, it was observed that this activity was enhanced when the task required them to evaluate characteristics that or may not have been associated with the image. Further evidence for the role of primary visual cortex in visual imagery has been reported by Sparing *et al* (Sparing et al., 2002). They found that the threshold at which phosphenes could be elicited by transcranial magnetic stimulation could be lowered when subjects were instructed to form visual images at the same time as the stimulation (a phosphene is the externally or internally induced visual

experience of a small fleck of light in the absence of occular input). This was interpreted as showing that visual imagery increases the excitability of the visual cortex. A review of the literature can be found in Thompson & Kosslyn (Thompson & Kosslyn, 2000). It is important to note that primary visual cortex is not the only region of interest during visual imagery; other extrastriate areas are also involved. In particular the precuneus has received attention in this respect. The precuneus is situated in the medial parietal lobe and is thought to be involved in conscious imagery and in the use of visual imagery as it facilitates memory retrieval – in particular episodic memory (Fletcher et al., 1995b; Fletcher et al., 1995a; Shallice et al., 1994). Indeed, Fletcher *et al* concur with Farah's speculations that the precuneus may fulfil the function of the visual imagery buffer (Farah, 1984). They are careful however, not to dismiss the involvement of striate cortex with visual imagery. Despite a lack of V1 activation during their experiment, they suggest that V1 is important for example, during the 'inspection' of detailed characteristics of the stimulus being imagined; a task that was lacking in their procedure. It is becoming apparent that despite a lack of resolution to the representation debate, there is an emerging consensus as to the cortical areas involved. There now follows an outline of work investigating mental imagery using EEG and magnetoencephalographic (MEG) methods as it relates to this accord.

5.2.1.2 Imagery and Electromagnetic Investigation

EEG work has been carried out to investigate the process of mental rotation. It has been proposed that mental rotation requires visuo-spatial areas of the cortex

known to be activated in spatial attention. For instance, several event-related potential (ERP) studies have indicated the involvement of parietal areas during rotation (Heil, 2002; Heil & Rolke, 2002; Yoshino, Inoue, & Suzuki, 2000). Furthermore, use of a repetitive transcranial magnetic stimulation technique has shown that performance of visuo-spatial imagery tasks deteriorates after stimulation of the posterior parietal lobe, indicating a possible causal role for parietal activity in such imagery (Aleman et al., 2002).

With regard to visual imagery, recent work carried out using MEG and EEG technologies has increased the evidence of visual cortex involvement in visual imagery. Using MEG, Raij (Raij, 1999) has found occipital activation and precuneus involvement in a task requiring participants to examine characteristics of a set of imagined letters of the alphabet. Williamson *et al* (Williamson, Kaufman, Lu, Wang, & Karron, 1997) have reported EEG alpha suppression over occipital areas as an indication of imagery-induced activation of those sites. Similar results have also been reported by Salenius and colleagues (Salenius, Kajola, Thompson, Kosslyn, & Hari, 1995). Using MEG, they found the greatest desynchronisation in the alpha band was over the parieto-occipital sulcus. However, their lack of findings of early visual cortex involvement may be due to problems associated with the 'invisibilty' of magnetic activity in the calcarine fissure to MEG, rather than any lack of activity itself. Other investigators have also used desynchronisation as an index of imagery activation in other modalities. Pfurtscheller & Neuper (Pfurtscheller & Neuper, 1994), Schnitzler *et al* (Schnitzler, Salenius, Salmelin, Jousmaki, & Hari, 1997) and McFarland *et al* (McFarland, Miner, Vaughan, & Wolpaw, 2000) have reported decreases in mu

and beta activity over motor cortices during motor imagery tasks. The reader is reminded that the reasoning behind the use of desynchronisation as an index of imagery is derived from the hypotheses regarding alpha as reflecting cortical idling (see section 2.2.3).

It should be noted however, that not all investigations of imagery using electromagnetic techniques have found alpha power to decrease. Indeed, many have found positive associations between alpha and imagery. Several of these (e.g. Bremner et al., 1972a; Bremner et al., 1972b; Grillon et al., 1987; Klinger et al., 1973; Ray et al., 1985a; Ray et al., 1985b; Schupp et al., 1994) were coming from the perspective of the intake-rejection hypthesis (see chapter 3). One possible reason for this alpha dichotomy is the nature of the experimental comparison being investigated. Most of the studies reporting desynchronisation use a resting EEG period as a control with which to contrast imagery, whereas most I-R studies tend to try to balance comparisons more between imagery and sensation. Thus the discrepancy between the findings may reflect imagery versus sensation as opposed to imagery versus doing nothing. However, it must be pointed out that equating a resting state with "doing nothing" is a big assumption; a means of assessing mentality during rest remains illusive (see Discussion below). This was a further reason for the development of the paradigm used in this and subsequent experiments which sought to directly compare imagery versus matched stimulus-intake tasks without making any assumptions as to the phenomenology of and the cognitive processes occurring during a 'control' / resting condition.

Apart from those coming from an I-R background, other recent studies have also reported positive changes in alpha activity during imagery tasks. Bhattacharya & Petsche (Bhattacharya & Petsche, 2002) found alpha phase synchrony to increase when artists and non-artists imagined looking at painting as opposed to looking at them. Von Stein & Sarnthein (von Stein et al., 2000b) observed characteristic coherence patterns in alpha when subjects imagined playing a musical instrument. Petsche *et al* (Petsche, Kaplan, von Stein, & Filz, 1997) found that inter-areal coherences in the alpha band evolved during visual imagery. These last two studies will be returned to and examined in more depth in section 8.3.

5.2.2 Hypotheses

It can be seen therefore that the relation between imagery and brain wave activity is far from straight forward. For example, results pertaining to alpha activity appear to be contradictory. With this in mind, and with the determination to explore mental imagery using a balanced protocol (sensory versus imagery) based on reasons described above (section 4.4.5) the following prediction was made: alpha activity should change as a function of attention. Three hypotheses arise from this prediction based on the opposing approaches to alpha activity and mental imagery:

1. *Alpha amplitudes at occipital sites will increase during internally directed attention, but not as difficulty factors increase.* This is based on the assumption that alpha activity reflects cortical idling and that sensory processing activates visual cortex more than imagery.

2. *Alpha amplitudes at occipital sites will be greater during externally directed attention and will not vary as a function of task difficulty.* Again, this is based on the cortical idling approach but incorporates the proposals that imagery increases activation in occipital areas and hence alpha desynchronises.

3. *Alpha amplitudes will be greater not only for internal attention as opposed to external attention but also for hard as opposed to easy tasks during mental imagery but not during sensory intake tasks.* This hypothesis is derived from the intake-rejection model.

The hypothesis derived from the I-R model regarding theta oscillations was unchanged from the first experiment:

4 Theta amplitudes will be greater during internally directed attention, and will increase as a function of task difficulty.

However, the hypotheses pertaining to delta activity are now contrasted with the contradictory findings from experiment 1, leading to the following hypotheses:

5 *Delta amplitudes will be greater during easy as opposed to hard tasks.* This prediction is based on the findings from the first experiment.

6 *Delta amplitudes will be increased during internal attention and in line with difficulty.* This is based on the I-R hypothesis.

The results from the first experiment regarding to the fast EEG components (beta 2, gamma 1 & 2) led us to hypothesise the following:

7 *Fast oscillatory activity will be associated positively with attention to internal processes, in this case mental imagery.*

5.3 METHOD

5.3.1 Subjects

12 participants (6 male & 6 female) were tested, ages ranged from 27 to 48 years (mean: 34.4). All participants reported normal hearing, haptic sensation, normal or corrected to normal vision and no known psychiatric or neurological problems. Participants gave written informed consent and were paid GB£15 for taking part. Ethics Committee approval was granted for this study.

5.3.2 EEG Recording

EEG set-up and recording was the same as in experiment 1.

5.3.3 Procedure

This protocol employed matched externally and internally directed attentional tasks. Both sets of tasks comprised of 3 levels of gradually increasing task demands. For each subject, all tasks were performed in each of the auditory, haptic and visual modalities. Order of modality was fully counter-balanced between subjects. Two sets of stimuli were employed for each modality: participants 1-6 used set 1; participants 7-12 used set 2. All recording sessions were conducted between 3.30pm and 6.30pm in an attempt to minimalise time of day effects. Immediately following testing, the participants were required to complete a subjective difficulty rating scale pertaining to the different experimental tasks.

5.3.3.1 Externally Directed Tasks

For each level participants were presented with a sequence of 6 randomly ordered stimuli (see external stimuli for details), repeated 3 times, with a pause of 4s between sequences. Stimulus durations were 0.5s, with an SOA of 0.7s. Level 1 required the participant simply to attend to the stimuli. Level 2 involved the answering of a simple question (e.g. "How many stimuli are there in each series?"). Level 3 involved the answering of a more demanding question (e.g. "How many different types of stimuli are there?"). Questions were asked prior to each presentation of the stimuli sequences, and responses were given post-stimulus presentation.

5.3.3.1.1 External Stimuli

Acoustic

A sequence comprised of 3 different pure tones at approximate natural scalar frequencies, pseudo-randomly ordered within the sequence. Stimulus set 1: F#, F#, F#, G, D, D (F#=370Hz; G=392Hz; D=293.7Hz). Stimulus set 2: D, C#, E, E, E, E (C#=277.2Hz; E=329.6Hz). These tones were generated by Neuroscan STIM software and were presented binaurally using STIM foam insert headphones at 90dB.

Haptic

A sequence comprised of 3 different grades/textures of sandpaper (grit size 40-1200g). Each stimulus was applied in sequence, by the experimenter, simultaneously to the opposed left and right index fingers of the participant. Stimulus set 1: S, M, R, M, S, M (S=1000g; M=180g; R=40g). Stimulus set 2: S, S, R, M, M, S (S=1200g; M=240g; R=60g).

Visual

A sequence comprised of 4 different stimuli: circles, squares, ellipses and triangles. Shapes were differentially coloured. Presentation was via a SVGA 15'' computer monitor and Neuroscan STIM software (see Figure 1).

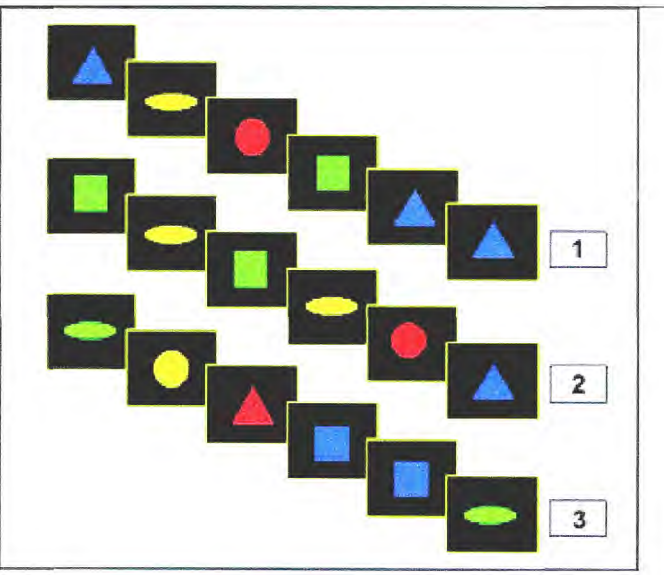


Figure 5.1: Schematic of external attention stimuli in the visual modality

5.3.3.2 Training Session

In order to assure successful completion of the internal tasks, a first step of training participants to be able to imagine the previously presented sequences of stimuli was instigated. Training took the form of repeated presentation of the stimuli until the participant reported confidence in their ability to imagine the sequence. On average, 2 presentations were necessary.

5.3.3.3 Internal Tasks

As in the external tasks three levels were employed. Level 1 involved the participant imagining the randomly ordered sequence of 6 stimuli, 3 times (Ss were instructed to try to replicate the timing and spacing of the original stimuli as

well as the stimuli themselves). Level 2 involved the participant imagining the sequences again and answering a simple question regarding the stimuli. Level 3 involved the participant imagining the sequence once again and answering a more demanding question. Questions were the same as in the external tasks and were asked prior to each imagination of the stimuli sequences. Responses were given post-stimulus imagination. The questions play the dual role of increasing task demands and providing the behavioural evidence that the participants had successfully 'imagined' the stimuli.

5.3.3.4 Subjective Difficulty Scale

Immediately following the completion of the experiment, the participants were required to rate the subjective difficulty of the various tasks they had performed on a scale of 1 – 5 (1 = easy; 5 = very hard). See appendix 9.1 for a full copy of the subjective difficulty scale used in this experiment.

5.3.4 Data Preparation

Ocular artefact rejection was carried out using methods described previously.(Croft et al., 2000a) The EEG data were epoched from 1000 – 11000ms after sequence onset and spline-fit to 8192 points. A fast-Fourier transform of the data enabled extraction of the various components from the raw EEG within the following frequency parameters: delta (δ) = 0.1-3.9 Hz; theta (θ) = 4-7.9 Hz; alpha (α) = 8-11.9 Hz; beta 1 ($\beta 1$) = 12-19.9 Hz; beta 2 ($\beta 2$) = 20-29.9 Hz; gamma 1 ($\gamma 1$) = 30-48 Hz; gamma 2 (γ) = 52-80 Hz.

In order to explore general topographical (sagittality and laterality) effects, the scalp electrodes were divided into 6 surface areas: left anterior (FP1, F3, F7, FTC1); right anterior (FP2, F4, F8, FTC2); left central (C3, T3, CP1, TCP1); right central (C4, T4, CP2, TCP2); left posterior (T5, P3, PO1, O1); right posterior (T6, P4, PO2, 02).

5.3.5 Statistical Analysis

Repeated measures polynomial contrasts were employed to test for differences in *attention* (external versus internal); *difficulty* (levels 1 - 3); *sagittality* (anterior, central and posterior sites); *laterality* (left versus right). An ANOVA model was used so as to facilitate both the planned contrasts between the experimental factors mentioned above and also to establish whether any interactions between *attention* and *difficulty* were to be found.

5.4 RESULTS

5.4.1 Subjective Difficulty Findings

The results of the subjective difficulty rating questionnaire can be seen in figure 5.2. They show a clear linear increase in experiential difficulty from level 1 to level 3. A repeated measures ANOVA (*modality* x *attention* x *difficulty*) revealed a significant main effect of task difficulty [$F(1,8) = 30.77$; $p < 0.001$].

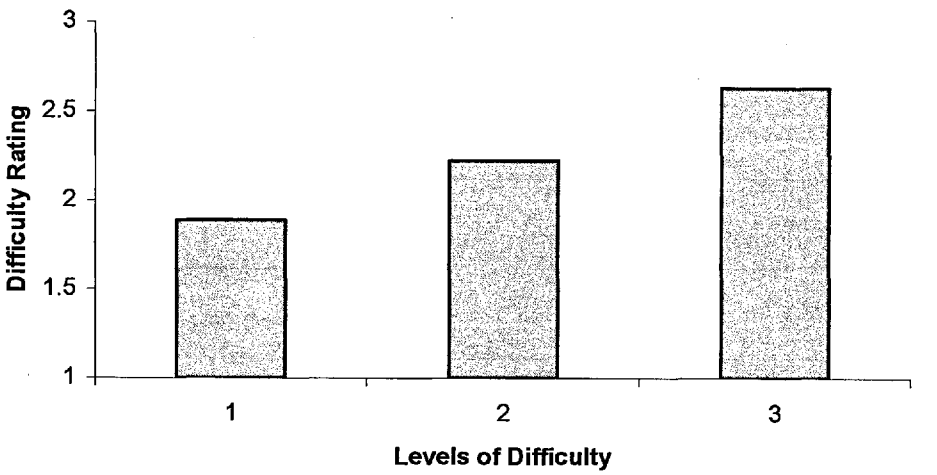


Figure 5.2: Subjective difficulty ratings collapsed across modalities and attentional state. Levels of difficulty: 1 = Easy, 2 = Medium, 3 = Hard.

5.4.2 EEG Findings

The EEG results will be presented according to the bandwidth in which they were observed. It is unclear whether the participants had their eyes open or shut during the internal attention conditions, consequently, the results for the visual modality will not be reported here (see section 5.5.5 for details).

5.4.2.1 Delta (0.1 – 3.9 Hz)

In contrast to both hypotheses derived from the intake-rejection model (hypothesis 6) or to the results from experiment 1 (hypothesis 5), no effects for *attention* or *difficulty* were observed in the delta band.

5.4.2.2 Theta (4 – 7.9 Hz)

In agreement with hypothesis 4, theta power was greater in hard as opposed to easy conditions in both the haptic modality [$F(1,10) = 9.14$; $p < 0.05$]

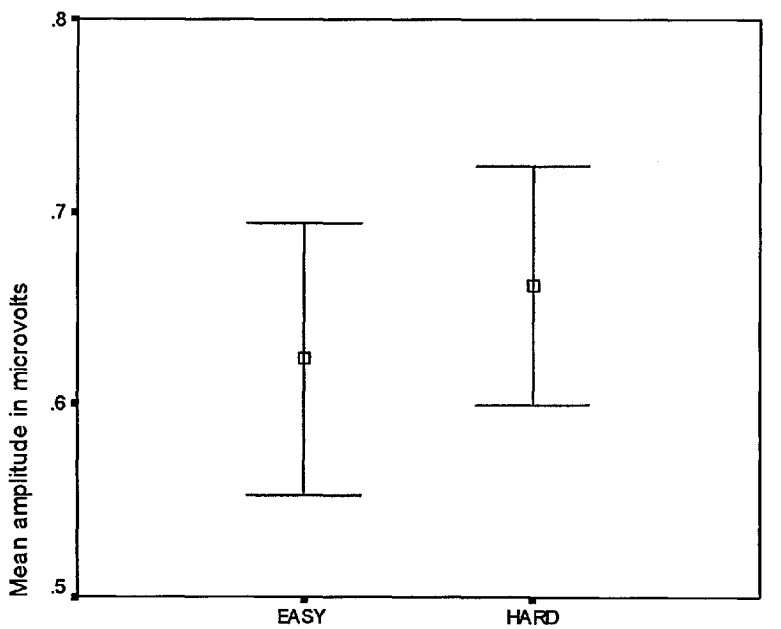


Figure 5.3: Mean amplitudes in the theta bandwidth for easy and hard haptic task conditions

5.4.2.3 Alpha (8 – 11.9 Hz)

Significant main effects for *attention* were observed in all modalities. Mean α-amplitudes were greater during internally as opposed to externally directed attention tasks (auditory [$F(1,11)=5.18$; $p<0.05$]; haptic [$F(1,10)=5.65$; $p<0.05$]; see Table 5.1).

In the auditory modality, the increase in mean α-amplitudes from external to internally directed attention was greater at anterior and posterior than central sites ([F(1,11)=18.9; p<0.001] see figure 5.4).

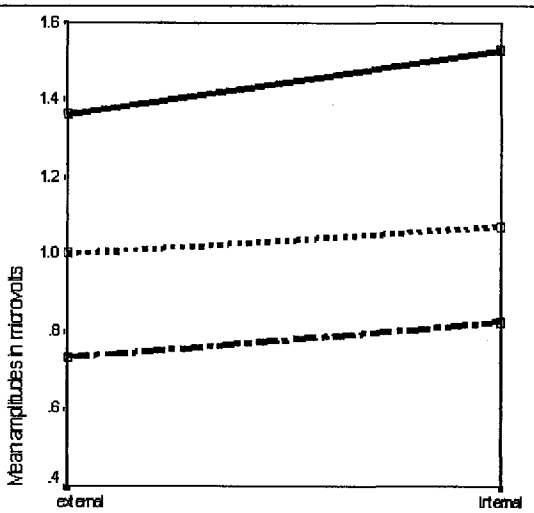


Figure 5.4: Attention x sagitallity interaction - Mean alpha amplitudes in the auditory modality revealing the differences between external and internal attention at frontal, central and posterior location.

Significant effects of task *difficulty* were found in the haptic modality. Mean α-amplitudes were greater in hard as opposed to easy conditions ([F(1,10) = 23.33; p < 0.001]. A similar trend was noted in the auditory modality [F(1,11) = 3.976; p = 0.072].

Table 5.1: Alpha Means & Standard deviations for Attention & Difficulty in μV

ACOUSTIC

		DIFFICULTY			
ATTENTION		**Easy**	**Medium**	**Hard**	**Grand mean**
External	mean	0.95	1.07	1.09	1.03
	sd	0.13	0.12	0.10	0.11
Internal	mean	1.12	1.17	1.13	1.14
	sd	0.12	0.11	0.13	0.12
Grand	mean	1.04	1.11	1.11	
	sd	0.12	0.11	0.11	

HAPTIC

		DIFFICULTY			
ATTENTION		**Easy**	**Medium**	**Hard**	**Grand mean**
External	mean	0.84	0.97	0.97	0.93
	sd	0.11	0.12	0.11	0.11
Internal	mean	0.99	1.05	1.10	1.05
	sd	0.13	0.12	0.13	0.12
Grand	mean	0.91	1.01	1.04	
	sd	0.11	0.12	0.11	

Graphs depicting amplitude values in the alpha band for easy, medium and hard tasks in both internally and externally directed attention are presented in Appendix 5.

5.4.2.4 Fast Activity (Beta and Gamma)

In partial agreement with hypothesis 7, derived from the findings of the first experiment, amplitudes in the fast EEG bandwidths were found to be significantly greater during internally directed attention. However, these effects were only observed in the auditory modality. The findings in detail are as follows.

5.4.2.5 Beta 1 (12 – 19.9 Hz)

A significant effect of difficulty was observed, such that in the haptic modality, amplitudes were greater during hard as opposed to easy tasks [$F(1,10) = 11.1$; $p < 0.01$] (see figure 5.6).

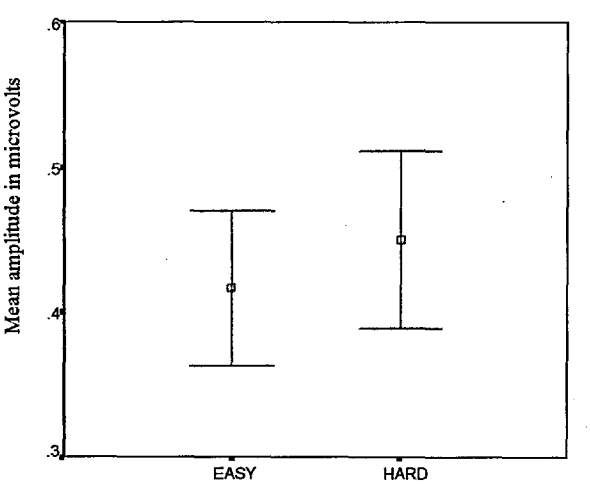


Figure 5.5: Mean amplitudes in the beta 1 bandwidth for easy and hard tasks in the haptic modality.

5.4.2.6 Beta 2 (20 – 29.9 Hz)

Greater β2-amplitudes were found during internal as opposed to external attention. Significantly so in the auditory modality [$F(1,11) = 4.91$; $p < 0.05$] and at trend for haptic tasks [$F(1,10) = 4.09$; $p = 0.071$]. See figure 5.7.

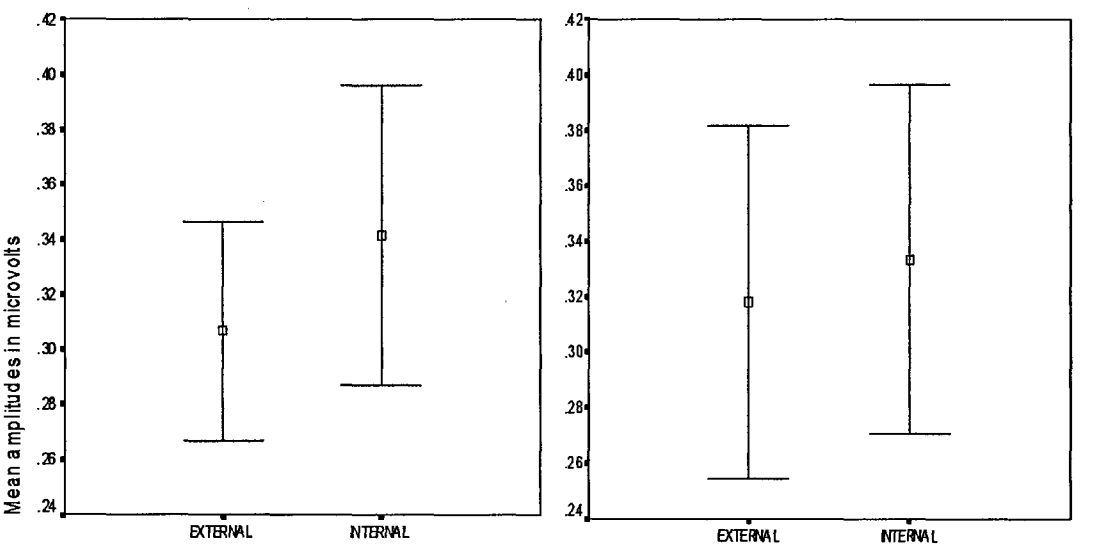


Figure 5.6: Mean amplitudes in beta 2 for external and internal attention.

5.4.2.7 Gamma 1 (30 – 48 Hz)

The effect of attention was such that γ1-amplitudes in the auditory modality were greater during internally as opposed to externally directed attention [$F(1,11) = 8.9$; $p < 0.05$] (see figure 5.8a).

5.4.2.8 Gamma 2 (52 – 80 Hz)

Again in the auditory modality, γ2-amplitudes were greater during internally directed attention [$F(1,11) = 16.18$; $p < 0.01$] (see figure 5.8b).

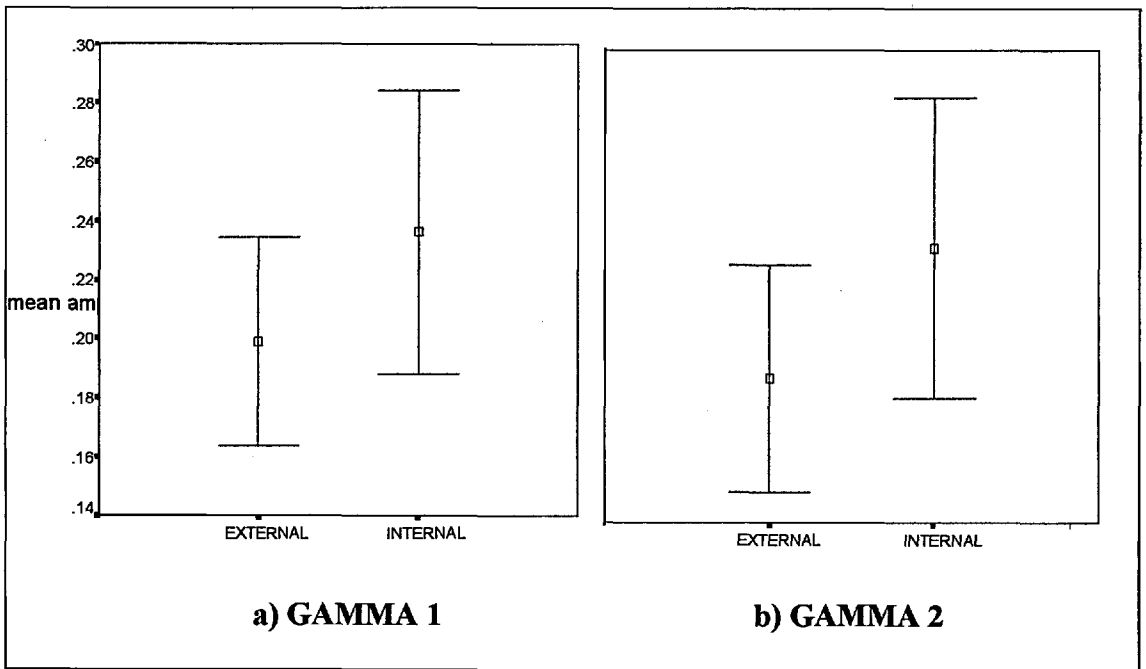


Figure 5.7: Mean amplitudes in the gamma bandwidths for external and internal attention in the auditory modality.

5.5 DISCUSSION

In order to attempt to clarify findings, the results will initially be presented according to the bandwidth in which they were found. Discussion will take place in light of both the results from the first experiment and the hypotheses derived from these and from the intake-rejection model.

- Delta: Unlike the first experiment, no effects of task difficulty were observed in the delta bandwidth. We found no evidence to confirm the findings of Harmony and colleagues (Harmony et al., 1996b; Harmony et al., 1999) linking increased delta activity with both internal attention and task difficulty. The possibility therefore has to be considered that delta cannot be viewed as an index of internally directed attention. Harmony *et al* had argued that delta facilitated internal attention by means of its role in class II selective inhibition of external / sensory stimuli (see section 3.1.2). There are two possible explanations as to why participants successfully carried out the imagery tasks without an accompanying increase in delta amplitudes. Firstly, as already stated, delta may not be an index of internally directed attention. Secondly, perhaps the internal tasks were so easy as to not require class II inhibition. This possibility warrants consideration. However, given that differences were found in the alpha band (see below) not only between internal and external attention but also between hard and easy tasks this second explanation seems unlikely.

- Theta: Unlike the first experiment, mean theta amplitudes increased in line with *difficulty* in the haptic modality. This finding is however consistent with proposals that theta activity, especially at frontal locations is associated with memory processes and executive functions. In this protocol, one way in which the easy and hard tasks differ is that the hard tasks make greater demands on working memory. Consequently, the observation that the hard tasks elicit more theta than the easy ones is entirely consistent with the previous proposals linking theta oscillations with activity in working-

memory networks (Burgess et al., 2000; Gevins et al., 1997; Grunwald et al., 2001; Ishii et al., 1999; Kubota et al., 2001).

- Alpha. With regard to attention, it was observed that mean alpha amplitudes were greater during internally directed attention than externally directed attention in all modalities. This effect was larger for the mean of anterior and posterior sites as opposed to central sites in the auditory modality but was more widespread during haptic tasks. Additionally, it was found that alpha amplitudes were greater with increased task demands, significantly so for haptic and at trend level for the auditory modality. This suggests that straightforward traditional explanations of alpha reflecting cortical idling are not tenable (hypotheses 1 and 2). The findings of increased alpha amplitudes during internally directed attention are in agreement with the findings of Ray & Cole (Ray et al., 1985b; Ray et al., 1985a) and consequently compatible with the intake-rejection hypothesis. However, the fact that alpha increases in line with task difficulty as a main effect introduces some problems with a straightforward I-R explanation. This finding reveals that alpha also increases during external attention as the task becomes harder (see appendix 5 for graphic illustration of this point). According to the intake-rejection model, one would expect this during internally directed attention but not during externally directed attention. One alternative explanation for the increases in alpha power is that it is an index of the greater degree of inhibition necessary for task completion not only during internally as opposed to externally directed attention but also as difficulty factors increase. This hypothesis has recently been proffered by

Klimesch and colleagues in attempt to explain a phenomenon that they refer to as 'paradoxical' task-related alpha increases (Klimesch, Doppelmayr, Rohm, Pollhuber, & Stadler, 2000; Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999). The work of Klimesch *et al* pertaining to this hypothesis will be explored in the following chapter.

- Beta 1. Greater beta 1 amplitudes were observed during hard tasks in the haptic modality. This finding is interesting in that it appears to reinforce ideas regarding beta activity and cognitive involvement. However, with regard to this experiment it was a serendipitous finding and as such much be treated in exploratory terms. Accordingly, beta 1 activity will be the subject of further investigation in the following experiment.

- Fast EEG activity. The experimental effects in the beta 2, gamma 1 and gamma 2 wavebands were all in the auditory modality. They all revealed greater amplitudes during internally as opposed to externally directed attention. This is in accordance with findings from the first experiment. However, given that no such findings were found in the other sensory modalities, it remains unclear whether these amplitude increases reflect a general attentional effect or something more specific to auditory processing and imagery.

5.5.1 Experimental Limitations

The results for the visual modality were not reported here as they can not be regarded as necessarily reflecting the requirements of the experiment. This is due to the possibility that some subjects may have closed their eyes during the imagination tasks. It is well established (e.g. Berger, 1929; Berger, 1930) that differences in EEG power between eyes-open and eyes-closed conditions exist (particularly in the alpha frequency band). This problem is addressed in experiment 2, where participants are required to keep their eyes open in all conditions. In the experiment described above, participants' eyes were closed for all conditions in the acoustic and haptic modalities.

5.5.2 Summary

The main findings and their implications for the study can be summarised in the following way:

- The theta *difficulty* effects in the haptic modaliy lend further support to the notion of a relationship between theta oscillations and working memory networks.

- Pan-modal effects of both *attention* and task *difficulty* were observed in the alpha band. These revealed alpha amplitudes to be greater during states requiring internally directed attention, and to have increased in line with

difficulty. The attentional findings are consistent with hypotheses derived from the intake-rejection model. However, the difficulty effects cast some doubt as to the completeness of this interpretation. Such results as those found here are compatible with ideas of increases in alpha reflecting the more generalised task-related inhibition proposed to be necessary for the successful completion of certain cognitive goals (e.g. Klimesch et al., 2000; Klimesch et al., 1999). It must be stressed however that this proposal is not the same as the traditional view of alpha reflecting cortical idling, indeed, the difficulty findings alone render this idea as no longer tenable.

- The association between task difficulty and increased beta 1 amplitudes in the haptic modality is in line with ideas linking beta activity with cognitive involvement in a task. What such involvement actually entails is yet unclear and will be the subject of further investigation in the following experiments but it seems reasonable to suggest that it would increase as task demands increase.

- The findings of increased fast wave activity during internally directed attention are compatible with similar findings from experiment one. However, the absence of this effect in the haptic modality raises the question that perhaps it is a modality-specific finding.

As outlined above, the limitations of this experiment require that one can not rely on the validity of the results from the visual modality; accordingly, they were not reported. Consequently, a constructive replication study was devised that sought

to address these limitations. Several modifications were made to the protocol that not only ensured that participants kept their eyes open in the visual modality but also in the auditory and haptic tasks. This would facilitate a comparison of findings between the two experiments to see if contrasts between external and internal attention differed depending on whether the participants' eyes were open or shut during all the tasks. The modifications to the protocol and their rationale will be presented in the following chapter (section 6.2.2).

6 EXPERIMENT 3

6.1 RATIONALE

The main purpose of this experiment is to serve as a constructive replication of experiment 2 in terms of results. It will also allow a more formal investigation of the 'inhibition' hypothesis introduced in the preceding discussion. This hypothesis posits that so called 'paradoxical' increases in alpha activity reflects task-specific inhibition of non task-relevant cortical areas.

6.2 INTRODUCTION

It was found in the last experiment that alpha amplitudes increased not only during internally directed attention in the form of mental imagery but also as function of task difficulty. The possibility was raised in the discussion section that these results may have the following implications: 1) the notion of alpha reflecting cortical idling is no longer tenable; 2) alpha may be more plausibly explained in terms of task-specific inhibition. This second interpretation is of course, compatible with the intake-rejection hypothesis, which equates alpha with the inhibition of 'interfering' sensory information during tasks that require internally directed attention. However, this idea also extends the I-R hypothesis, in the sense that alpha synchronisation is postulated to be required when any inhibition of task-irrelevant stimuli / processes is required. This approach (henceforth referred to in this study as the 'Inhibition Hypothesis') has been

championed in recent years by Klimesch and colleagues and will be described in greater detail in the following section.

6.2.1 On the Inhibition Hypothesis

This section will begin with a brief introduction to Klimesch's work regarding the EEG in order to explain the reasoning that led to the inhibition hypothesis. Klimesch and colleagues have hypothesised a wide role for neural networks oscillating at alpha frequencies in various cognitive processes involved in both attention and memory. An early finding by Klimesch *et al* that set him on this path was an observation of a relationship between alpha frequency and memory performance (Klimesch et al., 1990). In two experiments it was noted that good performers in a memory task has significantly higher alpha frequency than poor performers and were also faster to respond. These results led to the conclusion that alpha frequency may have a direct relation with the speed with which information can be recalled from memory. Further evidence for a link between alpha and memory was offered by Klimesch and colleagues revealing desynchronisation in the upper range of the alpha band during memory encoding (Klimesch, Pfurtscheller, & Schimke, 1992) and in a different experiment, desynchronisation during the presentation of a judgement stimulus in a semantic memory paradigm (Kroll & Klimesch, 1992). The basic principle to be understood here is that activation of an alpha neural network leads to desynchronisation (see Klimesch, 1997 for a review). With respect to attention, Klimesch *et al* have observed that desynchronisation can occur in the lower range of the alpha band at the time of a warning stimulus especially one

preceding a target stimulus and this is thought to reflect an increase in alertness and an allocation of processing resources (Klimesch, Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998; Klimesch et al., 1992; Klimesch, Pfurtscheller, & Schimke, 1993; Klimesch, Schimke, & Pfurtscheller, 1993).

More recently, Klimesch and colleagues (Klimesch et al., 2000; Klimesch et al., 1999) have reported that in certain circumstances they have observed what they refer to as a 'paradoxical' increase in alpha power. They employ this term as it emphasises the perceived contrary nature of the alpha activation (i.e. alpha synchronisation where one would have expected desynchronisation). They have proposed that alpha synchronisation may index inhibitory processes serving to increase signal to noise ratios – the greater the task demands within this network, the more inhibition needed, the greater the synchronisation. Klimesch's proposals are compatible with the notion of "surround inhibition" wherein active cortical areas, indexed by alpha desynchronisation are surrounded by a 'doughnut' of alpha synchronisation or inhibition (Suffczynski, Kalitzin, Pfurtscheller, & Lopes da Silva, 2001). Thus the surrounding inhibition, controlled by thalamo-cortical and reticular nucleus pacemaker cells, acts to increase the gain on the focally active area of alpha desynchronisation in a manner in keeping with Crick's spotlight of attention hypothesis (Crick, 1984). These findings suggest that alpha activity is not a simple index of cortical idling, but that it is a measure of active processing necessary for internally driven mental operations.

In the light of these proposals, the main aim of this experiment was to test the inhibition hypothesis. If the findings from the second experiment could be replicated with an improved protocol, the notion of task-related increases in alpha reflecting task-specific inhibition could be strengthened. The improvements to the protocol used previously are described in the following section.

6.2.2 Modifications to the Protocol

In order to clarify and replicate the findings from experiment 2, a number of modifications were made: 1) The levels of difficulty (for both internal and external conditions) were reduced from 3 to 2 in order to remove possible differences in subjective difficulty between questions two and three. 2) The questions constituting the hard difficulty level were standardised into the type "are the 1^{st} (2^{nd}/3^{rd}) and 4^{th} (5^{th}/6^{th}) stimuli the same"? 3) A new set of acoustic, haptic and visual stimuli was included in order to maintain modality and stimulus balance (see procedure). 4) In all conditions in all three modalities the participants were instructed to keep their eyes open at all times, and in order to facilitate the mental imagery, the participants fixated upon a plain black background. 5) Having found no interaction between *attention* and *difficulty* using an ANOVA model in the previous experiment, it was deemed appropriate to return to the randomisation t-test procedure described in the first experiment. This would facilitate a more detailed topographical analysis of the data.

6.3 METHOD

6.3.1 Subjects

18 participants (12 male & 6 female) were tested, ages ranged from 21 to 38 years (mean: 26.6). All participants reported normal hearing, haptic sensation, normal or corrected to normal vision and no known psychiatric or neurological problems. Ethics Committee approval was granted for this study.

6.3.2 EEG Recording

The EEG and EOG recording details were as for experiment 1.

6.3.3 Procedure

The protocol used was the same as for the second experiment with modifications as describes above. This resulted in the following configuration:

1. Easy External task – presentation of stimuli.
2. Hard External task - presentation of stimuli + question.
3. Training session – repeat of stimulus presentation until participant is able to successfully imagine them.
4. Easy Internal task – imagining of stimuli.
5. Hard Internal task - imagining of stimuli + question

In order to keep the stimuli balanced between subjects a new stimulus set (stimulus set 3) was introduced for all three modalities. Auditory set 3: E,G,E,D,D,G (E = 329.6Hz; G = 392Hz; D = 293.7Hz). Haptic set 3: M,R,S,S,R,M (Grit size: S=1200g;M=240g;R=40g). Visual set 3: see figure 5.1.

6.3.4 Data Preparation

Ocular artefact rejection was carried out using methods described previously (Croft et al., 2000a). The EEG data were epoched from 1000 – 11000ms after sequence onset and spline-fit to 8192 points. A fast-Fourier transform of the data enabled extraction of the various components from the raw EEG within the following frequency parameters: delta (δ) = 0.1-3.9 Hz; theta (θ) = 4-7.9 Hz; alpha (α) = 8-11.9 Hz; beta 1 ($\beta 1$) = 12-19.9 Hz; beta 2 ($\beta 2$) = 20-29.9 Hz; gamma 1 ($\gamma 1$) = 30-48 Hz; gamma 2 (γ) = 52-80 Hz.

6.3.5 Statistical Analysis

In order to obtain a more detailed picture of the topography of any EEG changes than available from the second experiment, electrode sites were examined individually rather than grouped into regions. Corresponding electrode amplitudes in different conditions (external v internal; easy v hard) were compared using Wilcoxon t-tests. Topographical maps were drawn using the resulting *z*-values according to the method of spherical splines (Perrin, Pernier, Bertrand, & Echallier, 1989). As in the first experiment, in order to compensate for Type I error due to the number of comparisons being calculated, a

randomisation test procedure was employed (Burgess et al., 1999; Burgess et al., 1997a; Edgington, 1987). See section 4.2.9.1 on randomisation t-tests.

6.4 RESULTS

Results for the comparisons of EEG amplitudes between externally and internally directed attention conditions can be seen in figures 6.1/4/5/6/8. Those for easy versus hard difficulty levels can be seen in Figures 6.2/3/7/9. Upper maps indicate *z*-values reflecting the difference between the two conditions. Brighter tones reflect increased amplitudes during internal or hard conditions. Lower (smaller) maps show the randomisation probability values for the differences. Results will be presented according to the bandwidth in which they were observed.

6.4.1 Delta

See figures 6.1 & 6.2 for topographical maps.

An effect of attention was found in the auditory modality, wherein δ-amplitudes were significantly greater during external compared to internal attention at electrode site C3. In the haptic modality, δ-amplitudes were greater during easy tasks at CP1.

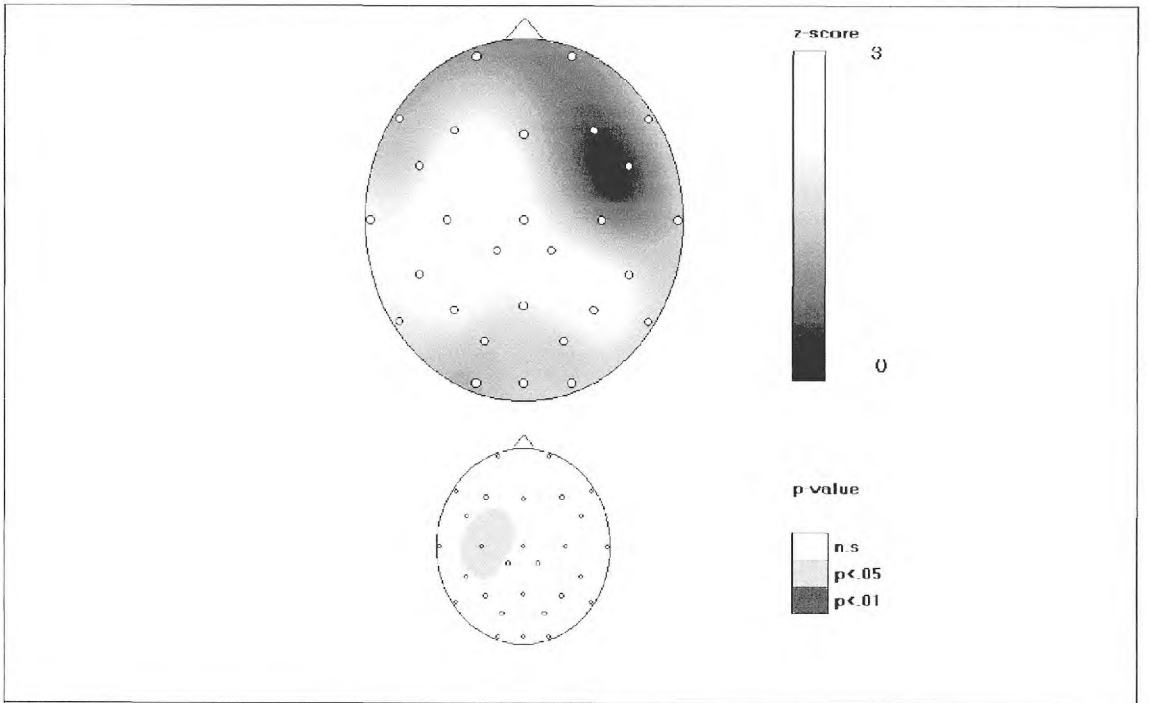


Figure 6.1: EEG amplitudes in the delta bandwidth measured during externally versus internally directed attention. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during externally directed attention. Lower (smaller) maps show the randomisation values for the differences.

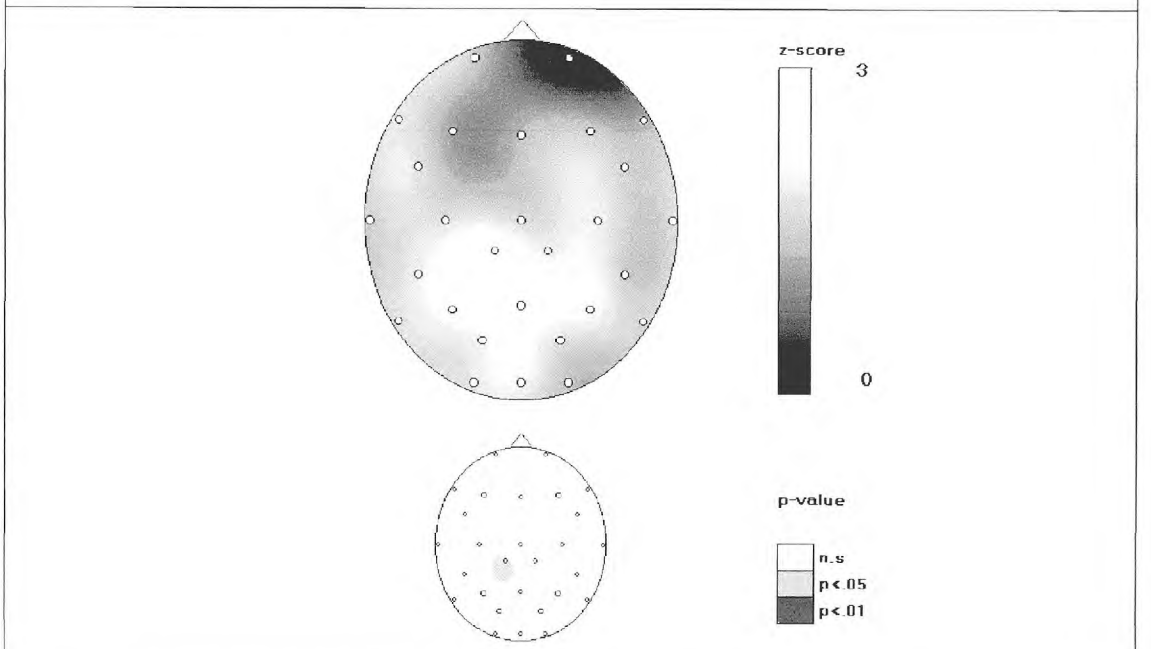


Figure 6.2: EEG amplitudes in the delta bandwidth measured during easy versus hard tasks. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during easy tasks. Lower (smaller) maps show the randomisation values for the differences.

6.4.2 Theta

See figure 6.3 for topographical map.

Significant differences in the θ-band were observed in the visual modality at F3, F4 and C4. Differences at trend levels were noted at C3, Fz, Cz, Pz, CP1 and CP2. These comparisons indicated greater amplitudes during hard tasks as opposed to easy ones.

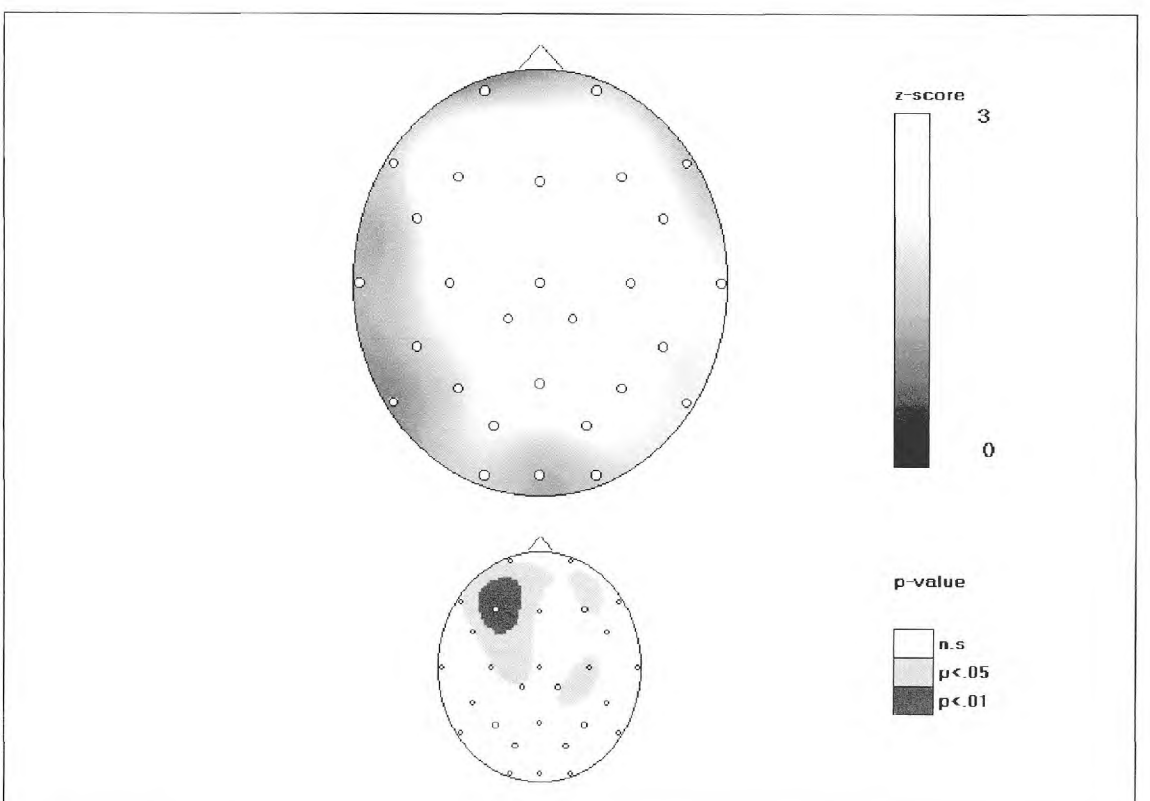


Figure 6.3: EEG amplitudes in the theta bandwidth measured during easy versus hard tasks. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during hard tasks. Lower (smaller) maps show the randomisation values for the differences.

6.4.3 Alpha:

As can be seen from figure 6.4, significant differences between attentional conditions were found in all three sensory modalities in the alpha band. These significances reflected greater α-amplitudes during internally as opposed to externally directed attention. In the auditory modality these differences were observed at O2, OZ, T6 and at trend level at O1. In the haptic modality, the significant differences were more widespread at FP2, F3, F4, C3, C4, P3, P4, O1, O2, F7, T4, Fz, Cz, Pz, Oz, FTC1, FTC2, TCP1, TCP2, CP1 and CP2 and at trend level at F8. In the visual modality, the observed differences were very similar to those in the auditory modality, being significant at O2 and Oz, and at trend level at O1 and T6.

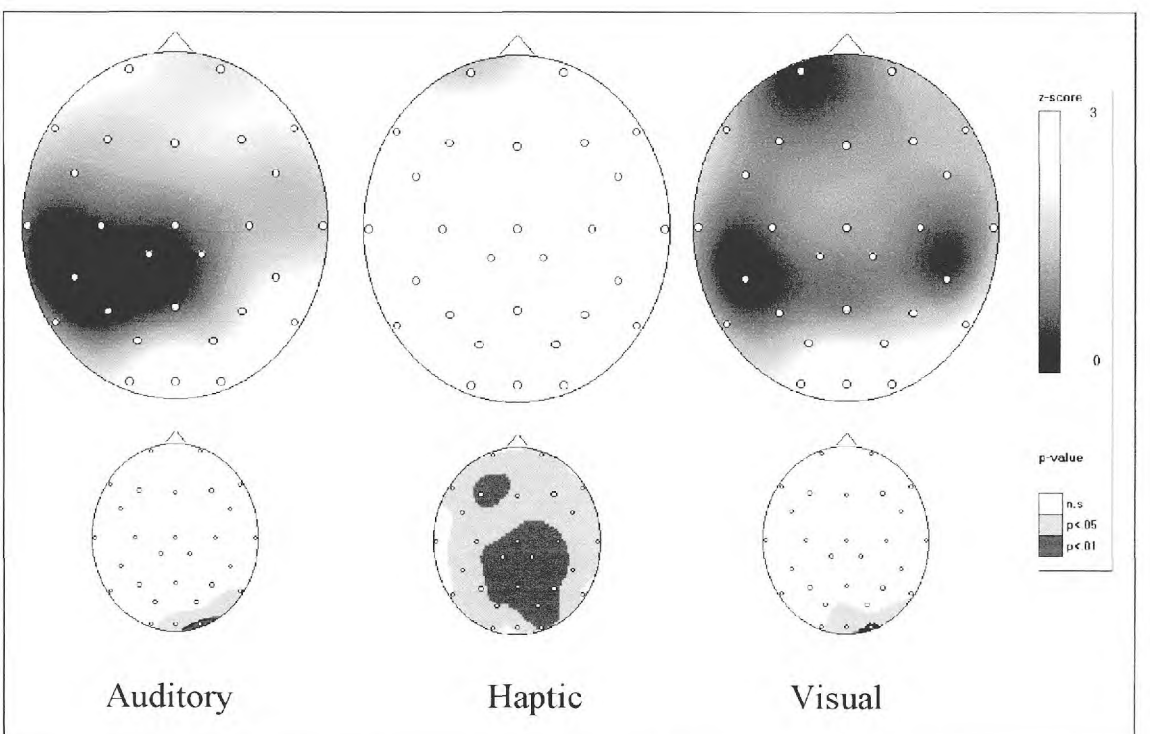


Figure 6.4: EEG amplitudes in the alpha bandwidth measured during externally versus internally directed attention. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during internally directed attention. Lower (smaller) maps show the randomisation values for the differences.

As can be seen from figure 6.5, significant effects of task difficulty were found in both the auditory and visual modalities in the alpha band. These significances reflected greater α-amplitudes during hard as opposed to easy tasks. In the auditory modality these differences were observed at FP1, P4, O2, T6, PO2 and at trend at TCP2. In the visual modality, the observed differences were significant at O2 and T6, and at trend level at C4 and FTC2. A similar yet small trend was also noted during haptic tasks at TCP2.

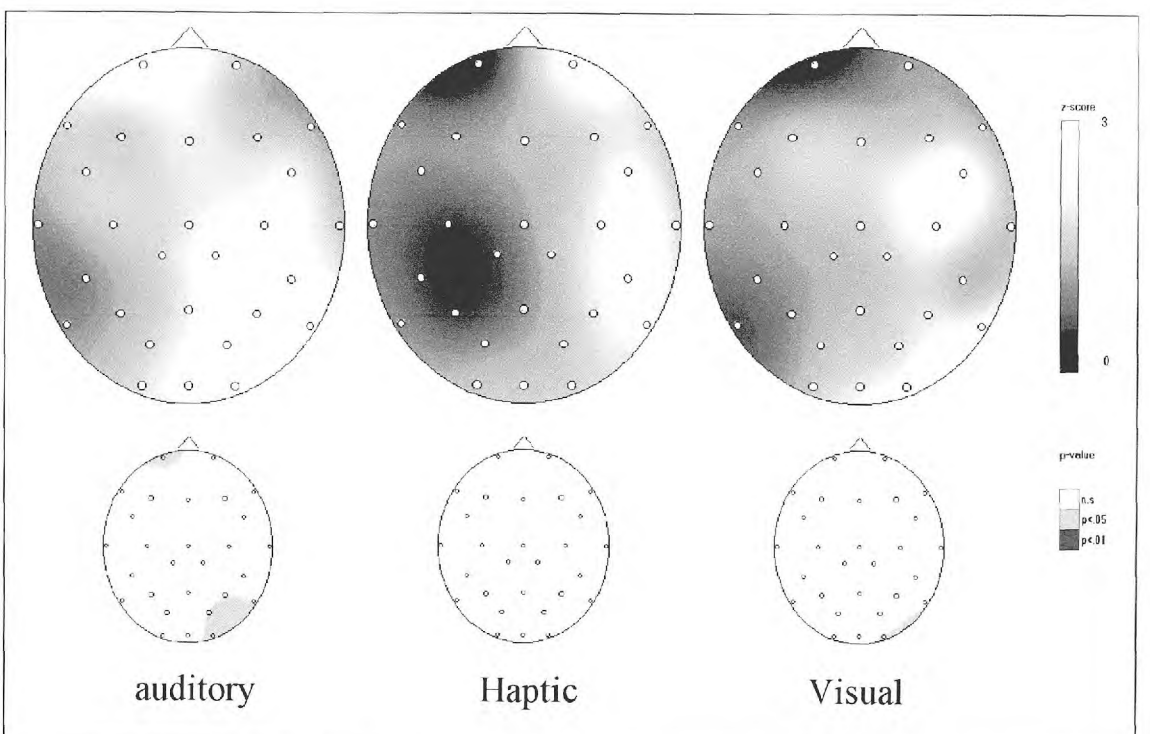


Figure 6.5: EEG amplitudes in the alpha bandwidth measured during externally versus internally directed attention. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during hard tasks. Lower (smaller) maps show the randomisation values for the differences.

Graphs and a table of means presenting the mean alpha amplitudes for easy and hard tasks in both externally and internally directed attention can be found in Appendix 6.

6.4.4 Beta 1

Significant effects for attention were observed in both the haptic and visual modalities. β1-amplitudes were greater during internally directed attention. In the haptic modality, these effects were extensive, and were significant at C3, C4, P3, P4, Cz, Pz, CP1, CP2, PO1 & PO2 and at trend at O1 & O2. In the visual modality the effect was less widespread, being significant at T4. See figure 6.6 for a map of β1 attention findings.

With regard to the difficulty factor, it was observed that beta 1 amplitudes in the visual modality were greater during hard as opposed to easy conditions at occipital sites O2 and Oz. See figure 6.7.

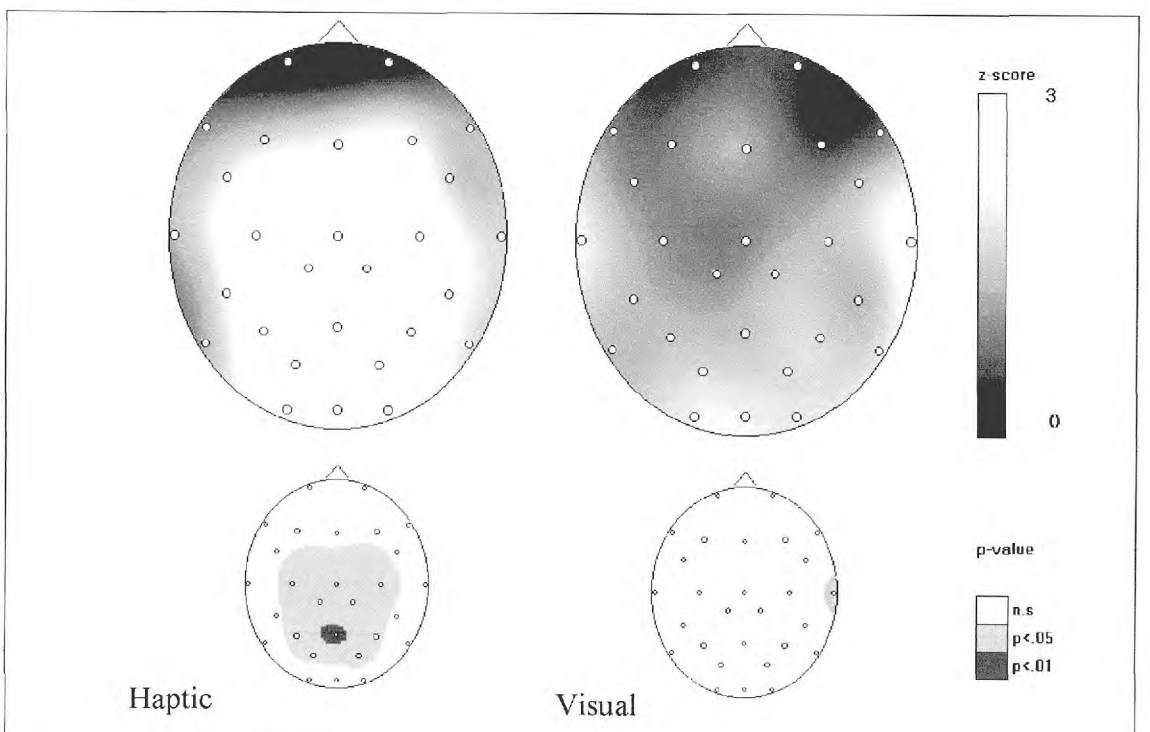


Figure 6.6: EEG amplitudes in the beta 1 bandwidth measured during externally versus internally directed attention. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during internal attention. Lower maps show the randomisation values for the differences.

6.4.5 Beta 2

The only experimental effect observed in the beta 2 bandwidth was a trend towards greater posterior β2-amplitudes during internally directed attention at PO1 & PO2 in the auditory modality.

See figure 6.8 for a map of β2 findings.

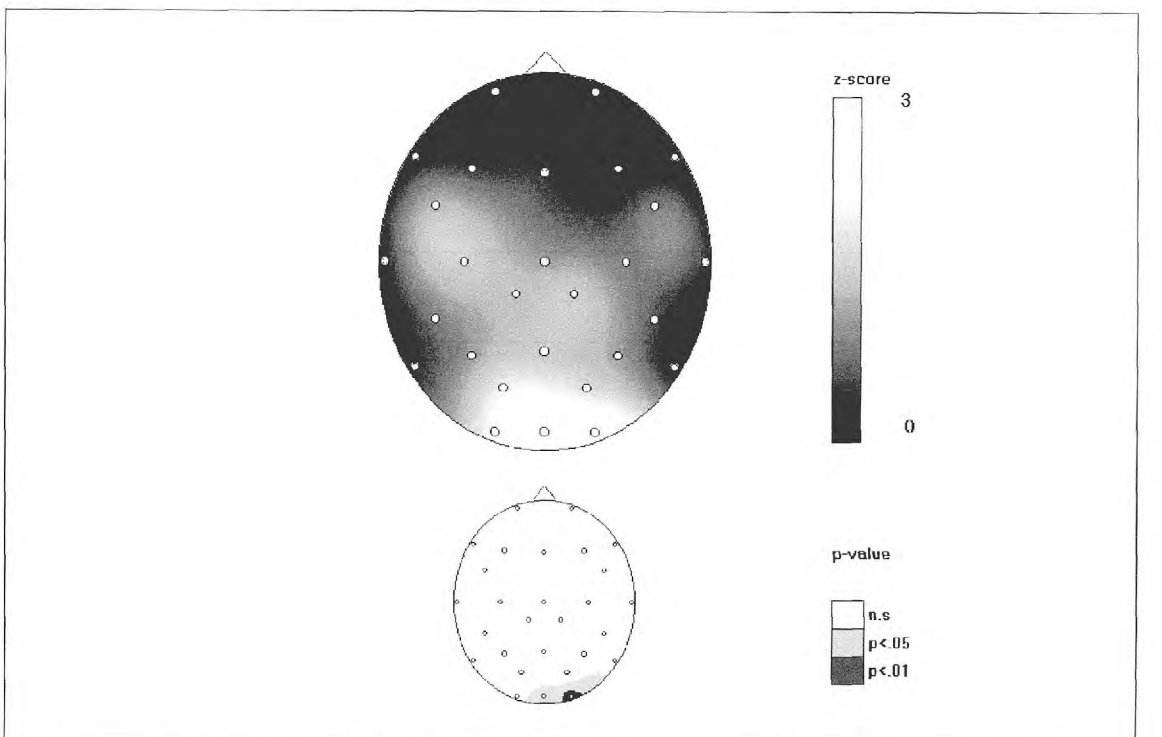


Figure 6.7: EEG amplitudes in the beta 1 bandwidth measured during hard versus easy tasks. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during hard tasks. Lower (smaller) maps show the randomisation values for the differences.

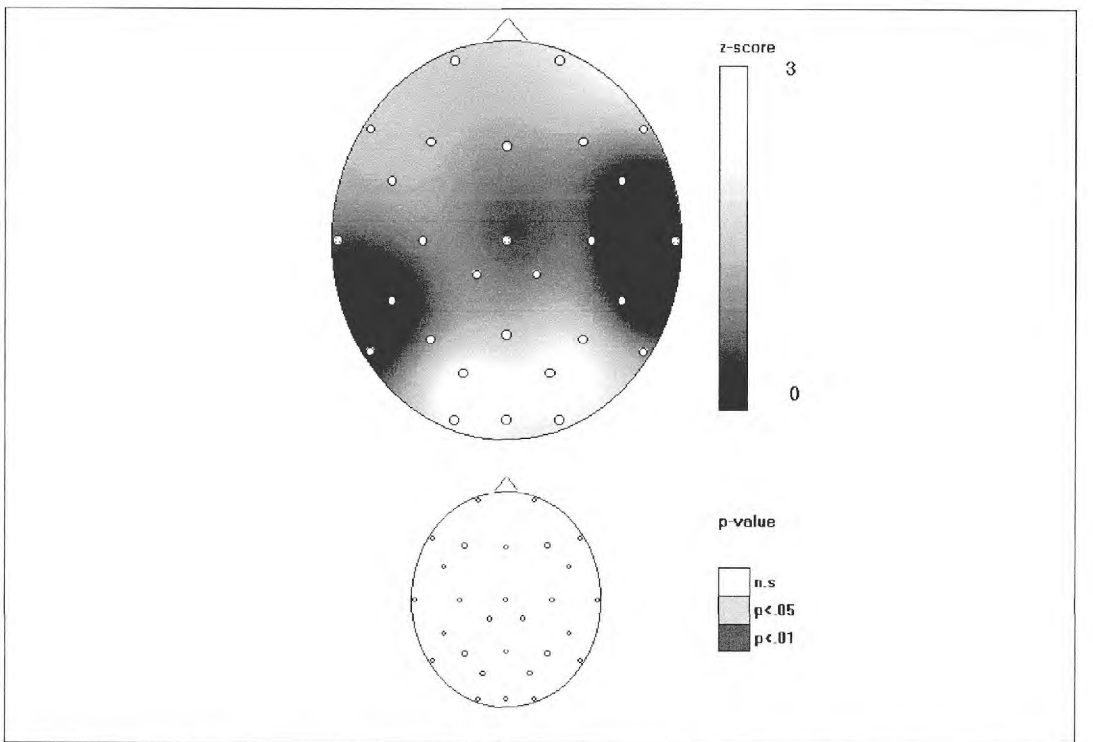


Figure 6.8: EEG amplitudes in beta 2 measured during externally versus internally directed attention. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during internally directed attention. Lower (smaller) maps show the randomisation values for the differences.

6.4.6 Gamma 1

As can be seen from figure 6.9, in the haptic modality, γ1-amplitudes were significantly greater during easy as opposed to hard tasks at frontal sites F3 & Fz and at trend at F4.

6.4.7 Gamma 2

Similar to lower gamma, γ2-amplitudes were also significantly greater during easy as opposed to hard tasks at frontal site Fz and at trend levels at FP1 & F3. See figure 6.9.

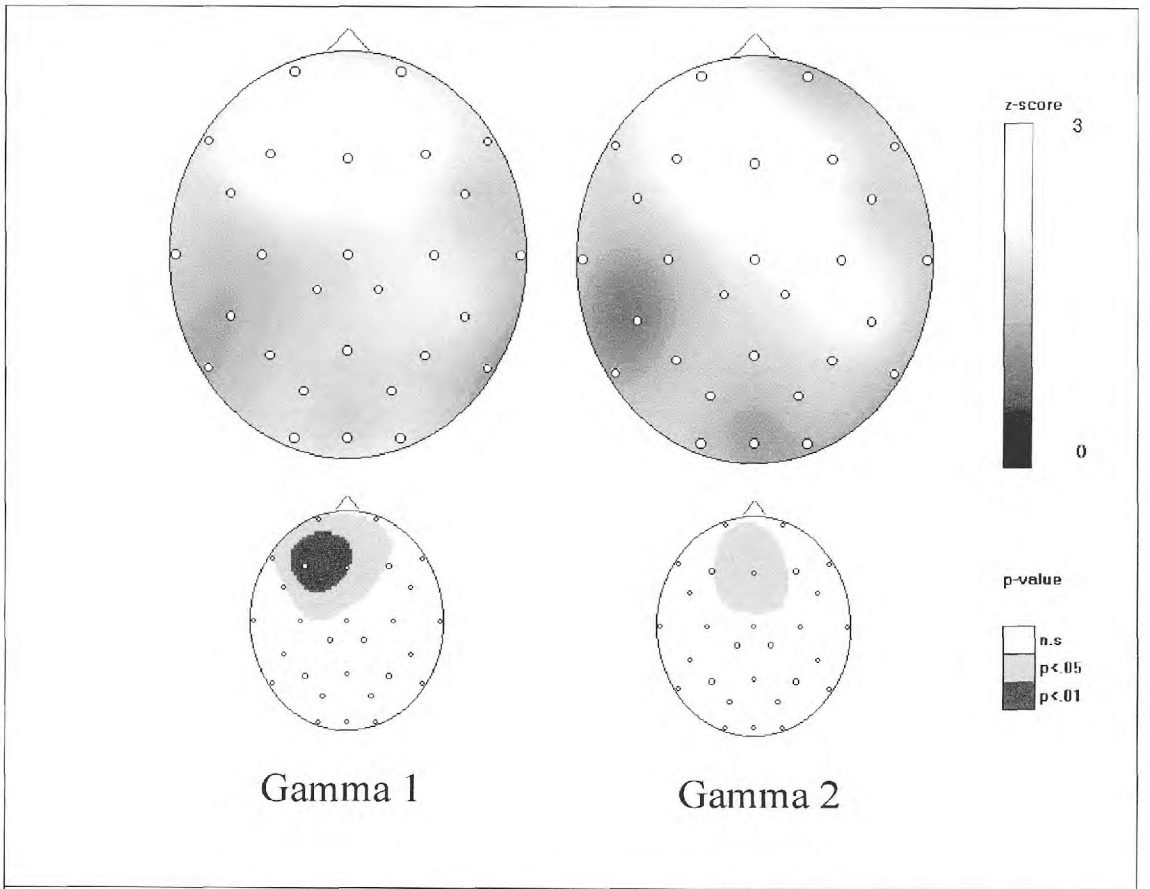


Figure 6.9: EEG amplitudes in the gamma bandwidths measured during easy versus hard tasks. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during easy tasks. Lower (smaller) maps show the randomisation values for the differences.

6.5 DISCUSSION

For reasons of clarity, the results will also be addressed according to the bandwidth in which they were observed.

6.5.1 Delta.

In accord with results from experiment 1, δ-activity was found to be negatively associated with internal attention and task difficulty. As stated before, this is

contrary to the findings of Harmony *et al* (Harmony et al., 1996b), who reported a positive association on both accounts. It is interesting to note that this relationship revealed itself through the more location-specific statistical methods employed in experiments 1 and 3 but not when electrode sites were grouped into regions as in experiment 2. One can only assume that these are subtle findings easily lost with lower signal to noise ratios.

6.5.2 Theta.

Findings of increased theta power as a function of difficulty were observed during visual tasks. This is in accord with results from experiment two. It is tempting to conclude that these findings are indeed as a result of the increased working memory demands apparent in hard as opposed to easy tasks (e.g. holding the 1st stimulus 'in mind' before reaching and comparing it to the 4th stimulus). This finding and its topographical location adds further weight to the body of evidence identifying theta oscillations (particularly at frontal sites) with working memory networks (Burgess et al., 2000; Gevins et al., 1997; Grunwald et al., 2001; Ishii et al., 1999; Kubota et al., 2001).

6.5.3 Alpha.

In line with results from experiment 2, greater mean α-amplitudes were observed in internally as opposed to externally directed attention at various electrode sites, in all modalities. In other words, further evidence was found in the EEG for increased alpha during imagination as opposed to sensory intake tasks. This was

particularly evident at sites near visual cortical areas, e.g. Oz and O2. The reader is reminded that the experimental findings of Ray & Cole (Ray et al., 1985b; Ray et al., 1985a) regarding increased alpha power during internal attention were located at temporal and parietal sites whereas those reported here are in occipital areas. However, in Ray & Cole's experiments, no occipital electrodes were employed and consequently any activity from this area would have been missed.

As far as task difficulty was concerned, mean α-amplitudes were greater for hard as opposed to easy tasks in the auditory and visual modalities, at sites similar to those for attention. The findings for *attention* and *difficulty* combined lend support to the hypothesis deriving from the work of Klimesch and others (Klimesch et al., 2000; Klimesch et al., 1999) that task-related increases in alpha reflect the inhibition of non-task relevant areas or processes. However, the locality of these findings introduces a note of caution. If, as proposed by the likes of Kosslyn and associates (see section 5.2.5.2), visual cortex is active during visual imagery then one would not expect inhibition in this area. However, this is exactly where our findings for both *attention* and *difficulty* were observed. Additionally, it is the opposite of that which would be expected if imagery were to be indexed by desynchronisation at these sites. The significant results for the auditory modality are almost identical to those in the visual modality, i.e. over occipital cortex. This initially puzzling result may be explained by recent findings by Schürmann *et al*, who have found MEG activity specific to auditory imagery in occipital locations (Schurmann, Raij, Fujiki, & Hari, 2002). Schürmann and colleagues have sought to explain this phenomenon by postulating that subjects employ visualisation strategies. This is not unheard

of previously; indeed, Platel *et al* (Platel et al., 1997) have found other areas associated with visual imagery, e.g. the precuneus, to be active during an auditory pitch-discrimination task similar to that employed in the present study. Additionally, in the present experiment, subjects reported using visualisation techniques in order to compare whether for example, the 2nd and 5th notes in a sequence were the same. With regard to the haptic modality, the task-related alpha increases were much more widespread, and were strongest at right occipital locations and central sites overlying sensori-motor cortex. It tempting to suggest that these findings reflect a combination of visual and touch imagery strategies.

We are now left with the problem of what are the mechanisms behind such imagery-related increases in alpha? It still may be the case that the inhibition hypothesis is applicable. This is more easily argued for visual tasks as it would imply inhibition of sensory input to the visual cortex but the plurality of the effects (e.g. the haptic results) make this explanation harder to entertain. Another recent proposal that may prove useful is that of the association between alpha activity and top-down processing. Several studies have found increased alpha coherences between distal cortical areas during tasks thought to be biased in favour of top-down processing requirements, such as mental imagery (e.g von Stein et al., 2000b). It should be noted that such studies are not using the term 'top-down' in the traditional information processing sense of the word but in a more recent, dynamic integrative sense (see Box 6.1).

Box 6.1: ***The Question of Top-down and Bottom-up Processing***

The notion of a central command centre in the brain, where information is compiled, decisions are made, actions planned and even, where consciousness may arise has largely gone the way of Descatres' pineal gland – laid to rest with fond remembrances of a quaint but untenable understanding of mind-brain interactions. The philosopher Dan Dennett emphasizes that neuroscientists need to beware of falling into what he terms this *trap of the Cartesian theatre* (Dennett, 1997; Dennett et al., 1992). Accordingly, evidence from modern neuroscience has led away from the homunculus in our heads (Gilbert Ryles' "Ghost in the Machine" - Ryle, 1949) and tends to highlight the dynamic, parallel processing, even emergent nature of the brain. However, some terminology still remains from this way of looking at brain processes, notably the two expressions: 'top-down' and 'bottom-up'.

Nevertheless, these terms can still serve a useful purpose even when used in a paradigm that assumes no central control mechanism or non-material intervention. If one accepts the premiss that the brain is a dynamic environment with continuously emerging and evolving patterns of activation that shape behaviour, then one can begin to understand the notions of top-down and bottom-up processes in a subtly different manner. In this context, top-down processes are in effect 'the state-of-play' of the brain at a given instant, whereas bottom-up processes are the immediate effects of sensory modulation upon this system. In other words, top-down processes are all those concerned with memory, attention, anticipation, goal-orientation et cetera and all 'serve the higher goals' or drives of homeostasis, survival and reproduction. They are facilitated by the huge amount of reciprocal connections between brain areas allowing not only feed-forward activity, but feed-backwards communication as well

(Edelman et al., 2000). Bottom-up processes are concerned with immediate sensory input and provide information concerning the external environment. The classic view derived from the information processing approach was that perception is a bottom-up process with a feed-forward hierarchy (von Stein, Chiang, & Konig, 2000a). However, this view has been in serious question ever since the classic paper by Moran & Desimone revealing the influence of attention on neurons in extrastriate visual cortex (Moran & Desimone, 1985).

The question is, how and to what extent do these two processes interact in the act of forming a percept? For some time debate raged as to their relative balance. On one hand, the importance of bottom-up mechanisms were championed by people such as Gibson. Coming from a psychophysiological background with a strong belief in the importance of ecological validity, Gibson argued that most, if not all the information necessary for visual perception was present in light itself. It is an easy effortless process, akin to a radio picking-up radio signals (Gibson, 1950; Gibson, 1966; Gibson, 1979). On the other hand, psychologists such as Gregory have emphasized the importance of top-down mechanisms. Gregory, drawing from his work with visual illusions has argued that the brain is a hypothesis-making machine and that perceptions can be usefully understood as predictive hypotheses (Gregory, 1970; Gregory, 1980; Gregory, 1997). Out of this seemingly dialectic position, something of a synthesis began to emerge, emphasizing the importance of both processes to perception. For instance, an influential proposal was made by Neisser of a cyclic theory of perception (Neisser, 1976). In this model, perceptual exploration samples the environment, that in turn modifies the relevant memory networks that consequently direct perceptual exploration and so on.

Latterly, there is general agreement that both processes play a role in the formation of percepts. The act of perception, involves the integration of sensory information with "internal constraints such as expectations, recent memories, planned actions et cetera" (von Stein, 1999). From such a stance, perception is shaped by knowledge, in the sense that knowledge is the physical embodiment of experience within the plastic neural networks of the brain (and arguably, perception is the experience of this plasticity taking place). In other words, memory and perception involve changes to the system, and previous changes to the system effect future changes.

To summarise, the once dualisticly-tainted terms of top-down and bottom-up processing have developed a new role in cognitive neuroscience emphasizing the dynamic nature of brain activity, in particular with respect to the balance between sensation and past experience in the formation of percepts.

However, before proposals of the association between alpha activity and top-down processing can be explored, it is important to test as fully as possible Klimesch's ideas, for as Popper suggested, the scientific merit of any theory is that it be falsifiable and it is the responsibility of any investigator to attempt such falsification (Popper, 1959). Thus, having established doubt as to the explanatory value of Klimesch's proposals regarding paradoxical alpha, it is the requirement of this study to investigate the recent proposals as to the details of the inhibition theory and thereby attempt to show them inadequate as an explanation for the present findings of this study. For instance, Klimesch has found that the mechanisms behind the task-related increases in alpha in his studies appear to be due to evoked activity; that is activity that is phase-locked to

the stimulus presentation (see section 7.1.1 for a more detailed explanation). However in the present study, such an explanation would lead one to expect task-related increases in alpha to be associated with the sensory intake aspect of the protocol (where behaviour was more tightly associated with stimulus presentation) as opposed to the mental imagery tasks where behaviour was less constrained temporally. We found the opposite to be the case, and therefore the notion that evoked activity may underlie our findings seems implausible.

One further caveat that warrants mention is related to the bandwidth parameters used in this study. It is possible that the problems associated with applying an inhibition hypothesis explanation to our present findings may arise from the traditional broadband demarcation of alpha used in this experiment. Typically, Klimesch and associates split alpha into three sub-bands (Klimesch, 1999). Consequently, one has to entertain the possibility that our results are not directly comparable with those of Klimesch *et al* (Klimesch et al., 2000; Klimesch et al., 1999). This provides further reason to test the inhibition hypothesis in detail, using as far as possible, the parameters and measures used by Klimesch and colleagues. This is the focus of the next experiment, presented in chapter seven.

6.5.4 Beta.

The findings of greater beta 1 activity during internal attention in the haptic and visual modalities, during hard tasks in the visual modality and also the trend of increased beta 2 activity at similar sites to beta 1 during internal attention may also be interpretable in terms of the idea of increased top-down requirements

introduced above. Consequently the role of beta oscillations will also be the target of focused investigation in the following chapter.

6.5.5 Gamma.

The findings of increased gamma activity (both gamma 1 and 2) at fronto-central sites during easy as opposed to hard haptic tasks was unexpected. It is possible that they are modality specific and reflect the perceptual binding processes ascribed to gamma oscillations and the subjective difficulty of the haptic tasks. The argument is as follows: haptic tasks were the hardest tasks according to the self-reports of the subjects; in the other two sensory modalities, perceptual binding was successful; however, in the haptic modality, the increased task demands of the hard difficulty level on top of an already very difficult task led to interference with perceptual binding and hence more observable gamma during easy tasks. However, this is a highly speculative suggestion and one that needs further investigation that is beyond the scope of the present study.

6.5.6 Summary

The results from experiment 3 replicated and extended those from experiment 2, particularly so in the alpha bandwidth and also to a lesser degree in the beta bands. It was found that in all modalities, alpha amplitudes were greater during internally as opposed to externally directed attention. Additionally, alpha was greater during hard tasks in all modalities, although only at trend levels in the haptic task. With regard to the inhibition hypothesis, a preliminary assessment of

the results would appear to lend further weight to this model. However, the scalp locations of these findings provide some doubt as to this conclusion. The models of Kosslyn and associates (e.g. Klein et al., 2000; Kosslyn et al., 2001; Salenius et al., 1995; Thompson et al., 2000) concerning the locality of mental imagery suggest that activity should not be inhibited in the areas found to be associated with more alpha activity in this experiment. These findings, in association with those of increased beta activity during certain internally directed or hard tasks suggest Klimesch's ideas regarding the inhibition hypothesis may not prove a plausible explanation of our findings. However, it may be that the use of traditional broadband alpha instead of the narrow band parameters favoured by Klimesch may have led to further problems of interpreting our results. Either way, it is important to test the inhibition hypothesis as rigorously and as completely as possible. Consequently, a further experiment was devised that sought to carry out a more detailed investigation of the inhibition hypothesis, particularly with regard to Klimesch's proposals for the componential make-up of 'paradoxical' alpha (Klimesch et al., 2000). This experiment and its findings is the subject of the next chapter.

As a final point, it is interesting to note the similarity in the findings in the alpha band between this and the previous experiment. This is despite the fact that in the second experiment, in the haptic and auditory tasks, subjects had their eyes closed for all tasks, whereas in the third experiment subjects kept their eyes open at all times. Thus the alpha findings reported here can be taken as reflecting the cognitive demands of the tasks in hand as opposed to differences in visual input requirements.

7 EXPERIMENT 4

7.1 INTRODUCTION

The results from the third experiment replicated those from experiment 2 with regard to the effects of attentional direction and task difficulty on alpha activity. On first inspection, these findings appear to lend support to the ideas regarding alpha as an index of task-related inhibition proposed by those such as Klimesch and colleagues (Klimesch et al., 2000; Klimesch et al., 1999). On the other hand, the locality of the EEG findings sheds some doubt on these proposals (see section 6.5). Klimesch has postulated that evoked activity may underlie such 'paradoxical' increases in alpha power (Klimesch et al., 2000). However, such a process would lead one to expect the opposite findings to those that were found in the previous two experiments. As a result, a new protocol was developed that sought to investigate in greater depth the inhibition hypothesis and the mechanisms proposed by Klimesch *et al* to underlie it. The main function of the new protocol was as follows: to balance completely the sensory intake tasks with the mental imagery tasks in terms of their temporal requirements. In other words, to ensure that imagery was as tightly time-locked to stimulus presentation as sensory intake behaviour was. This would allow the direct contrast of evoked and induced oscillatory activity between tasks, ensuring that any differences found would be due to experimental manipulations rather than possible stimulus differences. The methodology of this procedure is described in section 7.2.3, but first it may help to obtain a fuller understanding of the proposed mechanisms behind the task-related increases in alpha found by Klimesch.

7.1.1 On the Klimeschian Paradox

Klimesch's work has typically emphasised two main aspects of the EEG: individual differences and the non-homogenous nature of alpha waves. Individual differences in the EEG will be addressed in section 7.1.2. As far as the heterogeneous nature of alpha is concerned, working with narrow band parameters Klimesch has found that alpha appears to divide functionally into 3 separate bandwidths. The proposed functional significances of these sub-bands are as follows:

- Lower alpha 1 (c. 6 – 8 Hz) was observed to desynchronise following a warning stimulus and preceding a target stimulus and has been proposed to reflect attentional demands (Klimesch et al., 1998).
- Lower alpha 2 (c. 8 – 10 Hz) has been found to desynchronise when subject were waiting for an "imperative" stimulus (target or non-target) and has consequently been associated with expectancy (Klimesch et al., 1998).
- Upper alpha (c. 10 – 12 Hz) has been suggested to correlate with semantic memory performance. This is based on findings of increased alpha desynchronisation during the processing of semantically congruent pairs of words as opposed to non-congruent pairs. Klimesch has proposed that this is closely associated with theta activity that he argues increase during working or episodic memory tasks (Klimesch et al., 1997; Klimesch, Doppelmayr, Pachinger, & Russegger, 1997).

However, as reported in chapter 6, in recent years Klimesch and colleagues have also observed occasional task-related increases in alpha activity that they have

termed 'paradoxical' alpha. Klimesch *et al* (Klimesch et al., 2000; Klimesch et al., 1999) have shown a relationship between their findings of a paradoxical increases in alpha during a memory task and the evoked component of the activity. They have found that when the working memory requirements of a task reach a certain threshold (as far as difficulty is concerned) then evoked alpha activity shows an increase thought by Klimesch to underlie an inhibition of semantic long term memory mechanisms. More precisely, this evoked activity appears to be the result of the phase locking of the three alpha sub-bands in the 125-200ms post-stimulus presentation period. This phase locking accounts for 100% of the standard event-related potential (ERP) at Pz, 85% at PO1 and 36% at O1. There was also no evidence of any evoked alpha activity at frontal sites. Klimesch argues that this phase-locked activity is a transient response that precedes a desynchronisation and serves to increase signal to noise rations. In summary, there are two main aspects to Klimesch's views surrounding alpha. Firstly (and typically), alpha desynchronisation reflects activation of a neural networks whose optimal oscillatory rate at rest is within the 8-12 Hz range. Secondly (and more rarely), task-related increases in alpha power reflect the inhibition of non-task relevant (and possibly conflicting) neural networks, and this synchronisation is the result of an evoked phase resetting of the 3 alpha sub-bands.

Klimesch's work has also emphasised the individual differences in the EEG, particularly so with respect to the parameters of the alpha band. In order to account for such differences, Klimesch has developed a method for calculating bandwidth parameters on an individual basis (Klimesch, 1997; Klimesch, 1999).

If a full and fair test of the inhibition hypothesis is to be carried out then it is important to employ as closely as possible methods used by its main protagonist, particularly with respect to individual EEG differences. This approach is described in detail in box 7.1, and the g eneral theory behind its application is addressed in the following section.

7.1.2 Individual Alpha Frequencies

When examining a spectral analysis of a group of subjects, it is evident that there is a variation in both the frequency at which the peak alpha amplitude is to be found and in the parameters of the beginning and end of the alpha 'curve' (see figure 7.3 for an example graph of the spectral analysis of one individual). It follows therefore that assumptions about the bandwidth of the alpha component across subjects may be at best over simplified and at worst, misleadingly inaccurate. For instance, it is known that the mean peak alpha frequency of a person changes over the lifetime; there is a decrease from a mean of c.10.89 Hz at the age of 20 to c.8.24 at the age of 70 (Klimesch, 1997). Several researchers have sought to overcome this potential problem by adjusting the parameters of alpha on an individual basis (see Kaiser, 2001). However, techniques that only take into account one aspect of the individual differences, e.g. the frequency of the largest alpha amplitude, may still lead to inaccuracies as the alpha curve may have a negative or positive distribution depending on the individual. Klimesch and his colleagues have devised a method that corrects for these biases by creating a weighted average of each individual's alpha distribution and then calculating the bandwidth parameters accordingly (Klimesch, 1997; Klimesch,

1999). Based on his empirical findings, Klimesch has applied this approach to determine the bandwidths of theta and three separate alpha sub-bands. In this experiment we extended this method to include the lower beta band (beta 1). This method is explained in detail in box 7.1 (data preparation).

7.1.3 Hypotheses

The main hypotheses in this experiment are focused on the alpha band. With regard to the inhibition model, the following two hypotheses are made:

1. Alpha power will be greater during mental imagery as opposed to sensory-intake tasks.
2. Alpha power will be greater for hard as opposed to easy tasks.

Importantly, the inhibition model predicts that the task-related increases in alpha power (also observed in the previous two experiments) will result from evoked activity. An additional perspective to bear in mind when evaluating the results in relation to these hypotheses, will be that of the notion of different sub-bands of alpha reflecting different cognitive demands. Consequently, all three narrow-band alphas will be investigated for experimental effects.

The non-alpha hypotheses in this experiment are derived from the results from the previous experiments and are as follows:

3. Delta power will be greater during easy tasks and externally directed attentional.
4. Theta power will increase as a function of task difficulty.
5. Beta activity will also be the focus of investigation in an attempt to replicate previous findings of increased activity during internal attention and during hard tasks.

7.2 METHOD

This protocol aimed to broaden the auditory tasks carried out in experiments 2 and 3 in order to facilitate investigation of both evoked and induced oscillatory activity. This would facilitate the investigation of the proposal that task-related increases in alpha are dependent on evoked, stimulus-locked activity in that bandwidth (Klimesch et al., 2000). In order to have enough epochs to be able to reliably examine these event-related band power changes it was necessary to increase the number of trials to twenty (comprising of twenty internal, twenty external and twenty training tasks). This increase in the number of trials introduced a time constraint that necessitated a focusing of experimenter attention on to one sensory modality – auditory. The auditory modality was chosen for the following reasons: Firstly, most participants in earlier experiments had reported it easier to learn the auditory sequences than either the visual or haptic ones and consequently this would speed up the protocol and allow more trials; Secondly, not only had the auditory tasks produced robust experimental effects in experiments 2 and 3, they had also been the modality in which the unexpected fast wave findings in the second experiment were found.

7.2.1 Subjects

18 participants (12 male & 6 female) were tested with Ethics Committee approval. Ages ranged from 25 to 41 years (mean: 34.05). All participants had normal hearing and normal or corrected to normal vision and reported no known psychiatric or neurological problems.

7.2.2 EEG Recording

The EEG set-up and recording was the same as for experiment 1.

7.2.3 Protocol

Following the application of the EEG and EOG electrodes, the participants were seated in a dimly lit, sound attenuated, electrically shielded room (Faraday cage). Instructions were given to refrain from moving during test phases of the recording. Rests of 1-2 minutes were given between experimental blocks.

7.2.3.1 Individual Alpha Frequency

In order to be able to calculate the individual alpha frequency for each subject, resting-baseline EEG periods were recorded. These consisted of 2 x 3 minute periods at the beginning and the end of the experiment. During this time participants were verbally instructed to sit quietly, relax with their eyes closed and refrain from movement.

7.2.3.2 Eye movement calibration

Prior to testing the participants carried out the same electro-oculogram (EOG) calibration paradigm as in experiment one. See section 4.2.7.2 for details.

7.2.3.3 External versus Internal Paradigm

Prior to recording, one full practice trial was completed by each participant in order to familiarise them with the tasks. All tasks were preceded by a 'count-in', a sequence of 4 tones (frequency: 900Hz; duration:100 ms; SOA: 700 mS) that alerted attention and established sequence rhythm. There now follows a brief overview/schematic of one trial succeeded by a more detailed explanation of the tasks involved. A total of twenty trials were presented to each participant (see Appendix 9.3 for sequence details). Order of presentation of the trials was counter balanced across subjects.

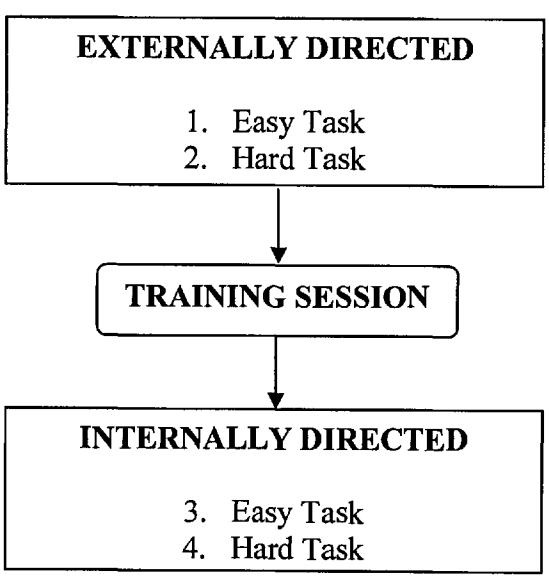


Figure 7.1: Schematic of protocol for Experiment 3. Repeated x20 per participant.

7.2.3.3.1 External Tasks

For each trial, two external tasks were employed: easy and hard. Both tasks (or blocks) involved the presentation to the participant of a randomly generated sequence of 6 tones repeated twice. Stimulus durations were 500mS, with an SOA of 700mS. There was a pause of 4000mS between sequences (see Fig.7.2).

The easy task involved the simple presentation of the sequence block plus instructions *"please listen to the following sequence of tones"*. The hard task involved the same sequence block plus the answering of a question (e.g. "*please listen to the following sequence of tones. Are the 1st/2nd/3rd and 4th/5th/6th tones the same?*"). The question was posed on a computer monitor before the presentation of the block of stimuli sequences and repeated post-presentation accompanied by instructions to *answer yes or no by button-press.* Order of questions was counter balanced within subjects.

7.2.3.3.2 Training Tasks

Participants were 'trained' to be able to imagine the previously presented sequences of stimuli. Training took the form of a further presentation of the block of stimuli sequences accompanied by the following instructions: "*Training session, listen and learn*".

7.2.3.3.3 Internal Tasks

For each trial, two internal tasks were employed: easy and hard. The easy task involved the participant imagining the previously learned stimulus block. This was preceded by the following instructions "*after the count, try to imagine the sequence of tones*". The task was then performed against a background of monotonous stimuli with identical count-in, timing, durations, SOA's etc. The pitch frequency of the monotonous tones was the same as the first note of the previously learned stimuli sequence and thus varied from trial to trial (see Appendix 9.3). The hard task involved the participant imagining the sequence once again against a background monotonous stimuli sequence and answering a question ("*after the count, try to imagine the sequence of tones. Are the* $1^{st}/2^{nd}/3^{rd}$ *and* $4^{th}/5^{th}/6^{th}$ *tones the same?*"). Again, the question was posed before the presentation of the block of stimuli sequences and repeated post-presentation accompanied by instructions to *answer yes or no by button-press*. The purpose of the 'count-in' and the monotonous stimuli during imagination was two-fold: firstly, to add a stricter time-constraint to the imagination tasks to facilitate a more reliable comparison between external and internal tasks; and secondly, to ensure that any differences found were not due to stimulus differences (e.g. presence or lack of evoked activity resulting from stimulus presentation).

7.2.3.3.4 Summary of Tasks

1. Read instructions from monitor: "*please listen to the following sequence of tones*".
2. Count-in.

3. Sequence block - a randomly generated sequence of 6 tones repeated twice. Stimulus durations were 500ms, with an SOA of 700ms. There was a pause of 4000ms between repetitions (see Fig.7.2).
4. Read instructions from monitor: "*please listen to the following sequence of tones. Are the 1st/2nd/3rd and 4th/5th/6th tones the same?*"
5. Count in.
6. Sequence block.
7. Reminder of question from monitor: "*were the 1st/2nd/3rd and 4th/5th/6th tones the same? Yes or No*".
8. Button-press response.
9. Training session. Participants were 'trained' to be able to imagine the previously presented sequences of stimuli. Training took the form of a further presentation of the block of stimuli sequences accompanied by the following instructions: "Training session, listen and learn".
10. Read instructions from monitor: "*after the count, try to imagine the sequence of tones*".
11. Count-in.
12. Imagination of sequence block. The task was performed against a background of monotonous stimuli with identical count-in, timing, durations, SOA's etc. The pitch frequency of these tones was the same as the first note of the previously learned stimuli sequence and thus varied from trial to trial (see Appendix 9.3).
13. Read instructions from monitor: "*after the count, try to imagine the sequence of tones. Are the 1st/2nd/3rd and 4th/5th/6th tones the same?*"
14. Count in.

15. Imagination of sequence block.

16. Reminder of question from monitor: "*were the 1st/2nd/3rd and 4th/5th/6th tones the same? Yes or No*".

17. Subjective difficulty rating: "*how hard was it to imagine the last sequence of stimuli?*" Button-press response: 1 = easy; 5 = very hard etc.

18. Repeat (1-17) x 20.

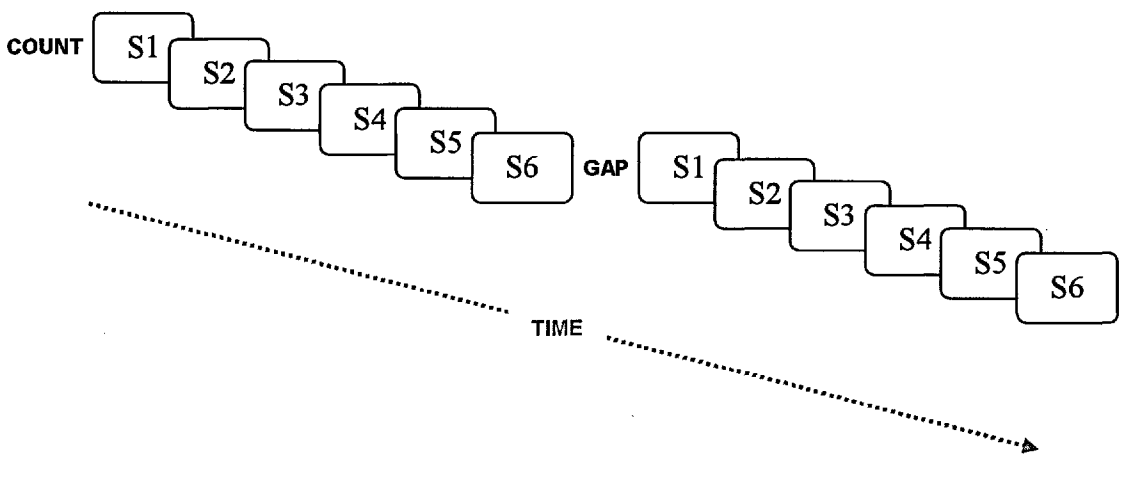


Figure 7.2: Schematic of the structure of a stimulus sequence. S1-6 = tones. Tone duration = 500mS, SOA = 700mS.

7.2.4 Data Preparation

Only trials where responses to both the external and internal tasks were correct were included for analysis. This resulted in an average of 25.55 / 40 matched blocks per subject (min = 12; max = 40). The raw EEG data were corrected for EOG artefact (see section 4.2.8.1). Training trials were not included in this analysis.

The raw EEG was epoched from –1000 to 4700 mS around the onset of tone S1 for each level of difficulty in both attentional conditions. This facilitated later trimming to remove filter artefact resulting in an epoch of 0 – 3700 mS. Epochs were assessed for contamination from movement artefact. Those with obvious noise or with signals greater than75mV were excluded from further analysis (for 4 subjects this was extended to 100mV due to large alpha oscillatory activity in those individuals). Prior to averaging, in order to address more specifically the theories of Klimesch and colleagues (Klimesch, 1999; Klimesch et al., 2000; Klimesch et al., 1999) concerning the role of alpha oscillations in cognition, a version of Klimesch's method for determining an individual's peak alpha frequency (IAF) was carried out (see Box 7.1). Individually adjusted EEG bandwidths could then be calculated.

Box 7.1: ***Individual Alpha Frequency (IAF)***

Drawing on empirical evidence from his own work, Klimesch has found that there appear to be (at least) 3 functionally discrete sub-bands of alpha activity. However, Klimesch argues that these differences are often missed due to individual differences in the parameters of these bandwidths. In order to overcome this possible problem a technique has been developed that facilitates the calculation of individual bandwidths based around a weighted average of measures centred around the individual's peak alpha frequency (i.e. the beginning (*f*1) and the end (*f*2) of the alpha curve – see figure 7.3). This method is used rather than just noting the peak frequency (i.e. the frequency at which the alpha curve is at its maximum) due to the somewhat skewed

distribution of most people's alpha band (positive or negative). It is important therefore to account for any skewness in the data and this can be achieved by using the weighted average technique. The method used in this experiment for each participant was as follows:

- The two baseline rest recordings were appended into a single data set.
- Data were epoched into 1-second periods (c.360 per subject).
- Epochs were averaged and a fast Fourier transform was carried out to reveal spectral band power.
- The beginning of the ascent and end of the descent of the alpha curve (*f*1 & *f*2) were identified. However, it must be noted that in particular, the identification of *f*2 can be problematic. There often is no actual 'end' to the alpha curve, just a gradual tailing-off that may continue up to 20 or 30 Hz. It was therefore decided to take the arbitrary cut-off point of 15 Hz for *f*2 if it had not already been identified at a slower frequency.
- The data were collapsed across electrodes and for each sampling point between *f*1 and *f*2, the frequency was multiplied by the amplitude and the average was calculated.
- This weighted mean was subsequently divided by the sum of the amplitude values between *f*1 and *f*2.

The resulting IAF was used as the reference point for calculating theta and the three alpha bandwidth parameters (see below). Additionally, it was also used to individually adjust the lower beta band in order to see if this was a useful extension to the individual analysis approach. However, delta, upper beta and the gamma bands

were not individually adjusted for the following reasons: Individually adjusting delta would have resulted in very slow and even negatively valued non-delta activity being included. Individually adjusting the upper beta and gamma bands has virtually identical results to using the traditional approach and thus was unnecessarily time consuming.

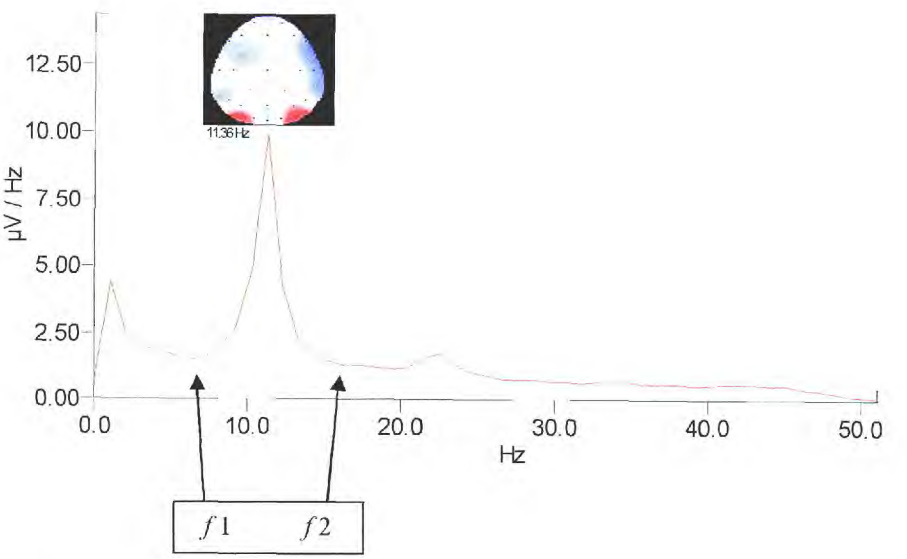


Figure 7.3: Spectral analysis of a single participant at rest revealing alpha peak

The data were filtered and averaged into the following bandwidths (roll-off of 48dB): Delta = 1 - 3 Hz; Theta = (IAF – 6 Hz) to (IAF – 4 Hz) Hz; Lower alpha 1 = (IAF – 4 Hz) to (IAF – 2 Hz); Lower alpha 2 = (IAF – 2 Hz) to IAF; Upper alpha = IAF to (IAF + 2 Hz); Lower Beta = (Median (IAF + 2 Hz and 20 Hz)) [6] +/- 4 Hz; Upper Beta = 20 – 30 Hz, Lower Gamma = 30 – 48 Hz and Upper Gamma = 52 – 80 Hz. Frequencies in the 48 – 52 Hz range were excluded due to possible contamination from mains electricity supply operating within this

waveband. The averaging process was carried out separately for both induced and evoked components (see box 4.2 for details).

7.2.5 Statistical Analyses

The randomisation t-test procedure explained in Experiment 1 was used to compare internally versus externally directed attention and easy versus hard tasks for both induced and evoked data sets. This randomisation procedure allows a rigorous comparison of experimental conditions without being overly conservative and without conflating type I error (see section 4.2.9.1).

Data from electrodes FP1 & FP2 were excluded from analysis due to excess noise contamination as were F7 (subject 14), F8 (subjects 7, 9 & 14), T3 (subjects 8, 11, 12 & 13) and O2 (subject 13).

7.3 RESULTS

7.3.1 Individual Alpha Parameters

The parameters for the individually adjusted alpha band were as follows. Mean individual alpha frequency for the group was 10.25 Hz (minimum = 8.97 Hz; maximum = 11.12 Hz. See figure 7.4). Group average ranges for sub-bands

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[6] Beta 1 parameters were calculated by finding the median frequency between the IAF + 2Hz and 20 Hz and then subtracting and adding 4 Hz for the high and low passes respectively.

were: Lower alpha 1 = 6.25 – 8.25 Hz. Lower alpha 2 = 8.25 – 10.25 Hz. Upper alpha = 10.25 – 12.25 Hz)

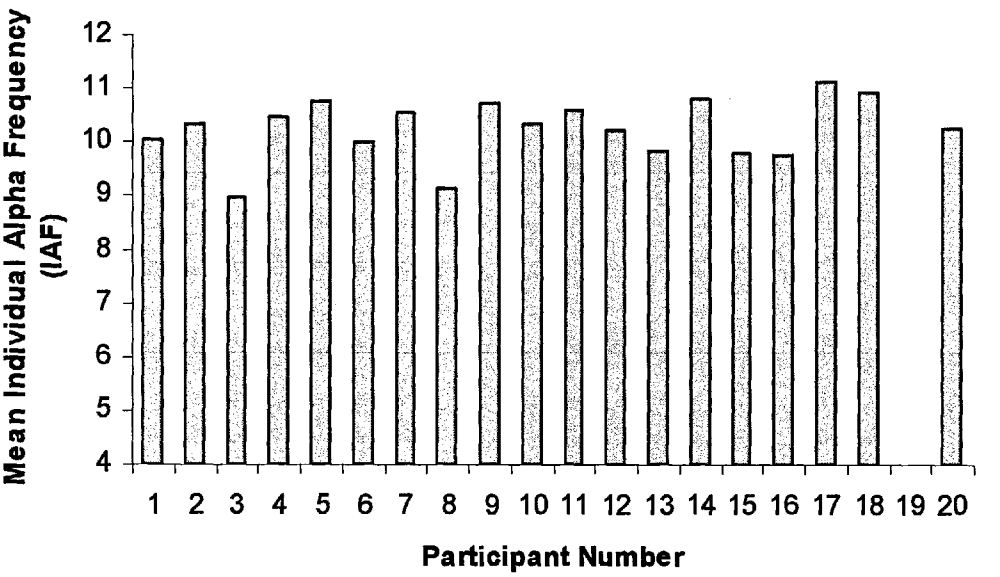


Figure 7.4: Chart representing individual alpha frequencies. No.20 = group average.

7.3.2 Delta

See figure 7.5 for a topographical representation of the delta findings. The observations are in full agreement with hypothesis 3.

Attention. Significantly greater evoked delta power was observed during external as opposed to internal attention at T5, T6, Cz and Pz and at trend levels at F4, P3, P4, O2, Fz, TCP2, CP1, CP2 and PO2.

Task Demands. A trend for greater induced delta power during easy as opposed to hard task demands was noted at F4 and C4. Significantly greater evoked delta power was observed during easy tasks at T3, T5, T6, PO2 & and at trend levels at C3, P3, P4, Pz, Oz and TCP1.

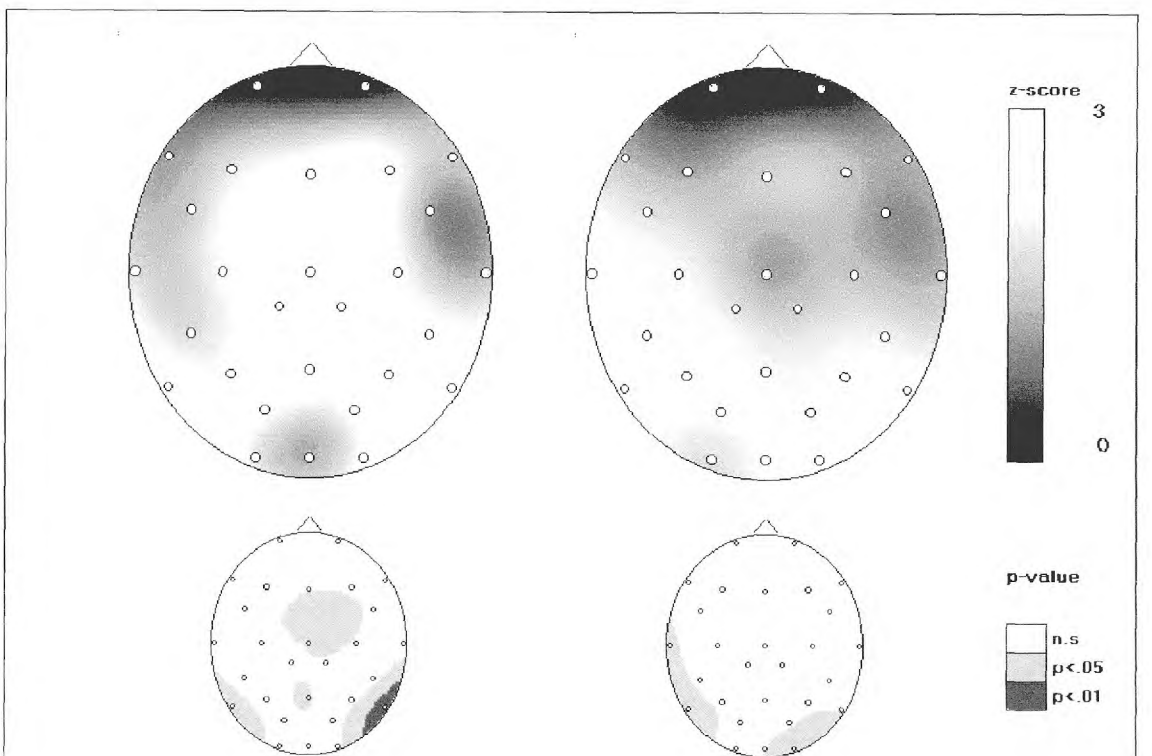


Figure 7.5: Results for the comparisons of evoked delta power between a) externally and internally directed attention & b) easy versus hard tasks. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during a) externally directed attention and b) easy tasks. Lower (smaller) maps show the randomisation values for the differences.

7.3.3 Theta

See figure 7.6 for a topographical representation of the theta findings.

Attention. Unexpectedly, a trend for greater induced theta power during internal attention was observed at F7. Evoked theta activity was greater during externally directed attention at T5, but it is possible that this isolated finding may reflect muscle artefact.

Task Demands. In accord with the fourth hypothesis, effects were noted such that induced theta power was significantly greater during hard tasks at F3 and at trend levels at F4, C3, Fz & Cz.

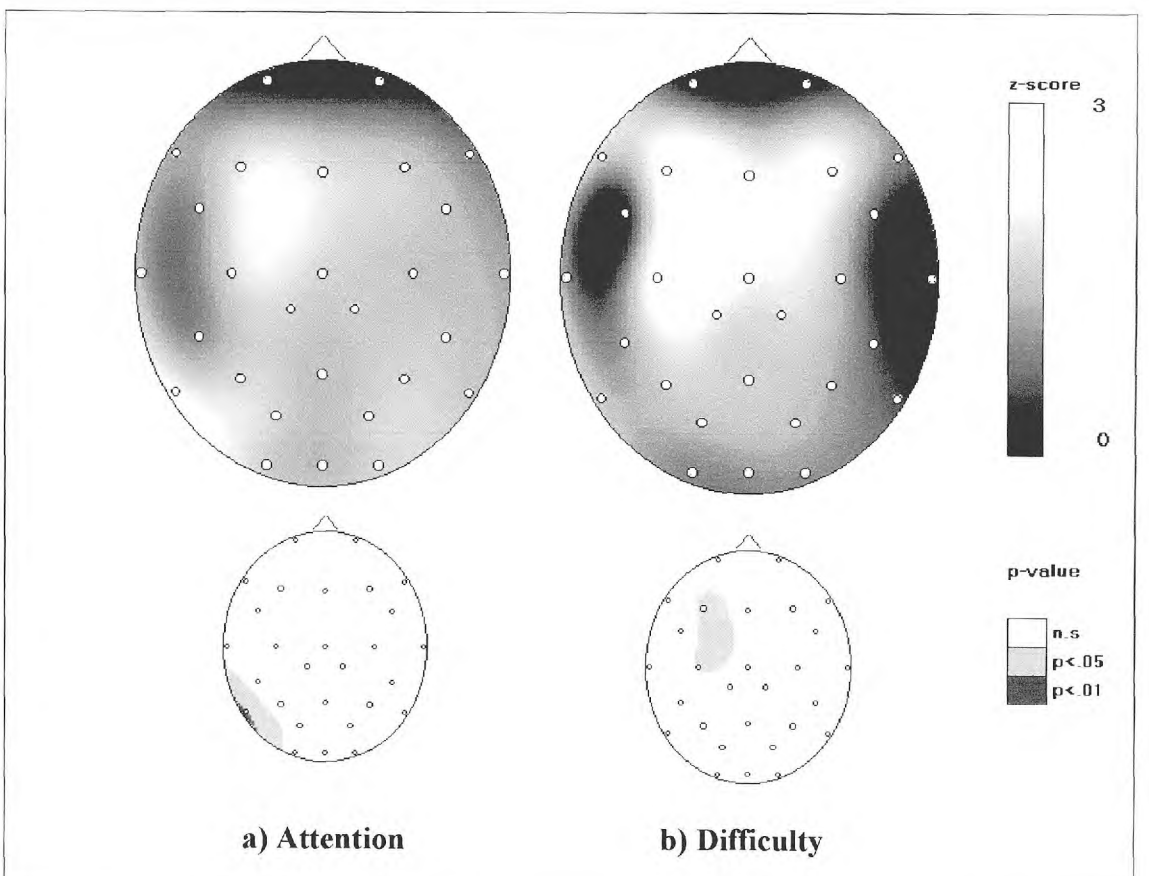


Figure 7.6: Results for the comparisons of theta power between a) externally and internally directed attention (evoked activity) & b) easy versus hard tasks (induced activity). Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during a) externally directed attention and b) hard tasks. Lower (smaller) maps show the randomisation values for the differences.

7.3.4 Alpha Activity

Findings in agreement with hypothesis 1 were found in all 3 sub-bands. However, contrary to expectations from hypothesis 2, no significant effects of task difficulty were observed. Indeed, the null hypothesis has to be accepted in all alpha sub-bands with regard to this factor. The findings for the three alpha sub-bands are as follows.

7.3.4.1 Lower Alpha 1

Attention. As can be seen from figure 7.7, there was significantly greater induced lower alpha 1 power during internal as opposed to external attention at F7. No significant effects were observed for evoked components.

Task Demands. No significant effects were observed for induced or evoked activity.

7.3.4.2 Lower Alpha 2

Attention. Significantly greater induced lower alpha 2 power was observed at F7 and at trend at F8 during internally directed attention. No significant effects were observed for evoked activity (see figure 7.7).

Task Demands. No significant effects were observed for induced or evoked activity.

7.3.4.3 Upper Alpha

Attention. Figure 7.7 reveals that significant effects were found at posterior sites, such that induced upper alpha power was greater for internal attention than for external attention at O1, O2, Oz and also frontally at F7. No significant effects were observed for evoked activity.

Task demands. No significant effects were observed in either induced or evoked oscillations.

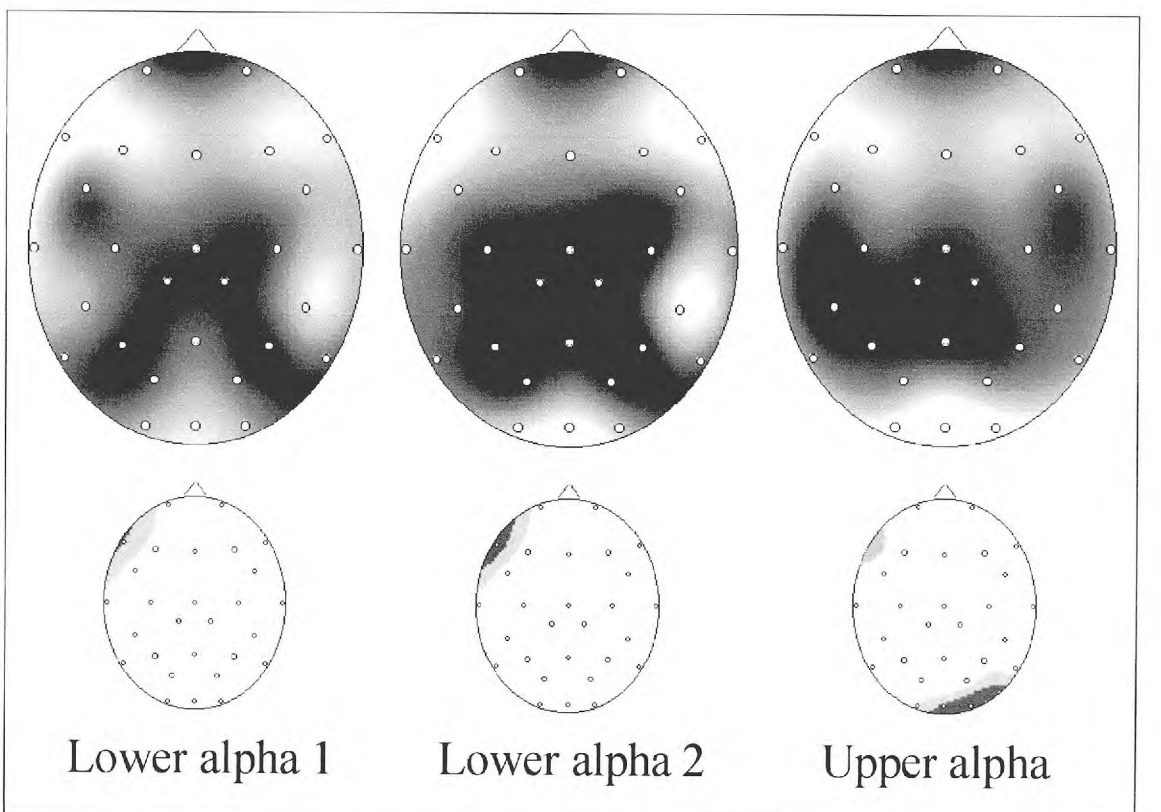


Figure 7.7: Results for the comparisons of induced alpha power between externally and internally directed attention. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during internally directed attention. Lower (smaller) maps show the randomisation values for the differences.

7.3.5 Beta 1

See figure 7.8 for a topographical representation of the beta findings.

Attention. In partial agreement with hypothesis 5, significantly greater induced beta 1 power was observed at 02 for internal compared to external attention.

Task Demands. Unlike the previous experiment, no significant effects were observed.

7.3.6 Beta 2

Attention. Significant differences were found at F4, P4, O2 and PO2, wherein induced beta 2 power was greater during internally directed attention. A trend for greater evoked beta 2 power during internal tasks was also noted at O2 (see figure 7.8).

Task Demands. No significant effects were observed in either induced or evoked oscillations.

7.3.7 Gamma 1

Attention. A trend for greater induced gamma 1 power was noted at F4 during internal tasks. No effects were observed for evoked activity.

Task Demands. No significant effects were observed in either induced or evoked oscillations

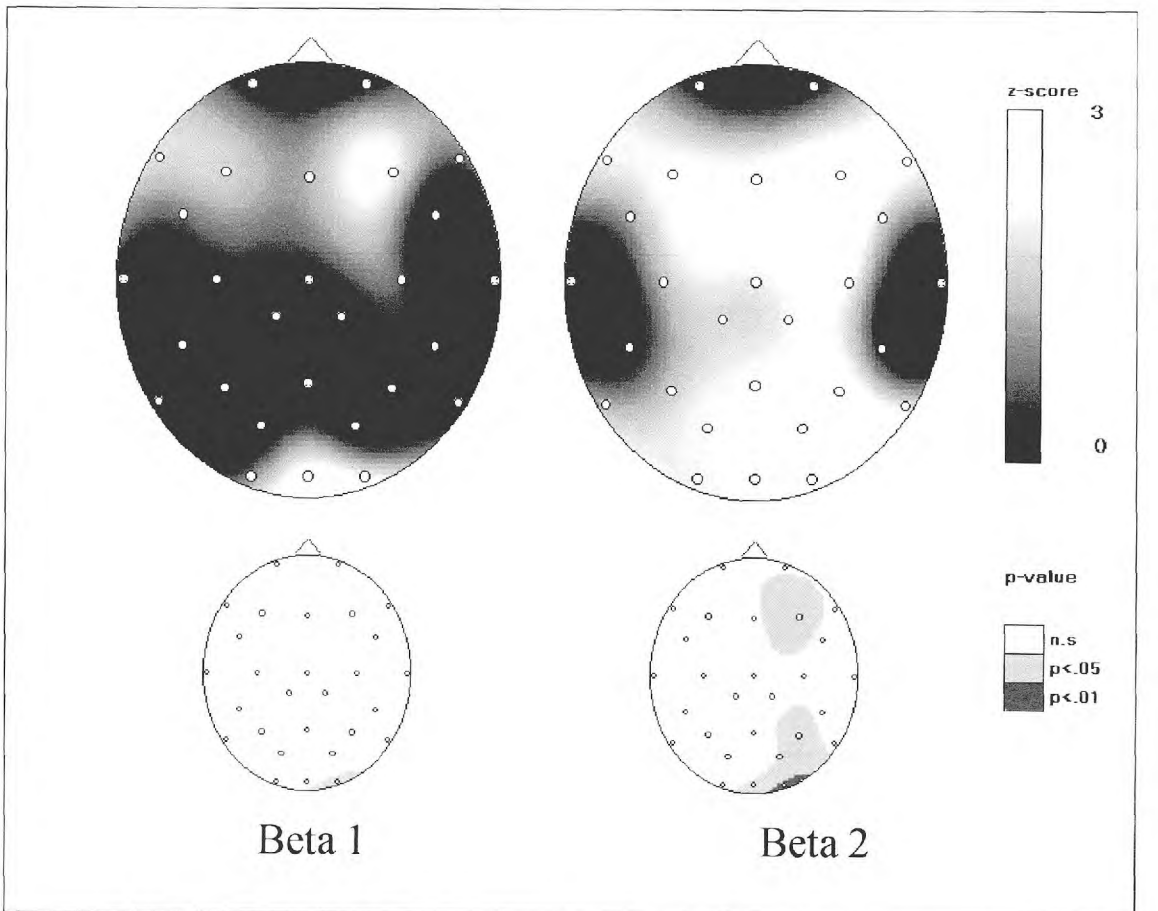


Figure 7.8: Results for the comparisons of induced beta power between externally and internally directed attention. Upper maps indicate z-values reflecting the difference between the two conditions. Lighter tones reflect increased amplitudes during internally directed attention. Lower (smaller) maps show the randomisation values for the differences.

7.3.8 Gamma 2

No significance differences were found for attention or task demands in either induced or evoked components.

7.4 DISCUSSION

This section will begin by focusing on the findings from this experiment as they relate to the hypotheses, before continuing with an exploration of the findings in the remaining EEG bands.

7.4.1 Alpha

The findings of experiments 2 and 3 of greater alpha activity during internally directed attention were replicated in all three alpha sub-bands. Interestingly, the locus of this activity varied between the sub-bands, being more frontal at the lower end of the alpha range and more posterior in upper alpha in terms of statistical significance. In addition to left frontal activity, the significant upper alpha activity was found at the same electrode sites as in the previous experiment, i.e. occipitally. As in the previous experiment this is noteworthy as it overlays visual cortical areas. Due to the inverse problem, one cannot make accurate localisations of brain activity from EEG recordings, but it is interesting to note that once again, the majority of subjects reported using visual imagery techniques[7] in this ostensibly auditory paradigm. This finding is in accordance with previous work showing activation of visual areas during auditory imagery and musical differentiation tasks (Platel et al., 1997; Schurmann et al., 2002). Thus based on the ideas of Kosslyn and others (e.g. Kosslyn et al., 2001; Kosslyn et al., 1993; Kosslyn, Behrmann, & Jeannerod, 1995; Sparing et al., 2002) of

[7] E.g. "I imagined the notes laid out on a grid-like structure".

visual cortex activation during mental imagery, these results once again create doubt as to the explanatory value of the inhibition hypothesis in this instance.

More crucially, as far as Klimesch's ideas about paradoxical alpha are concerned, is the componential nature of the alpha activity. Klimesch has argued that phase-locked (evoked) activity in the alpha band underlies the task-related increases in alpha noted in his memory paradigms (Klimesch et al., 2000). However, in this experiment we found that the differences between internally and externally directed attention where all found in induced, that is non-phase locked activity. The reader is reminded that both the stimuli and their timing were balanced between conditions and therefore the differences observed cannot be ascribed to stimulus disparity. In other words, participants were presented with strictly timed auditory stimuli in all tasks hence differences in the EEG between tasks are not attributable to differences in sensory (or bottom-up) input. It is tempting to conclude that Klimesch's observations have little relevance to the present findings with regard to mental imagery.

7.4.2 Beta.

The findings related to attention were similar for those found in the alpha bands. In particular, in both beta 1 and beta 2 significant differences were observed at occipital sites, wherein induced power was greater during internal attention. Additionally, in beta 2, activation was relatively widespread, with significant differences at right frontal areas. These findings taken in addition to those in alpha suggest another possibility as to the functional significance of alpha and

beta activity. This possibility is the suggestion made by von Stein and colleagues that alpha, beta and theta oscillations may form the media through which medium and long-range interareal communication can take place within the cortex (Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998; von Stein, 1999; von Stein et al., 2000a; von Stein, Rappelsberger, Sarnthein, & Petsche, 1999; von Stein et al., 2000b). The reason why the alpha and beta results observed here are relevant to this hypothesis is because it is proposed that 'top-down' tasks such as mental imagery require more information transfer between distal cortical areas than 'bottom-up' sensory intake and hence one would expect a positive association between alpha and beta activity and imagery. This is indeed what we found. This hypothesis and the problems associated with the definitions of the terms 'top-down' and 'bottom-up' are described and explored in the following chapter.

7.4.3 Theta

The main finding for theta activity was that of greater frontal activity during hard as opposed to easy tasks. Again, this is consistent with earlier findings both in this study and from other work showing a relationship between theta activity and various memory processes (e.g. Burgess et al., 2000; Gevins et al., 1997; Grunwald et al., 2001; Ishii et al., 1999; Kubota et al., 2001). It is also arguable that these findings are also interpretable in terms of the degree of interareal communication necessary for the successful completion of a task and hence our theta results may add to the evidence for the interpretation applied to both alpha and beta oscillations.

7.4.4 Delta

The main delta results were observed in evoked activity and revealed greater evoked delta power during externally directed attention and for easy as opposed to hard tasks. This is in complete accordance with findings from experiment 3 and also appears to reinforce the negative relationship between delta and task difficulty found in the first experiment. This matter will be addressed more fully in the general discussion.

7.4.5 Gamma

There were no significant experimental effects observed in either gamma 1 or gamma 2. There was a small trend towards an attentional effect at electrode F4, wherein induced gamma 1 power was greater for internally directed attention. It is of course possible that this reflects a type I error. However, the topographical similarity of the activation distribution to upper beta findings may provide reason against this interpretation. Additionally, this trend is complementary to the auditory task findings in experiment 2, but given the un-hypothesised nature of these results and their failure to reach significance levels in the present experiment it is unwise to speculate upon their function. However, these gamma observations may serve to temper the interpretations regarding the slower wave findings, in particular with regard to the specificity of EEG band functionality.

7.4.6 Summary

In summary, this experiment was carried out primarily to investigate in greater detail whether task-related increases in alpha activity are consistent with the hypothesis that they result from the inhibition of non-task relevant cortical areas or processes (Klimesch et al., 2000; Klimesch et al., 1999). In particular, its aim was to examine the proposal that such activity is due to evoked components of the EEG. In this experiment, it was observed that findings of greater alpha power during internally directed attention were the result of induced activity and are therefore incompatible with these mechanisms suggested to underlie the inhibition hypothesis.

A combination of factors, including the locality of the induced alpha findings, the similarity of the beta activity and the association between frontal theta oscillations and task difficulty suggest that perhaps a more parsimonious explanation of the functional significance of these wavebands may be found in terms of the balance between 'top-down' versus 'bottom-up' processing. This theory will be the focus of section 8.3.

8 GENERAL DISCUSSION

8.1 AIMS OF THE STUDY

The main aims of this study were two-fold: to investigate whether the intake-rejection hypothesis was a viable way of examining attention; and to explore and determine the functional significance of the related EEG bands. The question regarding the intake-rejection hypothesis can be viewed both in terms of the validity of the dichotomy of external versus internal attention and also as its usefulness as an investigative tool. This chapter will argue that despite the lack of evidence for a rigid discrimination between external and internal focus in terms of attentional mechanisms, it has still proven a useful model, at least in terms of facilitating investigation and providing the impetus for further hypotheses. It is however, no longer potent as an explanatory tool and should be regarded more as a 'stepping-stone' than a landmark finding. With regard to the functional significance of the EEG bands, this chapter will argue that ideas regarding alpha activity as indexing an idling, calm yet inactive brain are no longer tenable. Additionally, evidence will be discussed that undermines the validity of one of the main propositions seeking to replace the alpha-as-idling model, namely, the inhibition hypothesis. It is shown that interpretation of the results from these experiments in terms of the inhibition hypothesis leads to problems applying them to standard mental imagery models. Also, previous observations as to the componential make-up of the 'inhibitory' alpha wave activity (i.e. evoked not induced bandpower) were not replicated, leading to new explanatory proposals for EEG functional significance. The results of the

various experiments carried out in this study have been discussed in detail at the end of each appropriate chapter. However, it may prove useful to provide a synopsis of the main findings and their interpretations. There now follows a break-down of the aims and results of the study in terms of the experiments undertaken and of their relation to the intake–rejection and inhibition hypotheses.

8.2 EXPERIMENTAL SYNOPSIS

8.2.1 Experiment One

Experiment 1 sought to test the intake–rejection hypothesis. The aim was to examine whether changes in the EEG could be observed due to differences in whether a participant was attending externally, to the 'outside world' (sensory intake tasks) or internally, to the 'workings of their own mind' (thought to involve the rejection of sensory information). A paradigm was created that contrasted external attention tasks of identifying variously placed and pitched auditory tones, with internal attention tasks involving mental arithmetic. No evidence was found to substantiate previous findings linking internally directed attention with increases in delta power (Harmony et al., 1996b), theta activity (Aftanas et al., 2001) or alpha power (Ray et al., 1985b; Ray et al., 1985a). Indeed, the only results involving delta activity revealed greater amplitudes during easy as opposed to hard tasks. These are in direct opposition to those found by Harmony *et al* (Harmony et al., 1996b) and undermine their proposals of delta as a correlate of class II inhibition. Unexpected differences were observed in the faster wavebands (beta 2, gamma 1 & 2) wherein power in these

bands was greater during mental arithmetic than during sensory intake tasks. However, it was unclear whether these findings reflected true differences between the attentional conditions or were due to extraneous variables due to problems associated with experimental balance. For instance, there was the possibility of explicit sub-vocalisation during the arithmetic tasks that was not an issue during external attention. It was therefore deemed necessary to undertake a further examination of the intake–rejection hypothesis while addressing the issue of experimental balance. This was the aim of the second experiment.

8.2.2 Experiment Two

The rationale for the second experiment was both to carry out an additional investigation of the I-R hypothesis and to seek replication of the results pertaining to the fast EEG bands. A multi-modal protocol was devised that sought to contrast internal versus external attention using auditory, haptic and visual mental imagery tasks. The main effects of the experiment were observed in the alpha band, wherein amplitudes were greater not only during internal as compared to external attention but also for hard as opposed to easy tasks. This latter finding presents a problem with an interpretation based on the intake-rejection model. With I-R, one would expect alpha amplitudes to increase in line with task difficulty during internal attention but not external. However, the difficulty finding was a main effect and showed alpha to increase also during external attention. This led to the formation of the question that perhaps the 'inhibition' hypothesis could provide a better explanation of our results. The

inhibition hypothesis is related to the I-R model in the sense that both models are based on ideas of cortical inhibition but it extends the original proposal, suggesting that increases in alpha may index activity-related inhibition necessary for the successful completion of any task.

The findings of greater fast wave activity during internally directed attention go some way to substantiate those from the first experiment. However, they were only observed in the auditory modality and so may be more associated with modality-specific effects on the EEG than anything to do with attention per se. The theta results were congruent with previous findings from other researchers showing a relationship between theta oscillations and memory processing and will be discussed together with those from experiments 3 and 4 in section 8.2.5.

8.2.3 Experiment Three

The third experiment was primarily run as a constructive replication of experiment 2. This was necessary not only to establish the plausibility of the results from the previous experiment, but also to rectify certain procedural problems. The main findings from the previous experiment were fully replicated; alpha amplitudes were greater during internal attention and for hard tasks in all modalities. On first inspection these results appeared to strengthen the inhibition hypothesis in that task-related increases in alpha activity could be interpreted in terms of increased inhibition of non-task relevant areas or processes. However, the locality of many of the alpha findings, particularly those from electrode sites over visual processing areas led to some questioning of

this interpretation. For instance, findings of increased inhibition over occipital areas do not tally well with various studies in the field of mental imagery that have found activation of visual cortex during visual imagery tasks (e.g. Klein et al., 2000; Kosslyn et al., 2001; Kosslyn et al., 1993). Additionally, recent work has also found activation in occipital areas during auditory perceptual and imagery tasks (Platel et al., 1997; Schurmann et al., 2002). This was explained by the use of visual techniques employed by the subjects in order to successfully carry out the auditory tasks. Indeed, subjective reports by subjects in this study indicate that this was also the case during all three imagery experiments. A further reason to question the explanatory role of the inhibition hypothesis in this instance was the similar behaviour of beta activity to that of alpha. Beta 1 amplitudes were greater during internal attention in both the haptic and visual modalities and also in the visual modality during hard tasks. A similar trend was noted for attention during auditory tasks in the beta 2 bandwidth. Numerous studies have associated beta oscillations with cognitive activity, but a recent proposal has provided a model for both alpha and beta activation as the media for interareal cortical communication (von Stein et al., 2000b). Thus doubts were raised over the inhibition hypothesis as a means of explaining the results found in this particular study. However, it was deemed important to further explore the proposed mechanisms of the inhibition and so a further experiment was instigated in order to do this.

With regard to the fast EEG bands of gamma 1 and 2, no replication of increased activity during internally directed attention was found. Interestingly, as in experiment 1 delta activity was again found to be greater during external

attention (auditory modality) and in easy tasks (haptic modality). The theta results increased in line with task demands in the visual modality and will be addressed in section 8.2.5.

8.2.4 Experiment Four

The main focus of the fourth experiment was to examine the proposal that the task-related increases in alpha power indexing cortical inhibition are the result of changes in evoked activity. The new protocol necessary for such an investigation also facilitated the verification that changes in the EEG between internal and external attention were due to this experimental manipulation and not due to differences in stimuli or their presentation. The main experimental findings were of increased alpha power during internal attention in all three sub-bands and importantly, these differentials were based on induced not evoked activity. Additionally, similar observations were made in the beta bands also involving induced activity. Once again, it is interesting to note that main locus of these experimental findings was over occipital areas; where one would expect them to be if visualisation techniques were again being employed. Taken together, all of these results substantiate the doubts raised earlier regarding the inhibition hypothesis.

Gamma activity again failed to replicate the findings from the first two experiments. However, a note of caution should be sounded before concluding that fast EEG activity has no relationship with internally directed attention: a slight trend was noted in induced gamma 1 activity such that power was greater

during internal attention The implications of the sporadic gamma observations are discussed in section 8.4. As far as the delta results are concerned, the findings from the first and third experiments (of increased power during external and easy tasks) were replicated and were found to be the result of evoked activity. This is an important finding in that it contradicts one of the original hypotheses deployed in this study derived from the intake – rejection hypothesis. Harmony *et al* had argued that delta activity was "an indicator of attention to internal processing" (Harmony et al., 1996b) based on Vogel *et al*'s idea of class II inhibition (Vogel et al., 1967), i.e. inhibition of non-relevant sensory information during the performance of a 'mental' task. We found this not to be the case, not only during mental imagery but also previously during mathematical tasks. It is therefore tempting to conclude that delta activity is not a reliable index of internally directed attention. The theta results from this and the previous experiments will now be discussed in the following section.

8.2.5 Observations of Theta Activity

This section presents the results pertaining to the theta band separately for the following reason: rather than presenting a challenge to traditional interpretations of EEG bandwidths (as our alpha findings do) they represent an addition to them, being as they are, fully compatible with a growing body of evidence linking theta oscillations with the activation of various memory neural networks (Burgess et al., 2000; Gevins et al., 1997; Grunwald et al., 2001; Ishii et al., 1999; Klimesch, 1999; Kubota et al., 2001). Over the course of the three experiments using mental imagery protocols we found a positive association between task difficulty

and theta power in all three sensory modalities (i.e. experiment 2 – haptic and visual; experiment 3 – visual; experiment 4 – auditory). It should be noted that the theta results are not consistent across the entire study; in the auditory modality, they are only found in the final experiment. One possible reason for this result may be due to the fact that in experiments 2 and 3, the auditory modality was consistently deemed to be the easiest according to the self-reports of the participants and hence did not require the effort needed to produce changes in theta activity. It was not until the changes made to the last experiment that participants reported finding the auditory tasks taxing. It is unclear why there were no significant theta findings during the haptic tasks in experiment 3, however a trend level difference was observed.

It is proposed that the additional task requirements constituting the difficulty factor in these experiments work by increasing the load on working memory mechanisms. For instance, when executing the task instigated by the question "are the 1st and 4th tones the same?" the participant has to 'bear in mind' the first tone while at the same time running through and taking note of the stimulus sequence under scrutiny. Historically, the relation between theta and various cognitive tasks was understood in terms of class II inhibition of non-relevant information processing (e.g. Vogel et al., 1967; see section 3.1.3). However, recently it is more commonly being viewed as much more active processes. In particular, several studies have linked activity at anterior midline sites (frontal midline theta, fMθ) with anterior cingulate activity during attention and memory (Gevins et al., 1997; Ishii et al., 1999; Kubota et al., 2001; Rippon et al., 2002). Additionally, findings of theta generation in the hippocampus have strengthened

models of theta involvement in memory. It is within the confines of such an approach that the results pertaining to theta activity in this study can be most economically explained.

As a concluding remark to this section, it is interesting to note that whereas the notion of theta activity reflecting class II inhibition (see section 3.1.3) has to a large extent being overtaken by those ideas mentioned above of theta oscillations indexing more active cognitive processes, the same principle has still not been widely applied to understanding alpha activity. However, this approach is beginning to be seen and may provide useful insights into EEG functionality. Section 8.3 discusses this way of understanding alpha oscillations in greater detail.

8.2.6 Synopsis Summary

These results influence our appreciation of the intake – rejection hypothesis in the following ways:

- Delta – In three out of four experiments (1, 3, & 4) we found the opposite to that expected if delta were to be an indicator of attention to internal processes. Indeed, given the evoked nature of the findings in the first and last experiments, it is arguable that delta activity is more concerned with stimulus intake / registration of input.

- Theta – In three out of four experiments (2, 3, & 4) a positive association was observed between theta activity and task difficulty. This was interpreted in terms of increased working memory requirements. This can be viewed as compatible with expectations arising from the intake-rejection hypothesis. However, given other recent findings involving frontal midline theta (e.g. Gevins et al., 1997; Ishii et al., 1999; Kubota et al., 2001; Rippon et al., 2002) it is perhaps more readily explained as a more active cognitive process perhaps involving hippocampal and cingulate networks.

- Alpha – In three out of four experiments (2, 3, & 4) alpha was found to be greater during internally directed attention. This was fully compatible with intake-rejection ideas. However, the positive association between increased alpha and task difficulty found in two experiments (2 & 3) led us to reject the specificity of the intake-rejection model. A more generalised proposal was examined - the inhibition hypothesis. However, the location of the experimental findings together with the componential make-up of the activity (i.e. induced not evoked) led to the questioning of this model as a plausible explanation for the findings in this study. It is proposed that perhaps a more parsimonious interpretation of our results can be found in terms of long and medium-range interareal cortical communication, wherein EEG activity reflects the balance of top-down to bottom-up processing involved. This hypothesis is explored in depth in the following section.

8.3 THE EEG AND INTERAREAL COMMUNICATION

In recent years a growing body of evidence has begun to emerge that has cast some doubt onto traditional views of the functional significance of the alpha band (e.g. Basar et al., 1997; Bastiaansen, Posthuma, Groot, & de Geus, 2002; Jensen, Gelfand, Kounios, & Lisman, 2002; Klimesch et al., 2000; Klimesch et al., 1999; Krause, Lang, Laine, Kuusisto, & Porn, 1996; Krause, Salminen, Sillanmaki, & Holopainen, 2001; Nunez, Wingeier, & Silberstein, 2001; Schack & Klimesch, 2002). In several studies involving auditory memory tasks, Krause and associates have observed event-related synchronisation in the alpha band (particularly the upper range) during memory encoding. The so-called 'paradoxical' findings of Klimesch and colleagues have already been described elsewhere (section 7.1) but it is useful to note an additional set of findings pertaining to alpha activity during a memory scanning task recently published by Schack & Klimesch. They found increases in alpha oscillations in line with memory load during retention periods and increased phase-locking of this exact same frequency during retrieval. Schack & Klimesch argue that although in some ways their findings are interpretable in terms of the inhibition hypothesis, the phase-locking "suggests a more active function of alpha in working memory" (Schack et al., 2002 pg.110). This point of view has also been forwarded by Jensen and colleagues. Working with a modified Sternberg task[8] they too found increases in alpha power during the retention phase of the task. They speculate

[8] Sternberg task = presentation of a set of stimuli followed by a memory retention interval and then a probe stimulus. The task is to judge whether the probe was one of the original set of stimuli.

that perhaps "alpha band activity is directly involved in the neuronal mechanisms responsible for maintenance of working memory" (Jensen et al., 2002, pg. 882). Similar findings of increased power in the upper range of the alpha band during the retention period of a working memory task (in this instance, visuo-spatial) have been reported by Bastiaansen and colleagues (Bastiaansen et al., 2002). Başar and his group over several years have emphasised the importance of alpha band activity in various cognitive processes. For instance, Başar *et al* have found a positive relationship between dynamic memory performance and increase alpha synchronisation (Basar et al., 2001; Basar et al., 1997; Schurmann & Basar, 1999). Also, Başar has proposed a link between alpha activity and association mechanisms in the brain; he states "10 Hz processes may facilitate overall association mechanisms in the brain. When a sensory or cognitive input elicits '10 Hz wave trains' in several structures, then it can be expected that this general activity can serve as *a communication signal par excellence* between different structures" (Basar, 1999, pg. 350). On one level, it appears that this growing body of evidence (including the present study) is incompatible with previous, conventional understandings of the role of alpha activity in cognitive processes. However, recently a new model has been proposed that may begin to bridge the gap between these two positions. This approach is the subject of the next section.

8.3.1 Concerning Indices of Top-Down Processing

In an attempt to interpret apparently discordant findings pertaining to alpha activity during various cognitive tasks, von Stein and co-workers have hypothesised that the alpha rhythm may be viewed as an "extreme example of top-down processing" (von Stein et al., 2000a, pg. 14753). They come to this viewpoint by way of the following findings. (See box 6.1 for a description of the terms 'top-down' and 'bottom-up' and how these processes may interact in perception).

In 1997, Petsche *et al* published an article in which they reported findings indicating a relationship between 'creative thinking' and increased coherences over long distances in the alpha band (Petsche et al., 1997). They cite Thatcher et al (Thatcher, Krause, & Hrybyk, 1986) who suggested that such coherences reflect the activation of type-I pyramidal neurons with long axons (up to 25 cm) during information transfer between cortical areas. It is this notion of medium and long-range interareal communication that becomes emphasised in relation to various EEG bands in later studies. For instance, using a multi-modal semantic task[9] von Stein *et al* found a positive association connecting increased coherences in the low beta band between temporal and parietal sites and the creation of what was termed "supramodal conceptual representation[s]" (von Stein et al., 1999, pg. 138). They argue that such synchrony facilitates the large-

[9] Allow imagery to 'arise' following the presentation of pictorial, verbal and written stimuli.

scale 'binding' necessary between various sensory and executive mechanisms for the successful formation of semantically meaningful concepts.

This idea was developed further in a series of papers in 2000 (Bernasconi, von Stein, Chiang, & Konig, 2000; von Stein et al., 2000a; von Stein et al., 2000b). In one study, working with implanted electrodes in cats, von Stein *et al* investigated interareal interactions during tasks that relied on differing 'internal contexts' (i.e. with varying degrees of top-down control) using a modified go-no-go task. Implantation of the electrodes was carried out at various depths so as to record from different layers of the cortex. This was done as granular layers have been shown to reflect mainly 'feed-forward' activity (in terms of the visual processing hierarchy) and supra and infra-granular layers reflect mainly 'feed-backward' activity. Thus inferences could be drawn about the processing hierarchy according to the depth placement of the activity. They found that interareal correlations (e.g. between visual cortex and visual association cortex) were strongest in the slow EEG bands: delta, theta and alpha during successful 'go' but not 'no-go' tasks. Whereas local correlations, either within one area or joined by mono-synaptic connections were found in the gamma band to either task or to the presentation of novel stimuli that required no response. Furthermore it was observed that activity in visual association area (parietal cortex; area 7) preceded that in visual cortex (area 17) suggesting a feedback mechanism. This suggestion was reinforced by the finding that the most coupling was between the infra-granular layers of the visual association area and the supra-granular layers of the visual cortex; an effect compatible with feedback-mediated connectivity (see figure 8.1). Consequently, von Stein and

colleagues propose that whereas the slower frequency bands such as theta and alpha may play a role in top-down processing, gamma oscillations appear to be more related to the properties of the external stimulus and so may reflect the 'bottom-up' aspects of the task.

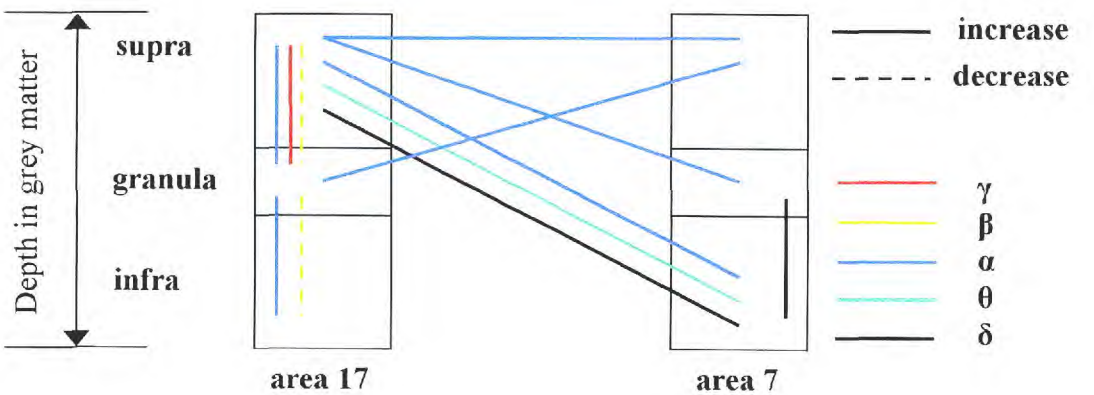


Figure 8.1: Schematic revealing electrode-pairs where cross-correlation differed significantly between go and no-go stimuli depicted with respect to their position in the different cortical layers (adapted from von Stein & Sarnthein 2000, PNAS).

In a further paper, working with human subjects, von Stein and Sarnthein have demonstrated a relationship between long distance fronto-parietal interactions in the theta and alpha bands and working memory and mental imagery (von Stein et al., 2000b). For instance, during the retention periods of both lexical and visuo-spatial working memory tasks, they observed significant coherences between electrodes over prefrontal and posterior cortex in the theta bandwidth. They relate this to previous findings of the involvement of prefrontal cortex and posterior association cortex in working memory processes (e.g. Goldman-Rakic, 1997; Tallon-Baudry, Bertrand, Bouchet, & Pernier, 1998), pg. 307). They also

postulate that working memory retention is a prototypical top-down process in that during it there is no external stimulation and it is therefore a "purely internal mental process" (von Stein et al., 2000b). Thus theta activity too can be associated with top-down processing. With regard to mental imagery, findings are reported, and re-interpreted of increased interareal coherence in theta and alpha during the mental imagery tasks previously described by Petsche *et al* (Petsche et al., 1997) and in alpha alone during a protocol that required the imaginary playing of a musical instrument. One important question addressed in this paper is that of the apparent dichotomy between these views of alpha activity and traditional approaches. They argue the following, "states with maximal alpha activity such as with eyes-closed and during rest do not reflect *inactive* brain states, but rather reflect states with *internal* mental activity. Rather than reflecting the absence of cortical processing they reflect the absence of *bottom-up* processing and thus can be classified a pure form of top-down activity" (von Stein et al., 2000b, pg. 311). This point not only has important theoretical implications but practical ones too. For instance, it calls into question the accepted notion of using a standard baseline measure when recording EEG for use as a comparison 'task'. It is arguable that when a subject is sitting calmly and relaxed and asked to do nothing but sit either with eyes closed or starring at a darkened computer screen that such top-down mechanisms would be in the ascendancy. For instance, at times such as these, when bottom-up processing is at a minimum, then internal mentation tends to arise spontaneously, giving rise to all kinds of unprovoked or non-task related thoughts. It was for reasons such as these that the mental imagery protocols described and employed in the present study were designed as they were; as straight-forward comparisons between

experimental conditions without the need or the possibly misleading presence of a baseline condition. A related point should also be made regarding the reference interval used during event-related desynchronisation or synchronisation studies. Typically, this period is taken as the several hundred milliseconds prior to stimulus presentation. Comparisons are then made between this period and that following the stimulus presentation and the percentage-change in EEG band powers can be calculated. However, it is increasingly clear that the brain is not a simple stimulus-response mechanism[10]. Indeed, at the time when a typical reference interval may be being recorded, processes such as anticipation, arousal, task-priming et cetera will be in effect. Inferences made from such comparisons as percentage-change ERD need to take this into account and be carefully put together.

A summary of the approach taken by von Stein and colleagues is as follows: over the course of several experiments, using EEG coherence techniques they have observed a relationship between cortical distance, EEG frequency and the balance between top-down and bottom-up processing. Namely, they have found that fast oscillations in the gamma band appear to be related to local (or mono-synaptic) intra-areal communication such as would facilitate the 'binding' of bottom-up, sensory information (von Stein et al., 2000a; von Stein et al., 2000b). Activity in the lower beta band was found to be positively associated with medium-range interareal communication (i.e. between parietal and occipital cortex) requisite for the formation of supramodal concepts (Sarnthein et al.,

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[10] Indeed, it is arguable that it evolved more as a response-stimulus mechanism (see Cotterill, 2001).

1998). Slow-medium wave oscillations in the theta and alpha bandwidth were observed to correlate with the long-range transfer of information between frontal and posterior cortex during tasks thought to require more top-down than bottom-up processing such as mental imagery and working memory retention (von Stein et al., 2000a; von Stein et al., 2000b).

8.3.2 Regarding Other Compatible Models

8.3.2.1 Global, Regional and Local Activation

The notion of long-range cortical communication facilitated by specific oscillatory activity in the alpha band and local coupling by fast EEG gamma activity is compatible with proposals from Silberstein (Silberstein, 1995). Using models of corticocortical coupling, Silberstein has found average global (long-range) and regional (medium range) resonances to be centred around 8Hz (on the cusp of the theta – alpha frequencies), whereas average local resonances are centred around 43Hz (in the gamma frequency band). Silberstein postulates that these local, regional and global resonant modes may be modulated by neurotransmitter levels. Specifically, that 5HT facilitates global-regional modes and inhibits local resonances. Whereas, local resonant modes are facilitated by NA, DA & ACh, and that these neuromodulators are active in the inhibition of long-range, global, corticocortical coupling. Silberstein and colleagues have also produced more direct findings compatible with a positive association between top-down processing and alpha activity. They observed increased inter-electrode coherences in the upper alpha range during mental calculation (Nunez et al.,

2001). Interestingly, these findings were most obvious at posterior sites. It should be noted however, that there were considerable individual differences between subjects. Nunez *et al* also make the important point that the techniques used to analyse and visualise one's data can have a dramatic effect on one's findings. This maybe one reason for many of the discrepancies found in particular with respect to observations of alpha activity. For instance, they found that when using a spatial filtering algorithm to create a 'dura image' (a virtual map of EEG potentials below the scalp) that global alpha was reduced compared to local activity. They explore this observation by discussing the fractal-like nature of the EEG – the closer one looks, the more detail one will find. However, this does not stop them emphasising the importance of global coherence effects for top-down processing. Global effects for instance can strongly affect local dynamics; a possible mechanism for how perception can be influenced by the present state of the system.

8.3.2.2 The Triangular Circuit of Attention

Although generally applied to traditional understandings of attention, i.e. externally directed, La Berge's triangular circuit of attention may provide some useful insights into both long-range interareal cortical communication and the observations made during the course of this study (LaBerge, 1995; LaBerge, 1997; LaBerge, 2001). The triangular aspect of this model is provided by the following three attentional mechanisms: expression, enhancement and control. Areas of attentional control, also referred to as sources of attention, are those neural networks located in frontal and pre-frontal cortex, normally associated

with executive-type functions (e.g. dorsal lateral prefrontal cortex). Enhancement is provided by the thalamus via thalamocortical mechanisms similar to those originally suggested by Crick's spotlight hypothesis (Crick, 1984). Attentional expression occurs in anterior and posterior networks associated with the encoding of percepts and their attributes (e.g. parietal association cortex). The triangle is activated when signals of note are picked up by frontal executive areas and consequently, the 'gain' is turned up on the relevant areas of attentional expression by way of the thalamus, also leading to increased corticocortical connectivity between the two areas. The important factor to bear in mind with regard to the present study is the identification and separation of the concepts of attentional source and expression. Thus for instance, the findings from the fourth experiment of greater alpha activity at occipital and left frontal sites could be considered compatible with such an idea; with the left-frontal activity resulting from attentional control and the occipital activity reflecting attentional expression in the form of visualization.

It is tempting to postulate that a model such as La Berge's could be adapted to accommodate the present findings, notions of alpha reflecting top-down control mechanisms and previous observations linking evoked alpha with inhibitory processes. Oscillations would provide the medium for the attentional 'binding'. The first step is to assume that task-specific inhibition is a form of top-down process and can therefore be incorporated into the top-down model. The second is to bear in mind that the activity observed during the course of the three imagery studies is facilitated by the numerous thalamocortical, corticothalamic and corticocortical feedback loops. In this scenario, goal-driven behaviour (i.e.

intention to create mental images) and/or lack of sensory input would nudge thalamic nuclei to inhibit input to primary sensory neural assemblies. At the same time, excitation of the requisite frontal, association and sensory areas could be expressed in the form of greater long-range corticocortical couplings. Despite the obvious speculative nature of such a model, it may hopefully provide a starting point for future research in this area.

8.4 CAVEATS AND POSSIBILITIES

An important caveat regarding the preceding preliminary model and indeed von Stein and colleagues' hypotheses per se is the possible problem with the strict distinction between local connectivity being mediated by gamma oscillations and the theta-alpha modulation of long-range connectivity. As mentioned above, the analysis methods used in a study can affect the observations made; to cite Nunez *et al* "experimental designs and data analysis methods may severely bias physiological interpretations in either local or global directions" (Nunez et al., 2001). One simple way in which the von Stein method may have influenced results was with the length of epoch chosen for analysis. With an epoch of 2000ms (e.g. Sarnthein et al., 1998), if, for example gamma activity were to be modulated at a slower frequency, as has been observed in a handful of studies (Bragin et al., 1995; Burgess & Ali, 2002; Chrobak & Buzsaki, 1998; Penttonen, Kamondi, Acsady, & Buzsaki, 1998), then the signal-to-noise ratio would be such that gamma activity would be 'lost' in the noise. Thus a further lesson learned from this study is that the length of epoch chosen may have a crucial

effect on the observations made and should therefore be carefully considered when planning future projects.

Also, with regard to the potentiality that the distinction between local gamma and global alpha is not as clear cut as hypothesized, one has to bear in mind the gamma results from the present study. Despite their intermittent and non-replicated nature, it is possible that the findings of greater gamma during internally directed attention in certain tasks in the first two experiments were actually reflecting true functional significance. It is possible that in the study as whole, a type II error[11] has been made and that gamma activity also accompanies mental tasks. If this were to be the case, then it is arguable that all EEG activity is a measure to some extent of top-down processes. Indeed, this possibility has been hinted at recently from various quarters (e.g. Makeig, 2002; Makeig et al., 2002). Perhaps a less stringent way of looking at it, is to think of the EEG in terms of reflecting the balance between top-down and bottom-up processes. This approach can be seen in the work of Gevins and Cutillo (Gevins & Cutillo, 1995, pg.332), who state "many areas probably are involved in a constellation of rapidly changing functional networks that provide the delicate balance between stimulus-locked behavior [bottom-up] and purely imaginary ideation [top-down]".

This emphasis on the dynamic, constantly changing nature of brain activity as expressed in the EEG is a topic that is currently receiving renewed interest and

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[11] The error of wrongly accepting the null hypothesis.

may provide a future avenue of investigation for the issue addressed in the present study. For instance, Edelman, Tononi and colleagues have developed a method for analyzing EEG that takes into account the complexity and non-linear nature of brain electrical activity (Edelman et al., 2000; Tononi & Edelman, 1998a; Tononi, Edelman, & Sporns, 1998b). They propose that higher order brain processes such as consciousness involve a balance between the functionally specific processes of the different neural networks involved and the homogenous, integrative nature of the system as a whole. Edelman & Tononi explain and justify their method with the following statement, "high levels of complexity correspond to an optimal synthesis of functional specialization and functional integration within a system. This is clearly the case for systems like the brain – different areas and different neurons do different things (they are differentiated) at the same time they interact to give rise to a single unified scene and to unify behaviors (they are integrated). By contrast, systems whose individual elements are either not integrated (such as gas) or not specialized (like a homogenous crystal) will have minimal complexity." (Edelman et al., 2000, pg. 130/1). There are obvious implications here for understandings of cognition based on ideas of global-local or inter-intra-areal communication. Clearly, applying such a measure as EEG-complexity to the carefully developed protocol from the present study, that ensures a fully matched balance between sensory-intake and mental imagery tasks should prove extremely useful in further determining the nature of the balance of processes involved.

The possibility of type II error in this study was introduced above. The other possibility of type I error[12] should also be addressed. There are two main possibilities as to how this may have happened in relation to the alpha findings. Firstly, one of the perennial problems associated with EEG studies is the small number of participants typically involved and the associated low statistical power. Thus it is possible that the alpha findings are purely down to random fluctuations in the EEG and / or skewed individual effects. However, the consistency of the alpha results across the three mental imagery experiments tends to suggest that they were not chance or artifactual findings. Instead we have a clear positive relationship in three modalities between alpha activity and top-down controlled mental imagery. The other possibility arises from the nature of alpha itself in comparison with the other EEG wavebands. Alpha (and indeed theta) oscillations have higher signal to noise ratios than delta, beta or gamma (Nunez et al., 2001, pg 149). This may account as to why we get consistent findings with alpha but not the other bands. However, the regular if not consistent delta observations (experiments 1, 3 and 4) tend to negate this idea; particularly as they are opposite to the alpha findings. Nevertheless, even if a 'worst case scenario' is assumed and experimental differences in other wavebands have been missed, the argument developed earlier in this section of EEG activity reflecting the balance of top-down versus bottom-up processes is still applicable.

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[12] The error of wrongly rejecting the null hypothesis.

8.4.1 Other Experimental Limitations

8.4.1.1 Sampling Rates and Gamma

A potential source of difficulty when examining the EEG is the relationship between fast activity and the speed of the sampling rate employed. Too slow a rate will lead to the 'aliasing' of the faster frequencies, i.e. the misrepresentation of frequencies that exceed half the sampling rate at slower frequencies (Gonzalez & Wintz, 1987). However, in all the experiments carried out in this study, the sampling rate was 500 Hz, leading to a Nyquist frequency of 250 Hz – well above the maximum range used for gamma in this study (i.e. 80 Hz).

8.4.1.2 Source Localisation

Another well known problem associated with the EEG is that of source localization. It is impossible to accurately assess the cephalic origins of the electrical potential one is measuring at the scalp. This has been dubbed the 'inverse problem'. In essence, this problem concerns the fact that any recorded array of electrical activity at the scalp, could have been generated by an infinite number of sources (Fender, 1987). Even if an ideal reference were devised (see box 4.1), one could still not mathematically prove that the signal one is recording arose from a specific area. Given the importance of the location of the alpha findings in this study with regard to their interpretation, further clarification of their origins is called for. Much past work has attributed the posterior alpha rhythm to activity arising in the visual cortex, but this cannot be taken for

granted in this instance. Functional magnetic resonance imaging studies (fMRI) have found activation of areas around the calcarine sulci during mental imagery tasks (e.g. Klein et al., 2000) but again we cannot be certain that this is the source of our imagery-related activity. Clearly, methods such as co-registration of EEG with fMRI would be of use in this respect. Another potentially useful approach to take is that of magnetoencephalography (MEG). The addition of evidence from MEG used in conjunction with a source localization technique such as SAM (Synthetic Aperture Magnetometry[13]) could, if appropriate, lend weight to the interpretations of those findings suggested above.

8.4.1.3 Individual Differences in Alpha Activity

Much work in recent years has focused on individual differences in alpha activity, particularly with respect to memory processes (e.g. Klimesch, 1997; Klimesch, 1999; Klimesch et al., 1997; Klimesch et al., 1990). Consequently, methods have been devised for individually adjusting alpha parameters on an individual basis. One such method also emphasizes the need to employ narrow bandwidth parameters when observing alpha, due to possible functional differences between the sub-bands (Klimesch, 1999). In the fourth experiment, this method was used in order to test more fully a theory pertaining to alpha, forwarded by the author of the method. The results were interesting, in the sense that the observations made in the earlier experiments were replicated in all sub-

[13] A method that provides continuous 3-D images of cortical power changes (Singh, Barnes, Hillebrand, Forde, & Williams, 2002).

bands, but at differing locations (i.e. more frontal for lower alpha 1 and 2, and more occipital for upper alpha). However, ambiguities remain as to the functional significance of this finding and also as to the usefulness and accuracy of the adjustment method involved. Given the intrinsic importance of these questions and the extremely time consuming nature of carrying out individually adjusted analyses of one's data, these issues need to be addressed. A useful avenue for future research would be to attempt to define the parameters of the bandwidths using independent component analysis (ICA)[14]. However, it is probable that uncertainties would still remain as arguably parameters may well change as task requirements change. Given the increasingly obvious dynamic, even fluid-like properties of the brain, this would seem a distinct possibility.

8.5 FUTURE RESEARCH

Another avenue of future research suggested by the results from this study would appear to be an undertaking that directly applies the von Stein model[15] to a sensory-intake versus mental imagery protocol such as that developed in this project. The important aspect of this model is that it emphasises the transfer of information between cortical areas some distance apart. In order to make this kind of assumption based on EEG data, von Stein and colleagues use coherence measures to assess the functional connectivity of the sites involved (von Stein et

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[14] a statistical technique for separation of independent signals, similar to principal component analysis.

[15] E.g. the equating of top-down control mechanisms with alpha activity etc (see section 8.3).

al., 2000b). Therefore, the first step would appear to be the application of a similar analysis technique. However, as mentioned above, there are certain potential problems associated with the specific technique employed by von Stein *et al.* Therefore functional connectivity should be assessed using for instance, phase coherence measures using smaller time-frames for analysis; thereby maximising signal-to-noise ratios in the faster EEG wavebands.

A further approach that may well prove fruitful would be to apply an analysis technique based on Edelman & Tononi's proposals of dynamic complexity (Edelman et al., 2000; Tononi et al., 1998b). This approach would allow a different and complementary means of examining functional connectivity between cortical areas during mental imagery versus sensory-intake tasks. This technique creates an index of 'complexity' within the cortex, which in this respect, is a measure of the balance between functional segregation (i.e. the modularity of the system) and functional integration (the dynamic, holistic aspects of the system). Such a measure appears well suited to establishing the relationship between the EEG, its constituent bandwidths and the balance of global versus local connectivity and relatedly, to the balance of top-down and bottom-up processes.

Perhaps one of the most important proposals regarding future research arising from this study, although admittedly a more general one, is that protocols need to take into account the possible balance of top-down and bottom-up processes. The careful planning and development of paradigms that fully match experimental stimuli and behavioural responses and can therefore make

inferences regarding this balance is of utmost concern. To date, much of the work investigating mental imagery in particular has been considerably undermined by such omissions.

One final caveat and one that is particularly apposite in a study such as this, is the use of language that implies that it is the oscillation rather than the binding that is important. For want of a better metaphor, the emphasis is often placed on the messenger rather than the message. Perhaps the distinction is semantically questionable, but it is arguable that the crux of the binding problem is not that it is realised by oscillations at a certain frequency or another. The crucial factor is that the activity is correlated, that coherent relations between neuronal events exist. As Kelso emphasises, "it is the coordination among distributed neuronal events that appears to be significant for binding, not the oscillation per se" (Kelso, 1995, pg. 251). This does not mean that all band-power measures of the EEG are irrelevant. It does mean however that when exploring the functional significance of the EEG we should not get carried away with assigning roles to rhythms for the purpose of creating neat (yet untenable) hypotheses. The lesson learned from this study in this respect has been to witness the gradual generalisation of the models tested. Beginning from a hypothesis of alpha activity indexing the inhibition of irrelevant sensory stimuli during internally focused tasks (the intake-rejection hypothesis), results ensured that this hypothesis was broadened to include the inhibition of all irrelevant processes or stimuli (the inhibition hypothesis) and finally proposals were made that alpha (and perhaps most EEG activity) reflects the balance of top-down to bottom-up processes (including where appropriate, inhibition). The point that we are left

with, is that certain tasks appear to require more in the way of 'top-down' processing than others (in this case, imagery needs more than sensory-intake) and this processing appears to be a function of oscillatory activity in the 8-12 Hz band, and importantly, this rhythm facilitates the correlation of activity, the binding, between the requisite spatially separate areas.

8.6 CONCLUSIONS AND OBSERVATIONS

This study was undertaken to examine the merit of the intake-rejection hypothesis as a means of investigating attention and to observe the associated functional significance of the various EEG bandwidths. In order to accomplish this aim, four experiments using EEG measures were carried out. Consistent results were obtained that led to the rejection of the intake-rejection hypothesis as a plausible model. Additionally, further evidence was generated against the traditional understanding of alpha activity (8-12Hz) reflecting cortical idling. Recent proposals suggesting that alpha may index the inhibition of non-task relevant areas or processes were also investigated. Results suggest that although this approach may go some way to explaining some of the observations made in recent years, it does not account for all of them. It is suggested that a more parsimonious explanation of the findings from this study can be found in terms of the relative balance between the levels of top-down and bottom-up processing, similar to proposals by von Stein and colleagues (von Stein, 1999; von Stein et al., 2000a; von Stein et al., 1999; von Stein et al., 2000b).

Although the intake-rejection hypothesis has been to some extent discredited by this study, its past usefulness as an approach to understanding attention should not be underestimated. It grew out of the psychophysiological work surrounding the area of stimulus-response specificity (e.g. Ax, 1953) and the directional fractionation of response[16] (Lacey, 1959). This understanding should not be overlooked when generalising from particular data sets. The I-R hypothesis has also led to the undertaking of several influential pieces of work (e.g. Cole et al., 1985; Ray et al., 1985b; Ray et al., 1985a) and has facilitated acceptance of many observations that would otherwise have been regarded as flying in the face of orthodoxy (e.g. task-related increases in alpha). However, the results from the present study have afforded the interpretation that most, if not all of these previous 'paradoxical' findings can be better understood in terms of the increased top-down control required for the task in hand.

The coincidence has not gone unnoticed between the observations from the present study and the recent upsurge in interest in and findings of task-related changes in alpha activity. Evidence is growing that traditional ways of understanding alpha are no longer tenable. Arguably this has been facilitated by new and more dynamic methods of analyzing EEG data (e.g. event-related bandpower, including identification of induced and evoked activity, coherence measures et cetera). Also findings from other electrophysiological areas have

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[16] Stimulus-response specificity refers to the "patterning of physiological responses according to the particular stimulus situation" (Andreassi, 2000, pg.405). The directional fractionation of response highlights the finding that different physiological measures can vary their direction in response to the same stimulus.

heightened the awareness of the importance of alpha oscillations in the nervous system as a whole. For instance, the work of Llinas and others has shown them to be virtually ubiquitous, ranging from the intrinsic oscillatory activity of individual nuclei (e.g. the inferior olive, Llinas, Walton, Hillman, & Sotelo, 1975) to the discrete periodic character of all movement – the "physiological tremor" (Schafer, 1886). This 'tremor' refers to the observations that all muscular movement is a discontinuous series of tetanic twitches and indeed can even be observed before and after movement, i.e. at rest (Goodman.D. & Kelso, 1983; Llinas, 2001). The point that Llinas emphasizes that has direct associations with the observations made throughout this study is that such a mechanism facilitates a "pulsatile control system" (Llinas, 2001, pg.33). Thus we see that the findings reported from this study complement and extend the growing, 'emergent' understanding that alpha oscillations sub-serve a critical and integral function in the brain as a controlling and facilitating medium. The questions remain, what is the exact nature of this control, and how does it interact with other EEG components? Hopefully, the recommendations for future research, made above, may go some way to addressing these issues.

8.6.1 Final Remarks

This study has presented evidence that contributes to the field of cognitive neuroscience in the following ways:

- The alpha-as-idling position is no longer tenable.

- The intake-rejection hypothesis was a useful but incomplete interpretation of attentional observations.
- The notion of increases in alpha power indexing the inhibition of non-task relevant areas or processes was thought to result from evoked activity. The finding of task-related increases in induced alpha activity undermines this position, as do the locations of the observations.
- A more parsimonious explanation may be found in terms of alpha (and theta and beta) reflecting an increase in the ratio of top-down to bottom-up processing involved in the task. Suggestions are made that this may extend to the EEG as a whole reflecting the balance of this ratio.
- Additionally, in line with numerous previous studies, further evidence was presented linking theta oscillatory activity with neural networks involved in working memory processes. This too may complement the notion of EEG reflecting top-down involvement in a task.

It remains the scope of future work to test further the relationship between EEG activity and the ratio of top-down to bottom-up processing. The first step would appear to be the implementation of phase coherence measures over short time intervals during an archetypal top-down task such as mental imagery. Additionally, analysis using complexity measures (e.g. Edelman et al., 2000; Tononi et al., 1998a; Tononi et al., 1998b) would develop the understanding of local-global interactions during such tasks and possibly shed further light on the role of alpha oscillations in higher-order processes.

It may appear from some perspectives that this study has proven mainly negatives (alpha is not idling; I-R and inhibition hypotheses are incomplete et cetera). If this outcome were to be the case, then so be it; such is often the character of scientific methodology. The main purpose of psychological and psychophysiological models is after all to facilitate hypothesis testing and thereby reject the ineffectual. Nevertheless, this project has carried this out by way of consistent positive findings.

Finally, it is important to emphasize these positive findings. In all three mental imagery experiments, task-related increases in alpha power were observed. Similar but less consistent findings were also observed in theta and beta bandwidths. These findings facilitated the rejection of three models of alpha functional significance. They also helped to give structure to a new emerging model – that of the intimate link between alpha oscillations (and other EEG components) and various cognitive control mechanisms. It is the requirement now, that this model be stringently tested; that it forms the basis for the next set of hypothesis testing.

9 APPENDICES

9.1 APPENDIX 1

QUESTIONNAIRE (for experiment 2).

Please try to remember how much effort you put into the tasks that you have just completed. Circle a number next to each question below to signify the amount of effort.

1 = No effort required
2 = A little effort required
3 = A moderate effort required
4 = A lot of effort required, but still able to do it
5 = A lot of effort required, and was unable to do it

For any tasks that you did not perform properly (e.g. got bored, did not concentrate etc.) please put an "X" next to the corresponding number.

The Visual Task: How much effort was required to.....?

1.	Stare at the screen	1 2 3 4 5
2.	Decide how many shapes there were	1 2 3 4 5
3.	Decide how many types of shape there were	1 2 3 4 5
4.	Imagine the previous sequence	1 2 3 4 5
5.	Imagine the previous sequence & decide what was the 3rd shape	1 2 3 4 5
6.	Imagine the previous sequence & decide if the 1st & 5th shapes were the same	1 2 3 4 5

The Auditory Task: How much effort was required to.....?

1.	Listen to the sequence of tones	1 2 3 4 5
2.	Decide how many sounds there were	1 2 3 4 5
3.	Decide how many types of shape there were	1 2 3 4 5
4.	Imagine the previous sequence	1 2 3 4 5
5.	Imagine the previous sequence & decide what was the 4th tone	1 2 3 4 5
6.	Imagine the previous sequence & decide if the 1st & 6th tones were the same	1 2 3 4 5

The Tactile Task: How much effort was required to.....?

1.	Feel the touches	1 2 3 4 5
2.	Decide how many touches there were	1 2 3 4 5
3.	Decide how many different textures there were	1 2 3 4 5
4.	Imagine the previous sequence	1 2 3 4 5
5.	Imagine the previous sequence & decide what was the 5th texture	1 2 3 4 5
6.	Imagine the previous sequence & decide if the 1st & 5th textures were the same	1 2 3 4 5

9.2 APPENDIX 2

On the following three pages, there is to be found a 'script' of the instructions given to the participants in experiment 3 and the questions asked of them. This script was consequently modified in experiment 4 for the reasons explained in chapter 5. The reasons for employing such a script were to minimise inter-subject variance in terms of the experimental procedure, and also to help eliminate experimenter bias.

EEG PROTOCOL - QUESTIONS **P =**

VISUAL

1. I am going to begin this section by showing you a series of shapes. This series will be repeated 3 times. To begin with I just want to you to watch the shapes.

2. I am now going to show you the series of shapes again. After you have seen the series 3 times I want you to answer the following question:
   How many shapes are there in each series?

   Answer: (6) Correct: Yes No

3. I am now going to show you the series of shapes again. After you have seen the series 3 times I want you to answer the following question:
   How many different types of shapes are there?

   Answer: (4) Correct: Yes No

4. In a moment I want you to be able to imagine the series of shapes in your mind's eye. I'm going to run the series by you for a further 3 times in order to try & train you to be able to do this. We can have as many training sessions as you like.

   Can do? Yes No

   OK After a count of three I want you to run through the series of shapes 3 times in your imagination. I'll say OK when it's time to stop. 3-2-1...

5. Now, after the count, I want you to run through the series of shapes again in your imagination. Try to do it another 3 times and at the end of it I'll say OK then you answer the following question:
   What is the 3rd shape in the series? 3-2-1...

   Answer: (S) Correct: Yes No

6. Now, after the count, I want you to run through the series of shapes again in your imagination. Try to do it another 3 times and at the end of it I'll say OK then you answer the following question:
   Are the 1st & 5th shapes the same? 3-2-1...

   Answer: (x) Correct: Yes No

Comments:

EEG PROTOCOL - QUESTIONS **P =**

ACOUSTIC

1. I am going to begin this section by playing you a series of tones. This sequence will be repeated 3 times. To begin with I just want to you to listen to the tones.

2. I am now going to play to you the series of tones again. After you have heard the sequence 3 times I want you to answer the following question:
   How many tones are there in each series?

   Answer: (6) Correct: Yes No

3. I am now going to play to you the series of tones again. After you have heard the sequence 3 times I want you to answer the following question:
   How many different notes are there?

   Answer: (3) Correct: Yes No

4. In a moment I want you to be able to imagine the series of tones in your head. I'm going to run the sequence by you for a further 3 times in order to try & train you to be able to do this. We can have as many training sessions as you like.

   Can hum it: Yes No Can imagine: Yes No

   OK After a count of three I want you to run through the series of tones 3 times in your imagination. I'll say OK when it's time to stop. 3-2-1...

5 Now, after the count, I want you to run through the series of tones again in your imagination. Try to do it another 3 times and at the end of it I'll say OK then you answer the following question:
   What is the 4^{th} note in the series: hi, mid or lo? Hum it to me. 3-2-1...

   Answer: (hi) Correct: Yes No

6 Now, after the count, I want you to run through the series of tones again in your imagination. Try to do it another 3 times and at the end of it I'll say OK then you answer the following question:
   Are the 1^{st} & 6^{th} notes the same? 3-2-1...

   Answer: (X) Correct: Yes No

Comments:

EEG PROTOCOL - QUESTIONS **P =**

HAPTIC

1. I am going to begin this section by touching your fingertips gently with a sequence of different grades/textures of sandpaper. This series will be repeated 3 times. To begin with I just want to you to feel the sequence. (click 1)

2. I am now going to repeat the sequence again. After you have felt the sequence 3 times I want you to answer the following question:
   How many touches are there in each series? (click 2)

   Answer: (6) Correct: Yes No

3. I am now going to repeat the sequence again. After you have felt the sequence 3 times I want you to answer the following question:
   How many different grades/textures of sandpaper are there? (click 3)

   Answer: (3) Correct: Yes No

4. In a moment I want you to be able to imagine the sequence of textures in your head. I'm going to run the sequence by you for a further 3 times in order to try & train you to be able to do this. We can have as many training sessions as you like.
   Can do? Yes No

   OK After a count of three I want you to run through the sequence of textures 3 times in your imagination. I'll say OK when it's time to stop. 3-2-1... (click 4)

5 Now, after the count, I want you to run through the sequence of textures again in your imagination. Try to do it another 3 times and at the end of it I'll say OK then you answer the following question:
   What is the 5th texture in the series: rough, medium or smooth? 3-2-1... (click11)

   Answer: (m) Correct: Yes No

6 Now, after the count, I want you to run through the sequence of textures again in your imagination. Try to do it another 3 times and at the end of it I'll say OK then you answer the following question:
   Are the 1st & 5th textures the same? 3-2-1... click12)

   Answer: (x) Correct: Yes No

Comments:

9.3 APPENDIX 3

Randomly generated stimulus sequences for experiments 4♠:

A = 440 Hz; **Bb** = 466 Hz; **B** = 493.9 Hz; **C** = 523.2 Hz; **C#** = 277.2 Hz; **D** = 293.7; **D# (Eb)** = 311 Hz; **E** = 329.6 Hz; **F** = 349 Hz; **F#** = 370 Hz; **G** = 392 Hz; **G# (Ab)** = 415.3 Hz.

1 C, B, B, F, F, B

2 G, Ab, Ab, E, Ab, E

3 F#, D, F#, E, D, F#

4 B, Ab, A, A, Ab, A

5 F#, Bb, Eb, F#, F#, Eb

6 C, C, E, Bb, E, E

7 C#, F, C#, C#, F#, F

8 B, Bb, Bb, C#, B, C#

9 Bb, Bb, A, A, F, A

10 E, E, C#, A, A, A

11 Ab, F#, D, F#, F#, D

12 G, F, A, A, F, G

13 A, A, G, G, A#, A#

14 F#, F#, F#, G, Bb, Bb

15 Eb, E, Ab, Eb, E, E

16 D, C, C, B, B, C

17 Ab, B, B, F#, B, B

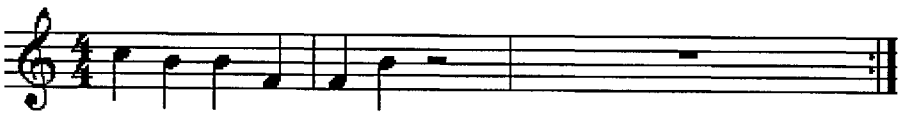
18 F, D, F#, F#, D, F#

19 C#, Ab, G, Ab, Ab, C#

20 Ab, Bb, Ab, Bb, E, Bb

♠ NB – First note of each sequence served as the tone for the monotonous (imagery) sequence

Example of auditory sequence (No.1) in musical notation:



9.4 APPENDIX 4

Publications and presentations based on research included in this thesis

Cooper, N.R., Croft, R.J., Dominey, S.J.J., Burgess, A.P. & Gruzelier, J.H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology* 47 65-74.

Cooper, N., Burgess, A., Croft, R. J., & Gruzelier, J. Investigating the role of evoked and induced activity in task-related alpha power increases. (*in prep*).

Cooper, N., Croft, R. J., Dominey, S., Burgess, A., & Gruzelier, J. (2001). Investigating the Alpha Component of the Human EEG During Internally and Externally Directed Attention. *The Annual Scientific Meeting of the British Psychophysiology Society. Aston University, September.*

Cooper, N., Sheri, A., Vernon, D., Egner, T., & Gruzelier, J. (2002). The Effect of Alpha Neurofeedback Training on Mental Imagery Abilities. *The Annual Scientific Meeting of the British Psychophysiology Society, University of Glasgow, September 22nd-25th.*

Cooper, N., Burgess, A., Croft, R., & Gruzelier, J. (2002). Investigating The Functional Significance of Alpha Oscillations During Externally versus Internally Directed Auditory Attention. *The Annual Scientific Meeting of the British Psychophysiology Society, University of Glasgow, September 22nd-25th.*

Vernon, D. J., Cooper, N., Egner, T., Compton, T., Neilands, C., Sheri, A., & Gruzelier, J. (2002). A comparison of Theta, Alpha and SMR Neurofeedback protocols, and their respective influence on Working Memory, Mental Rotation and Attention performance. *The British Psychological Society, Cognitive Section, University of Kent, September 9th-11th.*

Additional Publications and Presentations

Cooper, N., Loveday, C., & Baldwin, M. (1999). The Experience of Time: Measuring the Effect of Colour and Time of Day on Duration Estimation. *The British Psychological Society. University of London, December.*

Vernon, D., Egner, T., Cooper, N., Compton, T., Neilands, C., Sheri, A. & Gruzelier, J. (2003). The effects of training distinct neurofeedback protocols on aspects of cognitive performance. *International journal of Psychophysiology* 47 75-85.

EOG correction: A comparison of four methods. Croft, R. J. Chandler, J. S. Barry, R. J. Cooper, N. & Clarke, A. (*submitted*)

9.5 APPENDIX 5

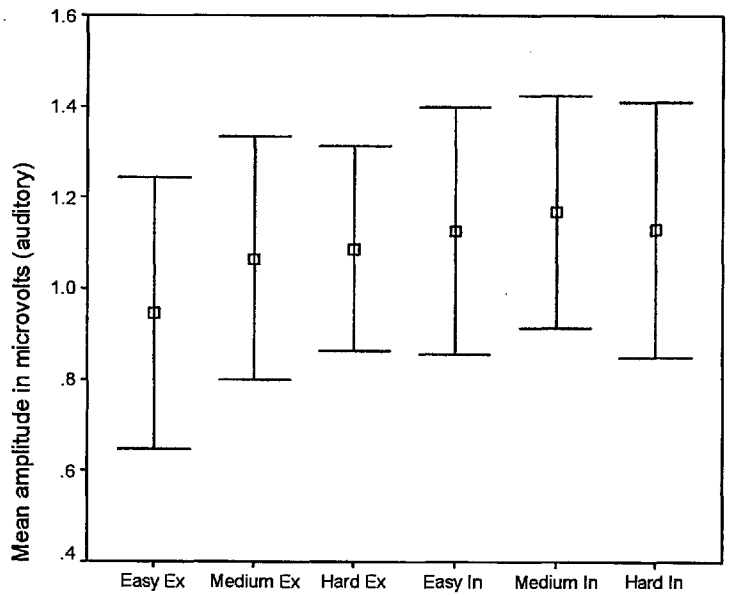


Figure 9.1: Graph depicting average alpha amplitudes for easy, medium and hard tasks in both externally and internally directed attention for the auditory modality (data from experiment 2).

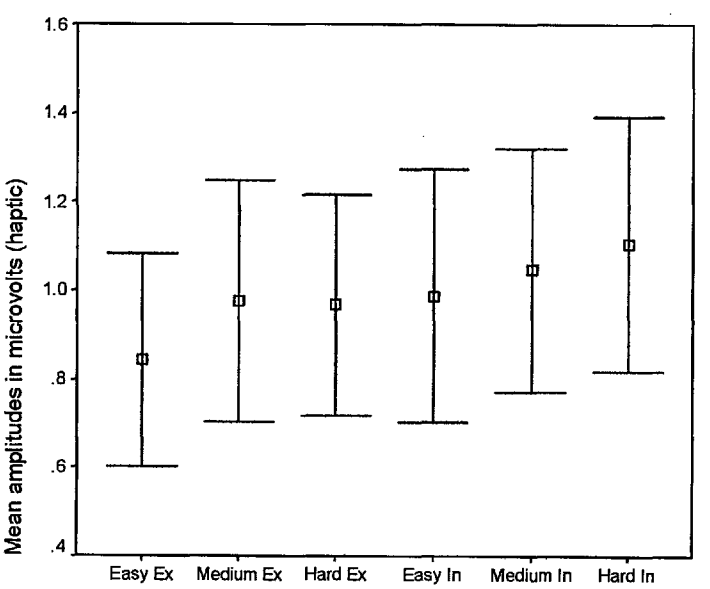


Figure 9.2: Graph depicting average alpha amplitudes for easy, medium and hard tasks in both externally and internally directed attention for the haptic modality (data from experiment 2).

Figures 9.1 and 9.2 reveal that mean alpha amplitudes increase in line with task difficulty in both externally and internally directed attention. However, in the internal auditory condition, the difficulty effect is only seen between the easy and medium difficulty conditions. As the results reported for task difficulty in experiment 2 are linear comparisons, only levels 1 & 3 (easy and difficult) are used in the analysis. This is arguably the reason for the fact that the main effect of task difficulty in the auditory modality was only observed at trend level – reflecting the "watering down" of the external difficulty effect by the internal findings. This coupled with questions pertaining to the subjective difficulty of the three difficulty conditions led to the number of levels of difficulty being reduced from three to two in the third and fourth experiments.

9.6 APPENDIX 6

As can be seen in figures 9.3. 9.4 and 9.5, the reduction from three to two levels of difficulty allows a clear difference between easy and hard tasks to emerge. This is observable in externally and internally directed attention in all three modalities

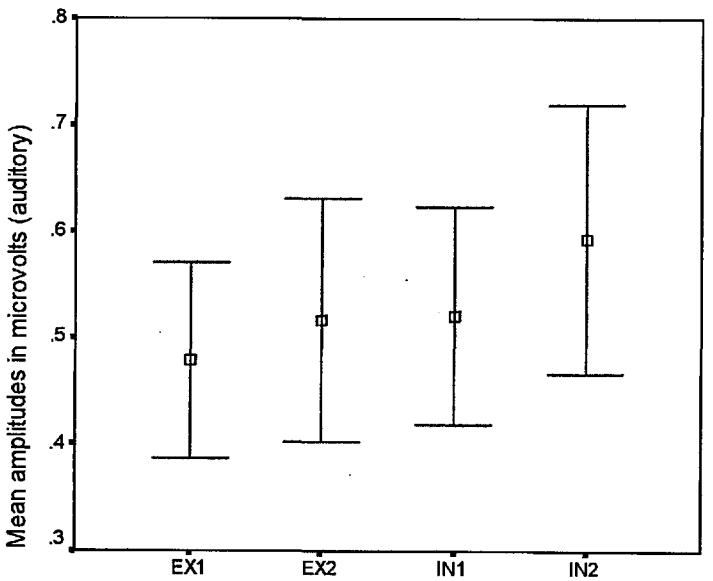


Figure 9.3: Graph depicting average alpha amplitudes for easy and hard tasks in both externally and internally directed attention for the auditory modality (data from experiment 3).

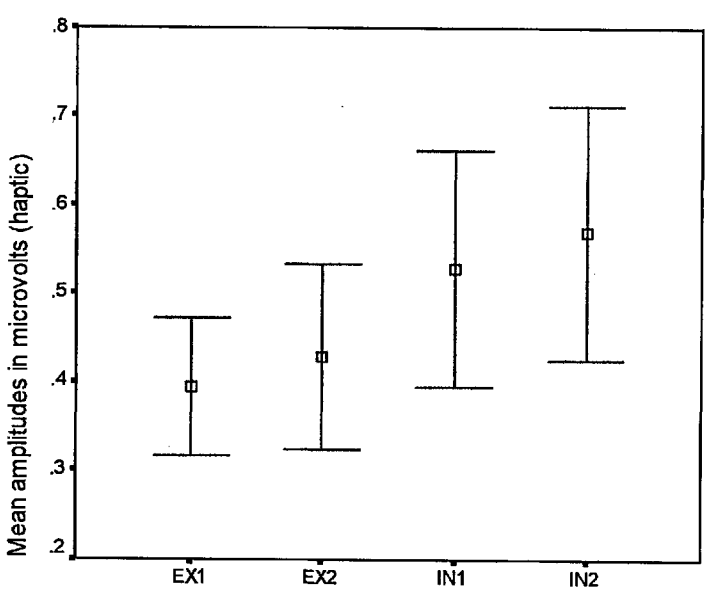


Figure 9.4: Graph depicting average alpha amplitudes for easy and hard tasks in both externally and internally directed attention for the haptic modality (data from experiment 3).

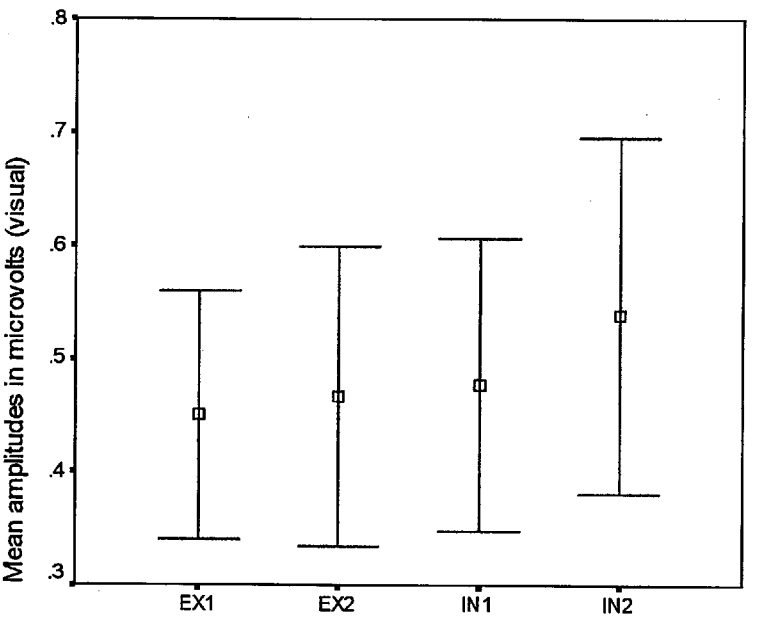


Figure 9.5: Graph depicting average alpha amplitudes for easy and hard tasks in both externally and internally directed attention for the visual modality (data from experiment 3).

Table 9.1 (shown overleaf) presents mean amplitude values and standard deviations for the attention and difficulty factors for all three sensory modalities in experiment 3.

Appendix 6 (continued)

Table 9.1: Alpha Means & Standard deviations for Attention & Difficulty in μV

ACOUSTIC

		DIFFICULTY	
ATTENTION		**Easy**	**Hard**
External	mean	0.48	0.52
	sd	0.18	0.23
Internal	mean	0.52	0.59
	sd	0.21	0.25

HAPTIC

		DIFFICULTY	
ATTENTION		**Easy**	**Hard**
External	mean	0.39	0.43
	sd	0.15	0.2
Internal	mean	0.53	0.57
	sd	0.26	0.27

VISUAL

		DIFFICULTY	
ATTENTION		**Easy**	**Hard**
External	mean	0.45	0.46
	sd	0.22	0.27
Internal	mean	0.47	0.54
	sd	0.26	0.31

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