

**NEURAL MECHANISMS MEDIATING VOLUNTARY  
SHIFTS OF SPATIAL ATTENTION**

by

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B.A., Simon Fraser University, 2004

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF ARTS

In the Department  
of  
Psychology

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SIMON FRASER UNIVERSITY

Summer 2006

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## **ABSTRACT**

The neural mechanisms underlying voluntary shifts of spatial attention were investigated by examining the event-related potentials (ERPs) to attention-directing cues and associated changes in alpha-band (8-14 Hz) electroencephalographic (EEG) activity. Intramodal auditory and visual shifts of attention were examined in Experiments 1 and 2, and crossmodal shifts of attention were examined in Experiments 3 and 4. Different patterns of ERP and alpha-band activities were observed across the four experiments. Frontal ERP activity (ADAN) was elicited by visual cues but not by auditory cues, which disconfirms previous claims that that this frontal activity reflects supramodal attentional control processes. Posterior ERP activity (LDAP) and associated changes in alpha-band EEG oscillations were observed in all experiments, but the scalp topographies of these activities depended on the modality of the task-relevant target. Such topographic differences suggest that the posterior ERP and alpha-band activities reflect attentional preparation in sensory-specific regions of cortex.

**Keywords:** Attentional control, Crossmodal attention, Multisensory, Supramodal, Event-related potentials

## **ACKNOWLEDGEMENTS**

I would like to thank my supervisor, Dr. John McDonald, for his ideas, insights, and feedback that were integral to this work, and for providing a motivating and inspiring lab for me to work in. Thanks also to Dr. Thomas Spalek for the many helpful ideas and discussions that contributed to this work.

I would also like to thank my lab mates, Clayton Hickey and Jen Whitman, for motivating discussions and research participation, and Julie Conder for emotional support and assistance with all the data collection. Thanks also to Glenn Landry and Shannon Gaudry for an enormous amount of support and advice, personal and academic.

Finally, thanks to my parents, who still don't understand what I do, but who are eternally proud and supportive anyway.

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# 1 INTRODUCTION

At any given moment our sensory systems are bombarded with information from our environment. Attention, the process of selectively focusing on one out of many possible stimuli, allows us to manage this abundance of sensory input by selecting only the most salient or task relevant information for further processing. In many cases a salient stimulus, such as a loud sound or a flash of light, will capture our attention involuntarily, but attention can also be focused on a particular object or location voluntarily. Attention can then be shifted from one object or location to another in order to efficiently obtain information about our environment. In the present study, the focus is on the voluntary shifting of attention to a spatial location in preparation for a task relevant stimulus.

The trial-by-trial cueing paradigm is often used to study voluntary spatial attention in the lab. In a prototypical cueing experiment, a symbolic cue is presented at fixation on each trial to indicate which of two or more possible target locations is to be attended before the task-relevant target is presented. Commonly these experiments involve a centrally presented arrow directing attention to a lateralized location to the left or right of fixation, followed by a target appearing either at the cued location (valid trials) or at the uncued location (invalid trials). When attention is voluntarily oriented to the location indicated by the symbolic cue participants are faster to respond to targets appearing at the attended location than to targets appearing at unattended locations (Posner, 1980). Similar cueing effects have also been found in studies of intramodal auditory attention (Mondor & Zatorre, 1995; Spence & Driver, 1994), and crossmodal attention (Mondor & Amirault, 1998; Spence & Driver, 1996; Spence et al., 2000). In general, voluntarily orienting attention to a specific spatial location will facilitate responses to target stimuli

appearing at the attended location even when the symbolic cue and response relevant target are presented in different sensory modalities (Driver & Spence, 2004).

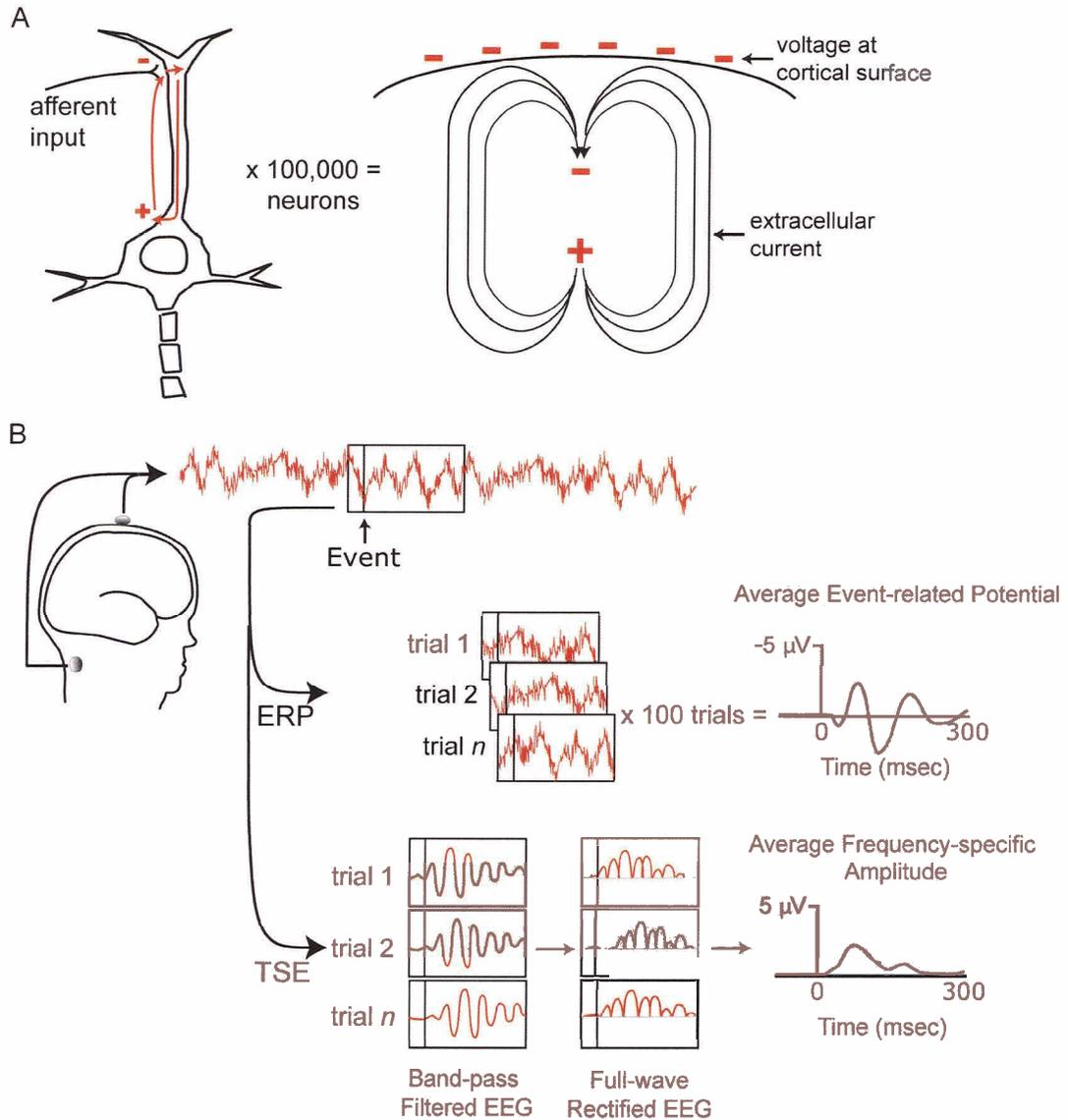
The similarity of cueing effects observed within the visual, auditory, and tactile modalities, as well as across modalities, suggests that a single *supramodal* neural system may exist that mediates shifts of attention to a particular spatial location independent of the modality of the relevant stimuli (e.g. Farah, Wong, Monheit, & Morrow, 1989). However, it is also possible that each sensory modality has an independent attention mechanism, but that links between these mechanisms exist to facilitate attention to multisensory objects when necessary (e.g. Spence & Driver, 1996). As such, similarities in the response-time cueing effects observed in unimodal and crossmodal studies may represent the interaction of separate unimodal attention mechanisms rather than a single supramodal system. One way to differentiate between these two possibilities is to examine the neural activity associated with shifting attention in space to determine if the same brain areas underlie the shifting of attention within and between modalities.

In recent years a number of researchers have focused on examining the neural mechanisms underlying spatial attention, particularly within the visual modality. Studies using functional neuroimaging techniques such as functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) are often utilized in order to provide high spatial resolution images of where activity in the brain is occurring. A number of studies using trial-by-trial cueing paradigms with these neuroimaging methods have indicated that voluntary shifts of visuospatial attention are mediated by activity of frontal, parietal, and midbrain structures (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2001; Hopfinger, Buonocore, & Mangun, 2000; Geisbrecht, Woldorff, Song, &

Mangun, 2003; Macaluso, Eimer, Frith, & Driver, 2003; Nobre et al., 1997; Rosen et al., 1999; Woldorff et al., 2004).

Although these neuroimaging studies have provided information about what specific brain areas are active during shifts of attention, there are two disadvantages to the neuroimaging techniques. First, they provide only an indirect measure of neural activity, measuring changes in metabolism or blood flow in the brain that follow the actual neural activity. Second, these techniques provide only a coarse estimation of the time course of activations. For example, PET and fMRI studies provide information about metabolic activity and blood flow, respectively, over the course of minutes, and event-related fMRI provides information about blood flow over the course of a few seconds.

Electrophysiological measures provide a more direct measure of neural activity and provide information about the time course of neural activity, although at the expense of some spatial information about where the activity is taking place. When post-synaptic potentials are produced simultaneously in large populations of cortical pyramidal cells (approx. 100,000), the electrical fields generated by the individual neurons sum together and can be recorded at the scalp as the electroencephalogram (EEG) (Figure 1-1A). The EEG can be recorded non-invasively from the human scalp while an experimental task is performed, and then epochs of EEG activity that are time-locked to a specific event of interest can be averaged together to create the event-related potential (ERP) (Figure 1-1B). Averaging over a large number of trials of the same event reduces activity that is not time and phase locked to the event of interest, producing a waveform that is representative of the neural response to the event of interest. If EEG is recorded from a sufficient number of electrodes across the scalp, then information about the spatial distribution of the activity can provide some indication of where in the brain the neural activity is being generated. If the distribution of activity varies across time within an



**Figure 1-1. Diagram of the generation of the electroencephalogram (EEG) (A), and the event-related potential (ERP) and temporal spectral evolution (TSE) methods of analyzing the EEG data (B).**

experimental condition or at the same point in time between experimental conditions it is indicative of different neural generators for the activity (Michel et al., 2004; Murray et al., 2005; Murray, Camen, Gonzalez Andino, Bovet, & Clarke, 2006). In addition, a number of techniques exist for estimating the neural sources of the scalp recorded activity. Thus, although less specificity in the brain areas that are active is available, the temporal

information and general spatial information provides complementary information to functional neuroimaging studies.

In addition to the EEG activity that is time and phase locked to the stimulus, it is possible to examine frequency specific oscillations in the ongoing EEG. It has long been presumed that the background EEG activity from which the ERPs are extracted is merely random electrophysiological noise that needs to be minimized, however it is now being recognized that changes in this seemingly random noise are induced by cognitive functions (e.g. Makeig et al., 2002; Mazaheri & Picton, 2005; Worden et al., 2000). Changes in oscillatory activity in the EEG can be induced by an event, but because on each trial the oscillation is not at precisely the same phase this activity is removed or greatly reduced by the averaging process. One particular way of examining this oscillatory activity is Temporal Spectral Evolution (TSE), a method that allows for the examination of EEG amplitudes within a chosen frequency band (e.g. between 8 Hz and 14 Hz to examine alpha activity) as a function of time (Salmelin & Hari, 1994). Although there is a small degree of temporal spread introduced by filtering of the data (<100 ms), and as such the timing of the frequency modulations are only approximations, TSE provides more accurate temporal information than other methods for examining EEG frequency power (Marrufo, Vaquero, Cardoso, & Gomez, 2001). By utilizing information from both ERPs and EEG oscillations, and relating it to the spatial information gained from functional neuroimaging studies, a more complete picture of the neural dynamics that underlie the consequences of attention on stimulus processing and the control processes mediating voluntary deployment of attention in space can be constructed.

To date, most electrophysiological studies of voluntary spatial attention have focused on the consequences of attention for the processing of attended as compared to unattended stimuli. ERPs elicited by visual and auditory targets are more negative when

a stimulus appears at an attended, or validly cued, location than when the same stimulus appears at an unattended, or invalidly cued, location. This negative difference (Nd) occurs in at least two phases, which suggests that voluntarily shifting attention to a particular spatial location modulates stimulus processing at multiple stages. In trial-by-trial cueing experiments the earliest negative difference, labelled the Nd1, begins approximately 140 ms after stimulus onset and is centred over the parietal scalp. A later negative difference, labelled the Nd2, begins approximately 200 ms after stimulus onset and is centred over the fronto-central scalp. The Nd1 appears to reflect processes that are involved in the reorienting of attention on invalid trials, whereas the Nd2 appears to reflect the facilitation of processing validly cued target stimuli that lead to faster response times (RTs) (Schröger & Eimer, 1997; Tata, Prime, McDonald, & Ward, 2001).

Voluntarily shifting attention to the location of visual targets can also amplify the P1 and N1 components over the lateral occipital scalp. The P1 and N1 components reflect the initial processing of the stimulus in extrastriate visual cortical areas, and attentional modulation of these components indicates that attention can also influence the early stages of cortical processing (e.g. Eimer, 1994; Mangun & Hillyard, 1991; Vogel & Luck, 2000).

To investigate the control processes that mediate the voluntary deployment of attention in space using the trial-by-trial cueing paradigm, researchers have examined the ERP waveforms elicited by the attention-directing cue stimuli, primarily within the visual modality (Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Jongen, Smulders, & Van Breukelen, 2006; Mangun, 1994; Nobre, Sebestyen, & Miniussi, 2000; Talsma, Slagter, Nieuwenhuis, Hage, & Kok, 2005; van der Lubbe, Neggers, Verleger, & Kenemans, 2006; Van der Stigchel, Heslenfeld, & Theeuwes, in press; Verleger, Vollmer, Wauschkuhn, van der Lubbe, & Wascher, 2000; Yamaguchi,

Tsuchiya, & Kobayashi, 1994). Based on these studies of visuospatial orienting, two components observed in the cue ERP waveforms have been associated with attentional control processes. These components are most commonly referred to as the anterior directing attention negativity (ADAN), and the late directing attention positivity (LDAP).<sup>1</sup> The ADAN appears as a relative negativity over anterior scalp sites contralateral to the to-be-attended location approximately 300-500 ms following an attention-directing cue. The LDAP component appears as a relative positivity over posterior scalp sites contralateral to the to-be-attended location beginning approximately 500 ms following an attention-directing cue and often lasting until the onset of the target stimulus.

The ADAN and LDAP observed during visuospatial shifts of attention were originally suggested to reflect the activity of a frontal lobe executive control mechanism for shifting attention and subsequent preparatory activity in the visual areas that would be activated by the upcoming target stimulus, respectively (Harter et al., 1989; Hopf & Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994). However, a number of recent studies have observed both the ADAN and the LDAP in crossmodal tasks where visual or auditory cues direct attention in anticipation of targets in the visual, auditory, or tactile modalities (Eimer, Forster, Fieger, & Harbich, 2004; Eimer & van Velzen, 2002; Eimer, van Velzen, & Driver, 2002; Eimer, van Velzen, Forster, & Driver, 2003; van Velzen, Forster, & Eimer, 2002). These latter observations have led to speculation that the ADAN and LDAP both reflect supramodal processes that are involved in the

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<sup>1</sup> A third cue-elicited ERP component (the early directing attention negativity, or EDAN) has been observed, but recent evidence indicates that it reflects the processing of the cue rather than the processes involved in shifting attention to the to-be-attended location (van Velzen & Eimer, 2003). The EDAN is only elicited when the attended portion of a visual cue stimulus is lateralized (e.g. the arrowhead of a central arrow cue), and since symmetric visual cues and auditory cues were used in the following experiments no EDAN was expected.

orienting of attention (Eimer & van Velzen, 2002; Eimer et al., 2002, 2003). Such processes would likely occur within the multisensory areas of the frontal and parietal lobes rather than within modality-specific areas of cortex such as the occipital lobe.

Despite the fact that the ADAN and LDAP can be seen prior to non-visual targets, there are at least two reasons to question whether these cue-elicited ERP components really reflect supramodal attentional control processes. First, the majority of experiments that investigated the supramodal nature of the ADAN and LDAP either presented visual cues to direct attention (Eimer et al., 2002) or presented visual as well as non-visual targets (Eimer & van Velzen, 2002; Eimer et al., 2003). This leaves open the possibility that the ADAN and LDAP are linked specifically to visual processing and not to supramodal attentional control. Second, auditory cues did not elicit the ADAN in a series of intramodal auditory experiments even though the cue-validity effects on auditory RTs were comparable to those found in an analogous intramodal visual experiment (Green, Teder-Sälejärvi, & McDonald, 2005). Auditory cues did elicit the LDAP in this study, but this component was focused primarily over the occipital scalp. This suggests that the LDAP may arise from multiple neural sources, some of which are located in extrastriate visual cortex.

The anterior ADAN and posterior LDAP components in the ERP waveforms are consistent with the results of fMRI studies of visuospatial attention, where pre-frontal and parietal cortical areas are commonly found to be activated and have been associated with a fronto-parietal network involved in controlling shifts of attention (Corbetta & Shulman, 2002; Posner & Petersen, 1990). Unfortunately, very few of the previous visual or crossmodal studies examining cue-elicited activity have adequately documented the spatial distribution of the ADAN or LDAP, making it difficult to know if the activity observed under a particular crossmodal cueing condition truly reflects the same activity

observed under other intramodal and crossmodal cueing conditions. Thus, it is possible that the ADAN and LDAP observed with different combinations of auditory, visual, and tactile cues and targets actually reflect the activity of different neural generators and not a single supramodal system.

In addition to changes in cue-elicited ERP activity, another way that voluntary shifts of attention could work to influence processing of the impending target is through the modulation of oscillatory activity in the multiple brain areas that are necessary for performance of the task. Recent work examining neural synchrony in cats and monkeys as well as the changes in oscillatory activity in the human brain as measured with EEG suggest that modulations of synchrony of oscillations may be the mechanism by which top-down signals bias sensory and motor processes (Engel, Fries, & Singer, 2001). Studies of cellular activity in cats and monkeys have found that during the interval between the presentation of a visual stimulus and a go-signal to make a response to the stimulus, synchronization of neural firing is observed in frontal, parietal, and visual areas in the cat (Roelfsema, Engel, König & Singer, 1997). In visual cortex, attention to a stimulus increases synchronization of neural activity relative to the response to the same stimulus when it is unattended (Fries, Reynolds, Rorie, & Desimone, 2001). Both of these studies demonstrated that attention increased the synchrony of neural firing, which indicates that expectation and preparation, both goal-directed processes likely mediated by prefrontal areas, can modulate synchrony not only in early sensory areas but also in widely distributed brain areas that perform other functions necessary for efficient task performance.

Recent work with humans has also associated low-frequency theta (4-8 Hz) and alpha (8-14 Hz) oscillations in the frontal and parietal lobes with the maintenance of information in spatial working memory (Sauseng, Klimesch, Schabus, & Doppelmayr,

2005; Schack, Klimesch, & Sauseng, 2005). This is consistent with previous findings that long range connections between distant brain areas, for example, between the frontal and parietal lobes, oscillate at low frequencies like theta and alpha, whereas connections within a smaller area, for example, within visual cortex, tend to display higher frequency oscillations (Gruber, Müller, Keil, & Elbert, 1999; Sauseng et al., 2005). As recent research suggests that overlap may exist in the neural mechanisms that underlie both shifts of spatial attention and spatial working memory (Awh, Anllo-Vento, & Hillyard, 2000; Awh & Jonides, 2001; Corbetta, Kincade, & Shulman, 2002), it is possible that synchronizations of frontal theta and posterior alpha rhythms may reflect the top-down control of spatial attentional orienting.

Akin to the ERP research on voluntary attention, most work examining the effects of attention on oscillatory activity have looked exclusively at the consequences that attention has on target processing (Mazaheri & Picton, 2005; Makeig et al., 2002; Marrufo et al., 2001). However, a few studies have now looked at oscillatory activity in anticipation of the target. Alpha-band (8-14 Hz) oscillatory activity in the EEG has been linked to anticipatory activity during voluntary attention (Foxe, Simpson, & Ahlfors, 1998; Fu et al., 2001), and this alpha modulation is spatially specific. That is, the alpha modulation is dependant on the locus of visuospatial attention (Worden, Foxe, Wang, & Simpson, 2000; Yamagishi, Goda, Callan, Anderson, & Kawato, 2005). These spatially specific differences in alpha activity have been interpreted to reflect either an increase in alpha contralateral to the uncued location as an anticipatory suppression of information from the to-be-ignored visual field prior to the target's occurrence (Worden et al., 2000), or a decrease in alpha contralateral to the cued location as an anticipatory enhancement of information from the to-be-attended visual field (Yamagishi et al., 2005).

Interestingly, the alpha modulation that has been associated with shifts of visuospatial attention occurred with a similar latency and scalp distribution to the LDAP observed in the ERP waveforms. However, the LDAP has now been observed in preparation for non-visual targets (Eimer et al., 2002, 2003, 2004; Eimer & van Velzen, 2002) and can be elicited in intramodal auditory cueing tasks (Green et al., 2005). There is some evidence that the presentation of a stimulus induces the phase resetting of ongoing oscillations to be time-locked to the stimulus, and that this plays a role in generating ERPs (Makeig et al., 2002). It has also been speculated that the EEG oscillations and ERPs share common neural generators (Engel et al., 2001; LaBerge, 2005; Mazaheri & Picton, 2005). Thus, if the LDAP and alpha modulation reflect the activity of a common neural generator then it is possible that the alpha modulation that has been observed during visuospatial shifts of attention will also be observed during auditory and crossmodal audiovisual shifts of attention.

The present series of experiments investigated the effects of attention on stimulus processing and the electrophysiological correlates of attentional control with both intramodal auditory and visual as well as crossmodal audiovisual cueing experiments. In Experiment 1, symbolic visual cues directed attention in preparation for subsequent visual targets, whereas in Experiment 2 symbolic auditory cues directed attention in preparation for subsequent auditory targets. In Experiments 3 and 4, the same cue and target stimuli were used but the modalities of the cues and targets were mixed such that symbolic auditory cues directed attention in preparation for subsequent visual targets in Experiment 3, whereas symbolic visual cues directed attention in preparation for subsequent auditory targets in Experiment 4.

Previous research has suggested that visual arrow cues elicit involuntary as well as voluntary shifts of attention (Ristic, Friesen, & Kingstone, 2002; Ristic & Kingstone, in

press). In addition, differences in the cue-elicited ERPs have been observed between well learned and novel symbolic cues in the visual and auditory modalities (Green, 2004). Thus, the visual and auditory cues used in the present series of experiments were designed to elicit only voluntary shifts of attention and to equate as closely as possible the amount of processing necessary to interpret the direction information provided by the cue. To this end, upward and downward pointing arrowheads were used as visual cue stimuli and upward and downward frequency glides were used as auditory cue stimuli.

These experiments were conducted with four primary goals. The first goal was to compare the effects of attention on response times and target-elicited ERP waveforms, including scalp topographies of the Nd1 and Nd2. The second goal was to determine if the presence of the ADAN is dependant on the modality of the cue, the modality of the target, or both. The third goal was to examine the scalp distribution of the LDAP to differentiate between supramodal parietal activity and sensory-specific preparatory activity. The fourth goal was to examine changes in alpha activity in auditory and crossmodal cueing conditions, as previous work has only examined this modulation within visual cueing.

The cue-validity effects on RTs and the target-elicited ERP waveforms were examined to determine whether participants followed instructions to shift attention to the cued location and to characterize the scalp topographies of the crossmodal attention effects on the target ERPs. Based on unpublished analyses of the cue-validity effects in the intramodal cueing studies done by Green et al. (2005), it is predicted that similar biphasic Nd waves will be observed in the intramodal and crossmodal experiments. This predicted pattern of results would provide evidence for the involvement of the same

supramodal attentional control system in intramodal and crossmodal audiovisual spatial attention.

With regard to the cue-elicited ERP effects, the intramodal visual and auditory studies (Experiments 1 and 2) were conducted to replicate the previous finding that the LDAP component, but not the ADAN component, is observed during intramodal auditory shifts of attention (Green et al., 2005). The crossmodal audiovisual studies (Experiments 3 and 4) were conducted to determine whether the presence or absence of the ADAN is related to the processing of a visual cue, the preparation for a visual target, or both. If the presence of the ADAN is dependant on shifting attention to a visual target then the ADAN should only be observed in Experiments 1 and 3, whereas if the presence of the ADAN is dependant on the use of a visual cue to direct attention then the ADAN should only be observed in Experiments 1 and 4. If any relevant visual stimuli will elicit the ADAN, then the ADAN should be present in all experiments except during intramodal auditory cueing (Experiment 2).

In addition to examining the conditions under which the ADAN is elicited, I also sought to determine whether the scalp distribution of the LDAP would be affected by the modality of the cue or target. It is possible that rather than reflecting either supramodal processes in the parietal lobe or preparatory activity in the occipital lobe, that the LDAP in fact reflects multiple processes (Green et al., 2005). If both attentional control and sensory specific preparation are contributing to the LDAP then it can be hypothesized that the contributions of these sources will vary depending on the modality of the cue and target stimuli. Thus, if the LDAP primarily reflects the activity of a supramodal control process in parietal cortex (cf. Eimer et al., 2002) then the LDAP should show a similar scalp topography regardless of the cue and target modalities, whereas if the LDAP partially reflects changes in activity in the cortical neurons required to process the

upcoming visual target (cf. Harter et al., 1989) then the LDAP should be focused over more ventral occipito-temporal scalp regions prior to visual targets (Experiments 1 and 3) than auditory targets (Experiments 2 and 4).

Finally, TSE waveforms were computed for the alpha activity during the cue-target interval to determine if alpha modulation occurs during intramodal auditory and crossmodal audiovisual shifts of attention. If modulations of alpha activity are not observed prior to auditory targets there are two possible explanations. First, the alpha modulations reported by Worden et al. (2000) and Yamagishi et al., (2005) may be purely visuospatial phenomena. Second, the modulations may be generated in sensory specific cortices. Alpha rhythms generated in the temporal lobe, sometimes referred to as *tau* rhythms, can be difficult to observe at the scalp with EEG and are usually only observed with magnetoencephalography (MEG) or intracranial recordings (Hari, Salmelin, Mäkelä, Salenius, & Helle, 1997; Niedermeyer, 1997). Thus, if anticipatory changes in alpha activity occur primarily in sensory cortices, alpha activity that is generated in visual cortex, but not alpha activity that is generated in auditory cortex, would be observed in the scalp recorded EEG. However, if modulations of alpha activity are observed prior to auditory targets it would suggest that, similar to the LDAP, the changes in alpha activity at least partially represent a modality unspecific attentional process, likely in parietal-occipital cortical areas.

## **2 EXPERIMENT 1 – VISUAL CUES AND VISUAL TARGETS**

The purpose of Experiment 1 was to replicate previous studies of spatial attention shifts in the visual modality to use as a comparison for the crossmodal and auditory studies that followed. Thus, it was expected that the ADAN and LDAP would both be observed in the cue-elicited waveforms, and that both the Nd1 and Nd2 would be present in the target-elicited waveforms. As has been previously reported, visuospatial shifts of attention are related to an increase in amplitude of oscillations in the alpha-band frequency range (8-14 Hz) at parietal and occipital scalp sites ipsilateral to the expected target location prior to target onset (Worden et al., 2000). I expect to replicate this finding in Experiment 1 as well.

### **2.1 Method**

#### **2.1.1 Participants**

Fifteen volunteers participated in this experiment after giving informed consent and were either paid for their participation or received course credit. Data from 3 participants were excluded from the analyses as more than 30-percent of trials were rejected due to blinking. Of the remaining 12 participants (6 females; ages 18-32 years, mean = 22.6 years) all reported normal hearing and normal or corrected-to-normal vision, and 2 reported being left-handed.

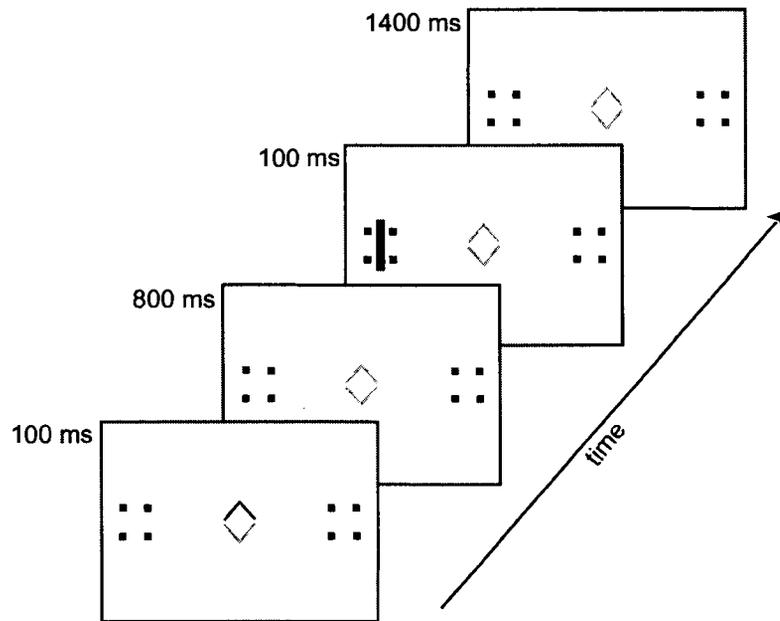
#### **2.1.2 Stimuli and apparatus**

The experiment was conducted in a sound-attenuated, electrically shielded chamber in which a 19-inch computer display was flanked by two loudspeakers. All visual stimuli were grey (RGB = 201, 201, 201) unless otherwise noted. Throughout the

experimental blocks two grey arrowheads (each arrowhead measuring  $1.4^\circ \times 0.7^\circ$ , one pointing up and one pointing down, formed a diamond that was presented at the center of the display to serve as fixation. The cue stimulus consisted of one of the fixation arrowheads changing colour to red (RGB = 255, 0, 0) to symbolically indicate the to-be-attended location. Two sets of four dots were located eight degrees to the left and right of the fixation cross. Each set was arranged at the corners of an imaginary rectangle ( $2.0^\circ \times 2.4^\circ$ ) and served as a landmark within which the target stimuli could be presented. The visual target stimuli was either a long ( $0.7^\circ \times 4.0^\circ$ ) or a short ( $0.7^\circ \times 2.9^\circ$ ) vertical bar. A light grey disk (RGB = 214, 214, 214;  $1.2^\circ \times 1.2^\circ$ ) served as a probe stimulus.

### **2.1.3 Procedure**

Participants were seated in an unlit chamber, 65 cm in front of the display. All participants were instructed to maintain their gaze on the central grey diamond throughout each experimental block. As shown in Figure 2-1, a 100-ms cue was presented to indicate the to-be-attended location (left or right) followed after a 900-ms stimulus-onset asynchrony (SOA) by a 100-ms target stimulus to the left or right of fixation. The inter-trial interval was 1400 ms. Participants were required to discriminate the length of the targets using the mouse (left button = short bar, right button = long bar) and to respond to the probe stimulus (left mouse button) only when it was presented at the validly cued location. Response hand was counterbalanced across participants, although the mouse buttons used to respond remained constant.



**Figure 2-1. Illustration of events occurring on a target (nonprobe) trial in Experiment 1.**

For half of the participants the upward pointing arrowhead indicated to attend to the left and the downward pointing arrowhead indicated to attend to the right. For the other half of participants the to-be-attended locations indicated by the arrows were reversed. The cue was spatially non-predictive but participants were instructed to attend to the location indicated by the cues. On one-third of the trials the target stimulus was replaced by a probe stimulus, which was only to be responded to when it appeared at the validly cued location. These probe trials were included to ensure that participants were following instructions to attend to the cued location. The entire experiment consisted of 30 blocks of 24 trials (16 target trials, 8 probe trials).

#### **2.1.4 Electrophysiological Recording**

EEG was recorded from 63 tin electrodes positioned at FP1, FPz, FP2, AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FC5, FC3, FC1, FCz, FC2, FC4, FC6, T7, C5, C3, C1, Cz, C2, C4, C6, T8, CP5, CP3, CP1, CPz, CP2, CP4, CP6, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, Iz, and M1 (American

Electroencephalographic Society, 1994) and five non-standard sites inferior to the standard occipital locations. All EEG signals were referenced to the right mastoid. The horizontal electrooculogram (EOG) was recorded bipolarly using two electrodes positioned lateral to the external canthi. Electrode impedances were kept below 10 kOhms. All signals were recorded with a bandpass of 0.1 - 100 Hz (-3 dB point; -12 dB per octave) and digitized at 250 Hz.

Artifact rejection was performed to remove epochs that contained eye movements, blinks, and amplifier blocking. Trials in which participants incorrectly respond to target stimuli were also removed prior to averaging. Artifact-free data were then used to create averaged ERP waveforms. Separate averages were created for leftward and rightward directing cues as well as for validly and invalidly cued target stimuli occurring at the left and right locations. The averaged waveforms were digitally low-pass filtered (-3 dB point at 25 Hz) and digitally re-referenced to the average of left and right mastoids.

## **2.1.5 Analysis**

### **2.1.5.1 Behavioural measures**

The behavioural analysis focused on the effects of cueing on speeded response time (RT), but response accuracy was also analyzed to test for speed-accuracy trade offs. Median RTs and error rates for the target discrimination task were analyzed using separate repeated-measures ANOVAs with factors for cued direction (left vs. right), validity (valid vs. invalid), and target type (short bar vs. long bar).

### **2.1.5.2 Target-elicited ERPs**

In order to assess the target-elicited Nd1 and Nd2, mean amplitudes of the target ERPs were measured at Pz and Fz in two post-target intervals that corresponded to the

Nd1 (120-180 ms) and Nd2 (240-360 ms). Mean amplitudes were measured relative to a 100-ms pre-stimulus baseline for analysis of the cue and target-elicited waveforms. The amplitudes of the Nd1 and Nd2 were analyzed separately at each electrode using repeated-measures ANOVAs with factors for target location (left vs. right) and validity (validly vs. invalidly cued). The cue validity effects of the target-elicited P1 and N1 components were also examined by measuring mean ERP amplitudes in two early latency windows (P1: 100-140 ms; N1: 170-210 ms) at a pair of lateral occipital electrodes (PO7 and PO8). The P1 and N1 were analyzed separately using a repeated-measures ANOVA with factors for target location (left vs. right), validity (validly vs. invalidly cued), and electrode lateralization (ipsilateral vs. contralateral, relative to the target location).

#### **2.1.5.3 Cue-elicited ERPs**

The control processes of voluntary spatial attention were investigated by examining the waveforms to the visual cues, focusing on the ADAN and LDAP components of the cue-elicited ERPs. To investigate the ADAN, mean amplitudes of the averaged cue ERPs for each participant were measured in the 300-500 ms post-cue interval at four pairs of anterior electrodes (F3/F4, F5/F6, F7/F8, and FC5/FC6). To investigate the LDAP, mean amplitudes of the averaged cue ERPs for each participant were measured in the 500-800 ms post-cue interval at four pairs of posterior electrodes (P3/P4, PO3/PO4, PO7/PO8, and CP5/CP6). The mean amplitudes for the ADAN and LDAP were analyzed separately using a repeated-measures analysis of variance (ANOVA) with factors for cued side (left vs. right), electrode lateralization (ipsilateral vs. contralateral, relative to cued side), and electrode location. When appropriate, Greenhouse-Geisser adjusted *p* values are reported. A significant main effect of electrode lateralization would indicate the presence of the lateralized ADAN or LDAP,

and a significant interaction between electrode location and electrode lateralization would indicate differences in the ADAN or LDAP across the electrode sites. Where differences were observed between the effects at the tested electrode pairs, additional analyses were performed for individual electrode pairs to determine the sites at which the effects were present.

#### **2.1.5.4 Cue-elicited oscillatory activity**

TSE waveforms were calculated first by digitally band-pass filtering the EEG in the frequency band of interest, 8-14 Hz, then full-wave rectifying the filtered EEG. Because the oscillatory activity is induced by the cue stimulus but not specifically time-locked to it, there can be differences in the phase of the oscillation between trials and between subjects, and averaging together these out-of-phase oscillations would result in an amplitude near zero. Rectification of the waveform (i.e. using the absolute values of the EEG amplitude at each time point to create a waveform that is only of a positive polarity) allows for an assessment of the amplitude of the oscillatory activity by removing the negative portion of the oscillation that would cancel out the positive portion of the oscillation when averaged across trials. (Marrufo et al., 2001; Salmelin & Hari, 1994; Worden et al., 2000). Following rectification, the EEG was averaged by experimental condition just as was performed to examine ERPs. Waveforms are displayed as a percentage of amplitude relative to a 100-ms pre-stimulus baseline interval, with positive percentages indicating increases in alpha activity and negative percentages indicating decreases in alpha activity.

Spatially specific modulations of alpha band activity were assessed by analyzing the TSE waveforms in the same time range as the LDAP (500-800 ms) at the same four electrode pairs (P3/4, PO3/4, PO7/8, and CP5/6) using a repeated-measures ANOVA with factors for cued side (left vs. right), electrode lateralization (ipsilateral vs.

contralateral, relative to cued side), and electrode location to test for differences in alpha modulation at these electrode pairs.

## **2.2 Results and Discussion**

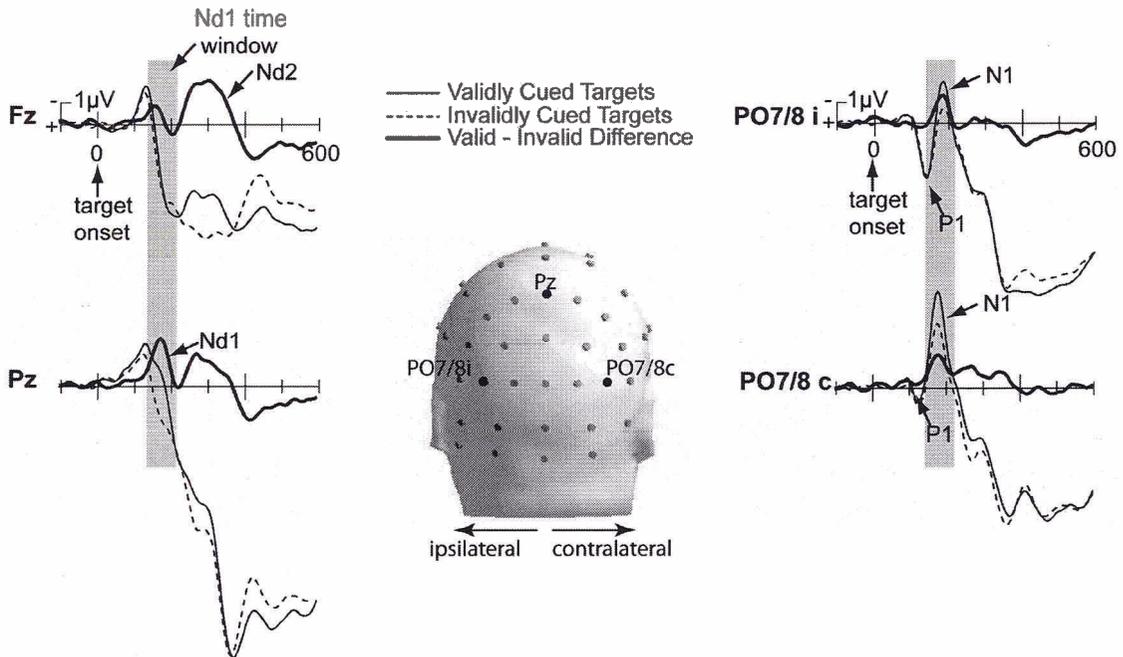
### **2.2.1 Behavioural measures**

Participants performed well on the probe task (mean hit rate on valid trials = 96%; mean false alarm rate on invalid trials = 5%), which indicates that they attended to the location indicated by the cues. The median RTs for valid and invalid trials differed statistically,  $F(1,11) = 4.8$ ,  $p = .049$ , with a shorter RT on valid trials (630 ms) than on invalid trials (664 ms). This 34-ms cueing effect indicates that participants shifted their attention to the cued location and that processing of targets appearing there was facilitated. There was no evidence of a speed-accuracy trade off (Error rates: valid = 5%, invalid = 5%,  $F(1,11) = .022$ ,  $p = .89$ ).

### **2.2.2 Target-elicited ERPs**

Figure 2-2 shows the ERP waveforms elicited by validly and invalidly cued targets at midline frontal, parietal, and lateral occipital sites (Fz, Pz, and PO7/8 respectively), along with difference waves that were created by subtracting the invalidly cued target ERP from the validly cued target ERP. The general morphologies of the ERPs were similar on valid and invalid trials. The posterior P1 and N1 components were observed over the lateral occipital scalp in both waveforms. The P1 peaked ipsilateral to the target about 140 ms after target onset, and the N1 peaked contralateral to the target about 180 ms after target onset. An earlier anterior N1 peaked over the frontal scalp about 120 ms after target onset. There was no effect of validity on the P1,  $F(1,11) = .17$ ,  $p = .68$ , but the N1 was larger on valid trials than on invalid trials,  $F(1,11) = 10.92$ ,  $p = .007$ . The N1 was larger for electrodes contralateral to the target location,  $F(1,11) = p =$

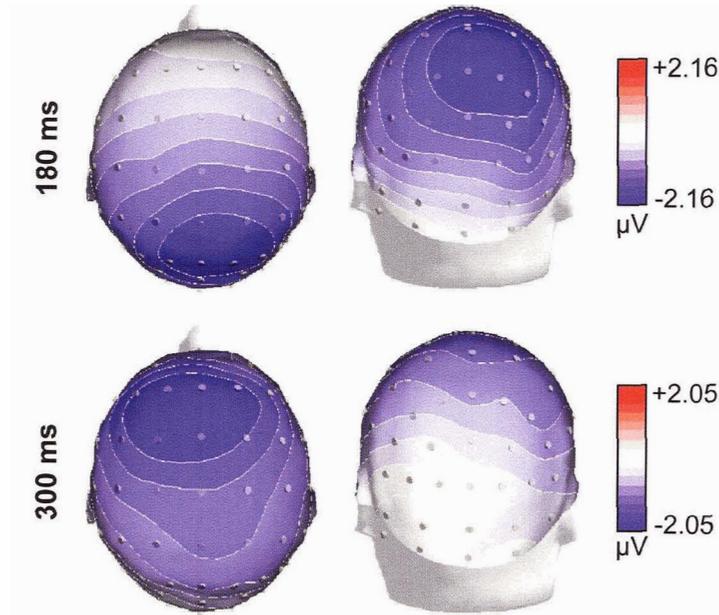
.04, but the main effect of target location and all the interactions were not significant (all  $p$ 's < .24). Thus, it appears that in this experiment voluntary shifts of attention elicited by visual cues have no affect on the early P1 component, but do influence the N1 component.



**Figure 2-2.** Grand-average ERP waveforms elicited by visual target stimuli in Experiment 1.

The Nd1 and Nd2 can be seen clearly as negative peaks in the valid-invalid difference waves. The Nd1 peaked at 160-190 ms and appeared larger over the parietal scalp than the frontal scalp, whereas the Nd2 peaked at 270-310 ms and appeared larger over the frontal scalp than the parietal scalp. These peaks are displayed in the topographic voltage maps in Figure 2-3, showing a clear parietal peak for the Nd1, and distinct fronto-central and parietal peaks during the time of the Nd2. The Nd1 was significant at Pz,  $F(1,11) = 7.33$ ,  $p = .02$ , and the Nd2 was significant at Fz,  $F(1,11) = 21.76$ ,  $p = .001$ , and at Pz,  $F(1,11) = 13.82$ ,  $p = .003$ . Neither the main effect of target

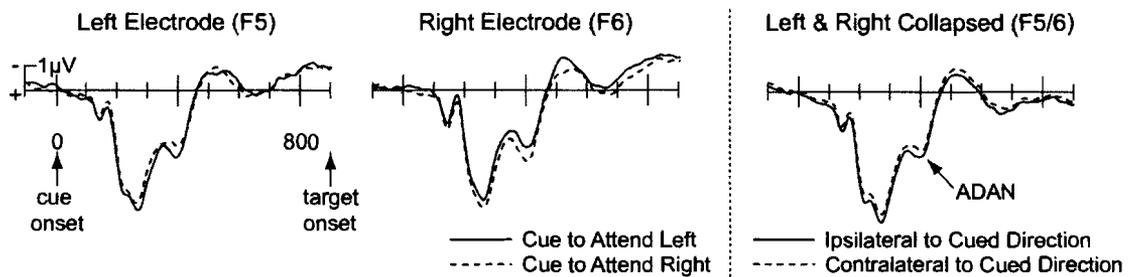
location nor the location X validity interaction was significant for the Nd1 or Nd2 at either electrode (all  $p$ 's > .3).



**Figure 2-3.** Topographical voltage maps of the Nd1 and Nd2 elicited by visual target stimuli in Experiment 1.

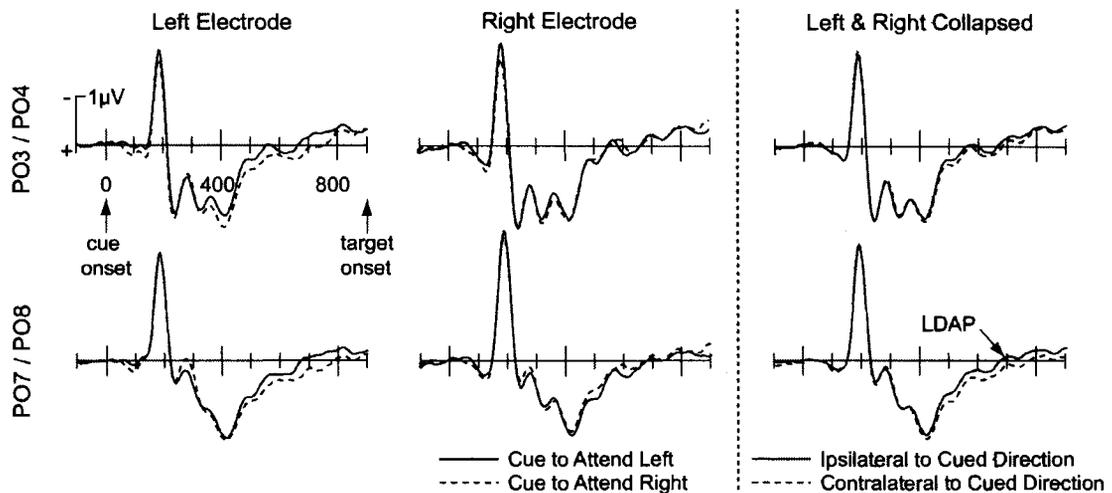
### 2.2.3 Cue-elicited ERPs

Figure 2-4 illustrates the ERPs to attend-left and attend-right cues at representative frontal electrode F5 and F6 along with the corresponding ERPs that show the waveforms at scalp sites ipsilateral and contralateral to the to-be-attended location. As can be seen in these later collapsed waveforms, the ADAN component was present following a visual cue stimulus, with the ERPs diverging approximately 300 ms following cue onset. The main effect of electrode lateralization was significant,  $F(1,11) = 5.734$ ,  $p = .03$ , which indicates the presence of the ADAN in this experiment. No other main effect or interactions were significant (all  $p$ 's < .1) which indicates that there were no significant differences in the ADAN effect at the electrode pairs tested.



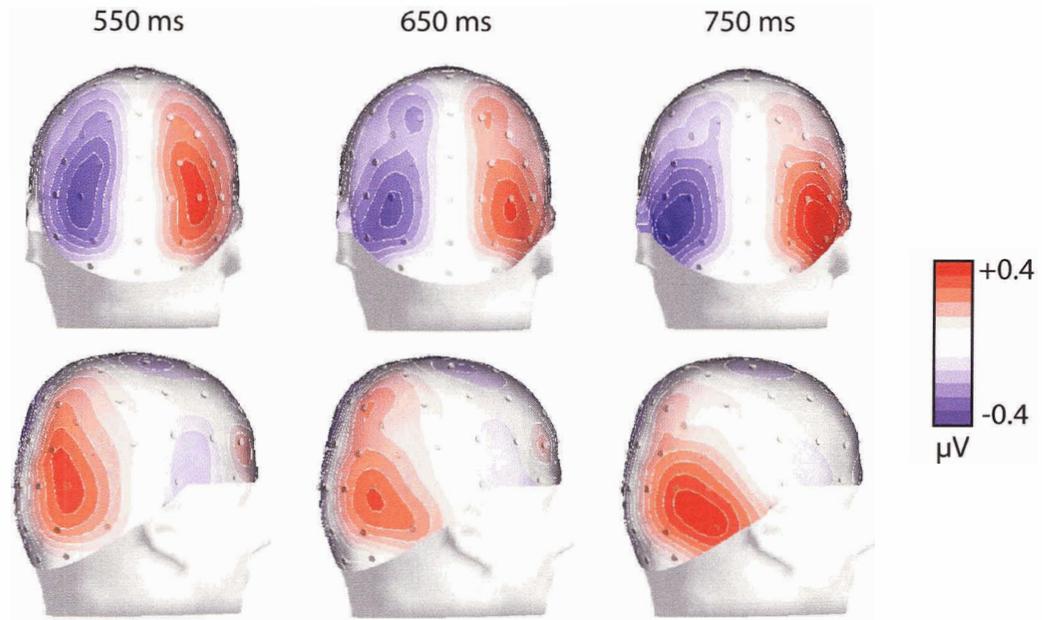
**Figure 2-4. Grand-average ERP waveforms elicited by attention-directing cues recorded at anterior electrodes F5 and F6.**

The LDAP was also elicited by the visual cues in this experiment, and waveforms for attend-left and attend-right cues as well as the collapsed waveforms for posterior electrodes PO3/PO4 and PO7/PO8 can be seen in Figure 2-5. The main effect of electrode location was significant,  $F(3,33) = 10.3, p = .003$ , as was the electrode location x electrode lateralization interaction,  $F(3,33) = 6.04, p = .032$ , which indicates a difference in the LDAP at the electrode pairs tested. To examine the differences between the electrode pairs,  $t$  tests comparing ipsilateral and contralateral waveforms were performed separately for each electrode pair. The LDAP was significant at PO7/8,  $t(10) = 3.12, p = .01$ , and PO3/4,  $t(10) = 3.08, p = .015$ , but not at CP5/6,  $t(10) = 1.19, p = .26$ , or P3/4,  $t(10) = 2.05, p = .07$ .



**Figure 2-5. Grand-average ERP waveforms elicited by attention-directing cues recorded at posterior electrodes PO3 and PO4 (top row) and PO7 and PO8 (bottom row).**

The topographical voltage maps of the LDAP in Figure 2-6 show the topography of the contralateral-ipsilateral difference wave, which is displayed on the right half of the head, and the mirror image difference is displayed over the left half of the head with values artificially zeroed at midline electrodes. The LDAP appears to be primarily generated in visual cortex in this experiment, possibly extending to inferior temporal areas in the later intervals (650 and 750 ms). This pattern is consistent with the hypothesis that the LDAP reflects preparatory activity in the areas that will process the upcoming target stimuli, in this case ventral stream visual areas involved in object recognition. Although the LDAP was not statistically significant at parietal electrodes P3/P4, the scalp topography shows activity over superior parietal scalp areas that appears to be distinct from the ventral occipital sources, seen most clearly in the maps of the activity at 650 ms. This suggests that there may be a parietal as well as an occipital source to the LDAP observed in the ERP waveforms.

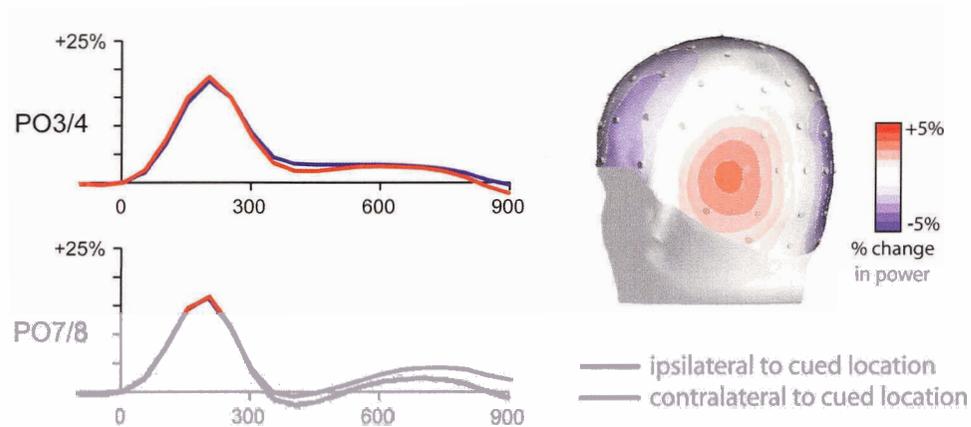


**Figure 2-6.** Topographical voltage maps of the LDAP elicited by visual cue stimuli in Experiment 1 at 550 ms (left), 650 ms (middle), and 750 ms (right) following the cue.

#### 2.2.4 Cue-elicited oscillatory activity

The alpha activity induced by the visual cues ipsilateral and contralateral to the to-be-attended location in this experiment at posterior electrodes PO3/PO4 and PO7/PO8 can be seen in Figure 2-7. An initial increase in alpha synchronization is apparent, lasting until approximately 350 ms following the onset of the cue. This peak reflects the phase-locked activity observed in the ERP waveforms, the P1, N1, P2, and N2 sequence of components, which have a frequency within the alpha range. Following this peak of alpha synchronization the activity over ipsilateral and contralateral electrode sites began to diverge, with increased alpha activity observed over posterior scalp sites ipsilateral to the cued location lasting until target onset. The main effect of electrode location was significant,  $F(3,33) = 4.27, p = .04$ , as was the electrode location x electrode lateralization interaction,  $F(3,33) = 4.38, p = .04$ , which indicates a difference

in alpha modulation at the electrode pairs tested. To examine the differences between the electrode pairs, *t* tests comparing ipsilateral and contralateral waveforms were performed separately for each electrode pair. Lateralized alpha-band modulation was only evident at PO7/8,  $t(10) = 3.82, p = .003$ , not at PO3/4,  $t(10) = 1.12, p = .29$ , CP5/6,  $t(10) = .32, p = .75$ , or P3/4,  $t(10) = .74, p = .47$ .



**Figure 2-7. Grand-average TSE waveforms of alpha (8-14 Hz) activity induced by attention-directing cues at posterior electrode PO3/4 and PO7/8. Topographical map displays the distribution of the contralateral-ipsilateral difference wave from 500-800 ms post-cue.**

The alpha modulation observed in Experiment 1 is consistent with that previously observed by Worden et al. (2000) in a similar visual cueing task, and appears to be topographically similar to the LDAP observed in the ERP waveforms. Based on these topographical similarities it is interesting to speculate that alpha-band specific differences in activity underlie the ERP differences observed in this time interval, and may be particularly linked to the preparatory activity in visual cortical areas prior to the target stimulus, as no parietal differences in alpha were observed in the TSE waveforms.

## **3 EXPERIMENT 2 – AUDITORY CUES AND AUDITORY TARGETS**

Previous research has shown that no ADAN is elicited when auditory cues are used to direct attention to auditory targets (Green et al., 2005). In Experiment 2 I expected to replicate this finding using auditory cues analogous to the visual cues used in Experiment 1 to direct attention to auditory targets. If no ADAN is observed this will support the hypothesis that this component is related to visual processing and not the activity of a supramodal attention mechanism. The LDAP component and the target-elicited Nd1 and Nd2 have previously been reported during intramodal auditory shifts of attention, and thus I expect to observe them in this experiment as well.

The TSE waveforms for the alpha-band EEG activity were also examined to determine if the alpha modulation observed in Experiment 1 during intramodal visual shifts of attention also occurs during intramodal auditory shifts of attention. The presence of alpha modulation in an intramodal auditory task where no visual stimulation is present would indicate that this change in oscillatory activity is related to spatial attention, possibly in a modality unspecific way.

### **3.1 Method**

#### **3.1.1 Participants**

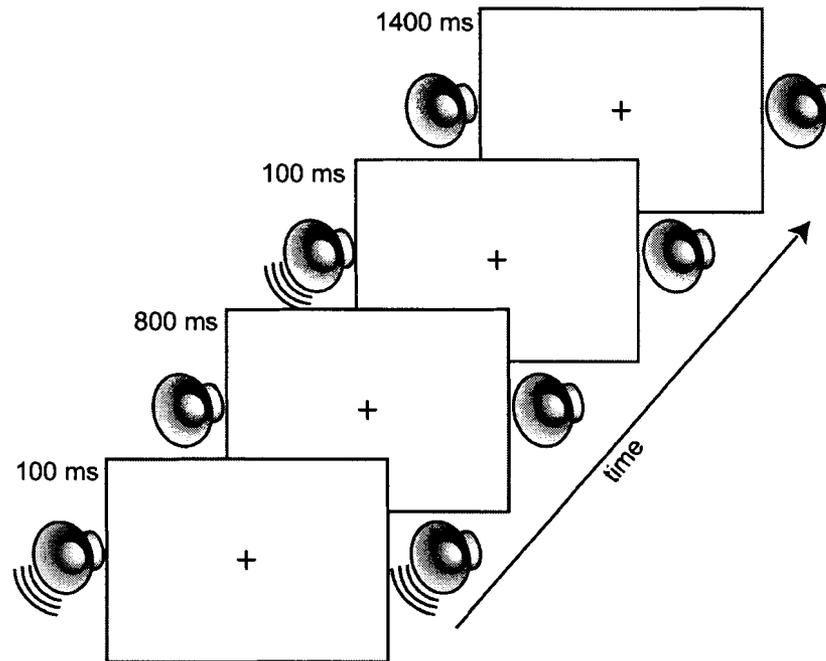
Fifteen volunteers participated in this experiment after giving informed consent and were either paid for their participation or received course credit. Data from 3 participants was excluded from the analyses as more than 30-percent of trials were rejected due to blinking. Of the remaining 12 participants (7 females; ages 18-30 years, mean = 21.8 years) all reported normal hearing and normal or corrected-to-normal vision, and all reported being right-handed.

### **3.1.2 Stimuli and apparatus**

The auditory cue stimuli were upward and downward frequency sweeps that ranged from 750 Hz to 1250 Hz. Both upward and downward sweeps were digitized at 44 kHz and included 5-ms linear rise and fall times. The cues were 100 ms in duration and were presented from both speakers simultaneously such that they appeared to be emanating from the center of the computer display. The sounds were approximately 70 dB SPL at the location of the participants' ears. The target sounds consisted of bursts of white noise, one having a 5-ms gap of silence in the middle, the other with a 20-ms gap in the middle. Both target sound were digitized at 44 kHz and included 5-ms linear rise and fall times. The targets were 100 ms in duration and were approximately 70 dB SPL at the location of the participants' ears. A cowbell (350 ms duration, 72 dB SPL) served as a probe stimulus. Throughout each experimental block a small cross ( $0.9^\circ \times 0.9^\circ$ ; RGB = 201, 201, 201) was presented at the center of the display to serve as a fixation point.

### **3.1.3 Procedure**

For half of the participants the upward frequency glide indicated to attend to the left and the downward frequency glide indicated to attend to the right. For the other half of participants the to-be-attended locations indicated by the sounds were reversed. Participants were required to discriminate the length of the gap in the target sounds using the mouse (left button = short gap, right button = long gap) and respond to the cowbell probe stimulus (left mouse button) only when it was presented at the validly cued location. All other aspects of the procedure were identical to Experiment 1.



**Figure 3-1. Illustration of events occurring on a target (nonprobe) trial in Experiment 2.**

### **3.1.4 Electrophysiological Recording**

All electrophysiological recording procedures were identical to those used in Experiment 1.

### **3.1.5 Analysis**

All analysis procedures were identical to those used in Experiment 1 with the exception that analyses of the cueing effects on the visual P1 and N1 components were omitted as the targets were presented in the auditory modality. Attention effects on the auditory P1 and N1 are not observed in transient spatial cueing (e.g. Schroger & Eimer, 1997), thus the target-elicited ERPs were only examined for the Nd1 and Nd2 effects.

## 3.2 Results and Discussion

### 3.2.1 Behavioural measures

Participants performed well on the probe task (mean hit rate on valid trials = 83%; mean false alarm rate on invalid trials = 11%), which indicates that they attended to the location indicated by the cues. The median RTs for valid and invalid trials differed statistically,  $F(1,11) = 5.19, p = .04$ , with a shorter RT on valid trials (719 ms) than on invalid trials (747 ms). This 28-ms cueing effect indicates that participants shifted their attention to the cued location and that processing of targets appearing there was facilitated. There was no evidence of a speed-accuracy trade off (Error rates: valid = 13%, invalid = 13%,  $F(1,11) = .11, p = .74$ ).

### 3.2.2 Target-elicited ERPs

Figure 3-2 shows the ERP waveforms elicited by validly and invalidly cued targets at midline frontal and parietal sites (Fz and Pz, respectively), along with difference waves that were created by subtracting the invalidly cued target ERP from the validly cued target ERP. The general morphologies of the ERPs on valid and invalid trials were similar, with small positive and negative deflections (P1 and N1) followed by a large positive peak (P2) about 210 ms after target onset at frontal scalp sites. The Nd1 and Nd2 can be seen clearly as negative peaks in the valid-invalid difference waves. The Nd1 peaked at 150-160 ms and was larger over the parietal scalp than the frontal scalp, whereas the Nd2 peaked at 310-330 ms and was larger over the frontal scalp than the parietal scalp. These peaks are displayed in the topographic voltage maps in Figure 3-3, showing a clear parietal peak for the Nd1, and distinct fronto-central and parietal peaks during the time of the Nd2. The Nd1 was significant at Pz,  $F(1,11) = 22.48, p = .001$ , and the Nd2 was significant at Fz,  $F(1,11) = 10.63, p = .008$ , and at Pz,

$F(1,11) = 9.51, p = .01$ . Neither the main effect of target location nor the location X validity interaction was significant for the Nd1 or Nd2 at either electrode (all  $p$ 's > .23).

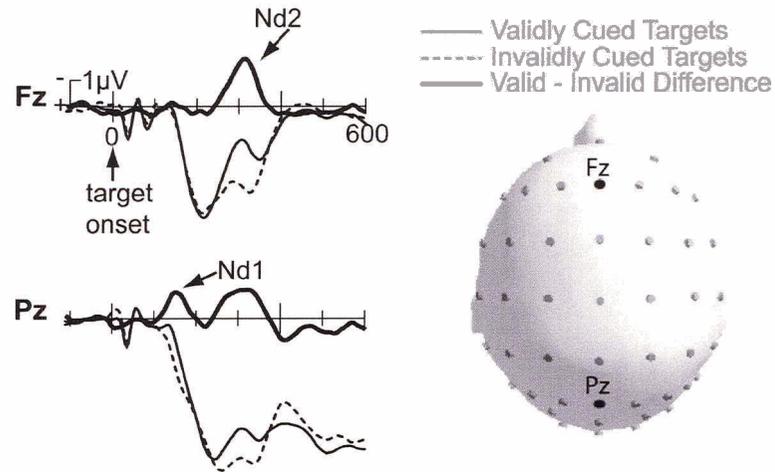


Figure 3-2. Grand-average ERP waveforms elicited by auditory target stimuli in Experiment 2.

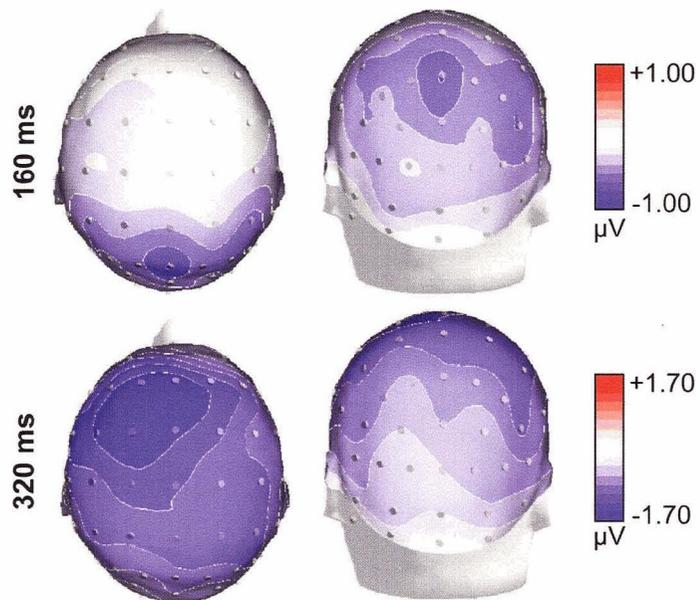
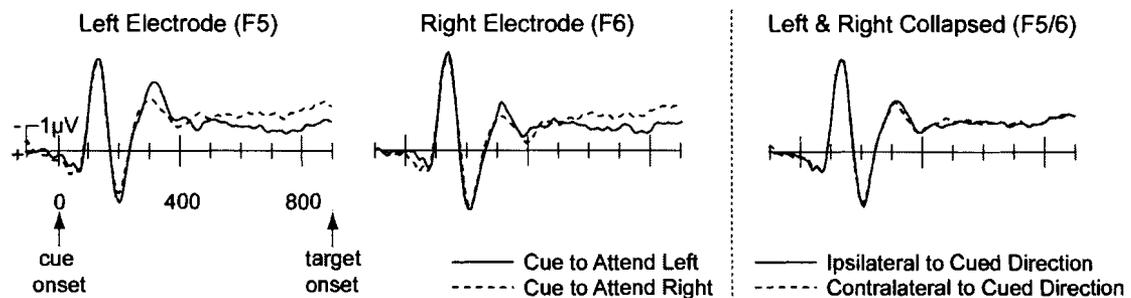


Figure 3-3. Topographical voltage maps of the Nd1 and Nd2 elicited by auditory target stimuli in Experiment 2.

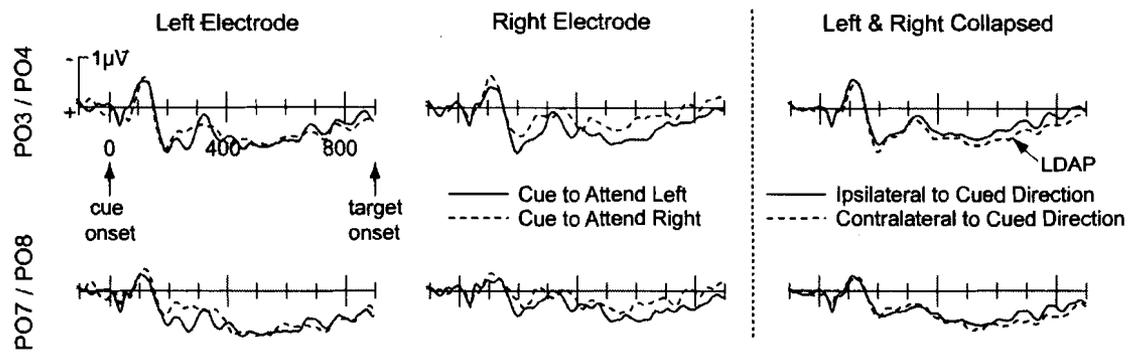
### 3.2.3 Cue-elicited ERPs

As can be seen in Figure 3-4, ERP waveforms contralateral and ipsilateral to the cued location did not differ at frontal electrode sites. All main effects and interactions were not significant (all  $p$ 's > .24), which indicates that the ADAN was not present in the auditory cue-elicited ERPs, replicating the previous findings of Green et al. (2005).



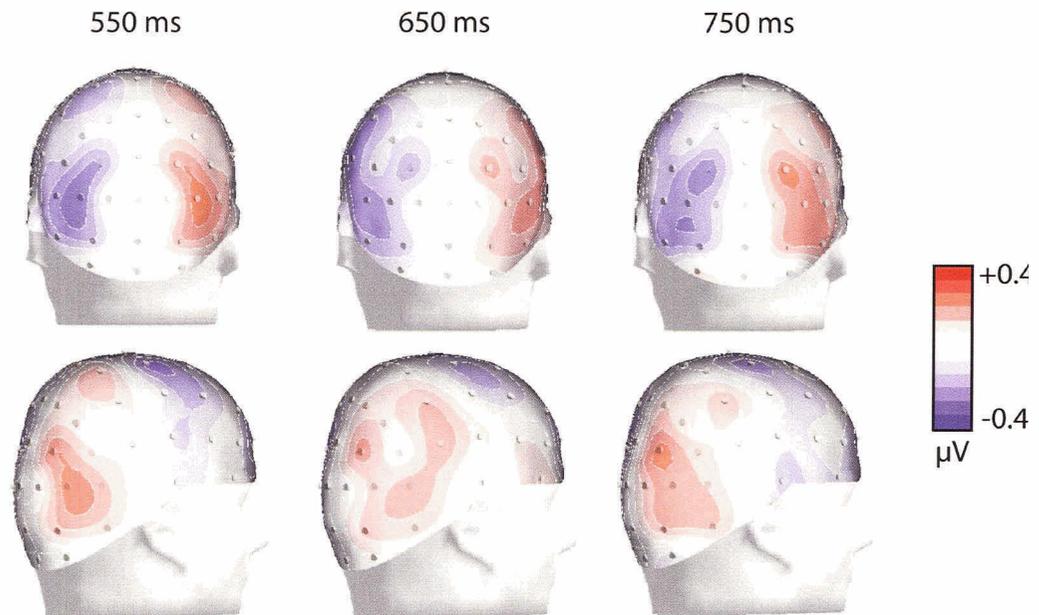
**Figure 3-4. Grand-average ERP waveforms elicited by attention-directing cues recorded at anterior electrodes F5 and F6.**

The LDAP elicited by the auditory cues in this experiment at posterior electrodes PO3/PO4 and PO7/PO8 can be seen in Figure 3-5. The main effect of electrode lateralization was significant,  $F(1,11) = 6.83$ ,  $p = .004$ , as was the interaction between electrode lateralization and electrode location,  $F(3,33) = 13.53$ ,  $p = .004$ , which indicates a difference in the LDAP at the tested electrode pairs. To examine the differences between the electrode pairs,  $t$  tests comparing ipsilateral and contralateral waveforms were performed separately for each electrode pair. The LDAP was significant at P3/4,  $t(10) = 3.56$ ,  $p = .004$ , CP5/6,  $t(10) = 4.25$ ,  $p = .001$ , and PO3/4,  $t(10) = 2.94$ ,  $p = .01$ , but not at PO7/8,  $t(10) = 1.42$ ,  $p = .18$ .



**Figure 3-5. Grand-average ERP waveforms elicited by attention-directing cues recorded at posterior electrodes PO3 and PO4 (top row) and PO7 and PO8 (bottom row).**

The topographical voltage maps of the LDAP in Figure 3-6 show a different scalp distribution than that observed in Experiment 1. The strong occipital source observed in Experiment 1 does not appear to be present in the auditory cue-elicited LDAP. The LDAP was smaller and appeared to have a more temporo-parietal distribution in this experiment. It is possible that the LDAP observed in intramodal auditory cueing reflects the activities of a parietal generator common to shifts of attention in all modalities as well as a generator in temporal lobe auditory areas that is analogous to the preparatory visual cortical activity observed in intramodal visual cueing.

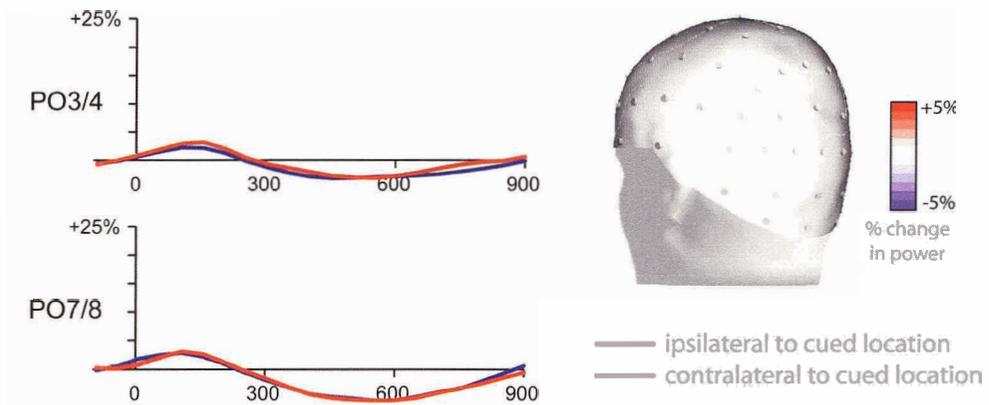


**Figure 3-6.** Topographical voltage maps of the LDAP elicited by auditory cue stimuli in Experiment 2 at 550 ms (left), 650 ms (middle), and 750 ms (right) following the cue.

### 3.2.4 Cue-elicited oscillatory activity

The TSE waveforms for the alpha activity induced by the auditory cues in this experiment at posterior electrodes PO3/PO4 and PO7/PO8 can be seen in Figure 3-7. None of the main effects or interactions were significant (all  $p$ 's > .198), which indicates that no significant modulation of alpha activity was observed during intramodal auditory shifts of attention. There are two possible reasons for this lack of alpha activity. First, it is possible that the alpha modulation observed in Experiment 1 is specific to preparation for a visual target stimulus. Second, it is possible that the alpha modulation is dependant on the use of a visual cue stimulus. Regardless of whether the cue or target modality is important for inducing alpha activity, the lack of alpha modulation in this experiment decouples the changes in alpha activity from the LDAP component in the ERP waveforms, because the LDAP was observed here even though no changes in alpha

were seen. It is possible that changes in occipitally generated alpha activity reflect modality specific visual preparation processes and that anticipatory changes within the auditory modality do not occur within the alpha band or are not visible in the scalp recorded EEG (Hari et al., 1997; Niedermeyer, 1997).



**Figure 3-7.** Grand-average TSE waveforms of alpha (8-14 Hz) activity induced by attention-directing cues at posterior electrode PO3/4 and PO7/8. Topographical map displays the distribution of the contralateral-ipsilateral difference wave from 500-800 ms post-cue.

## 4 EXPERIMENT 3 – AUDITORY CUES AND VISUAL TARGETS

In order to determine if the ADAN reflects activity specifically associated with visual processing, Experiment 3 used auditory cues to direct attention to the location of a visual target<sup>2</sup>. If the ADAN reflects supramodal processes or if it is related to shifting attention in the visual modality, it should be observed in this experiment as the target stimuli are visual. However, if the ADAN specifically reflects processing of a visual cue stimulus, then I expect no ADAN to be observed in this experiment. As in Experiment 2, previous crossmodal research suggests that an LDAP will be observed in this experiment, as will the target-elicited negative differences.

In addition, I examined the modulation of alpha activity when auditory cues were used to direct attention to the location of an upcoming visual target. Based on the lack of spatially specific alpha activity during intramodal auditory shifts of attention, it is possible that like the ADAN the visual cue or target is driving the modulation of alpha activity. Thus, if alpha modulation reflects preparatory changes in neural activity prior to a visual target then similar alpha activity to that observed in Experiment 1 should be observed, whereas if the alpha modulation reflects activity dependant on a visual cue stimulus then no alpha modulation should be observed in this experiment when auditory cues are used to direct attention.

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<sup>2</sup> The cue and target-elicited ERP data from Experiments 3 and 4 were previously published (Green & McDonald, 2006). The TSE analysis for all the experiments in this work is new analysis and was not included in that publication.

## **4.1 Method**

### **4.1.1 Participants**

Fifteen volunteers participated in this experiment after giving informed consent and were either paid for their participation or received course credit. Data from one participant was excluded from the analyses as more than 30-percent of trials were rejected due to blinking. Of the remaining 14 participants (7 females; ages 18 - 27 years, mean = 21.2 years), all reported normal hearing and normal or corrected-to-normal vision, and all reported being right-handed.

### **4.1.2 Stimuli and apparatus**

The auditory cue stimuli were identical to those used in Experiment 2, and the visual target and probe stimuli were identical to those used in Experiment 1.

### **4.1.3 Procedure**

As depicted in Figure 4-1, the experimental procedures were identical to those used in Experiments 1 and 2, with the exception that the cue and target were now presented in different sensory modalities.

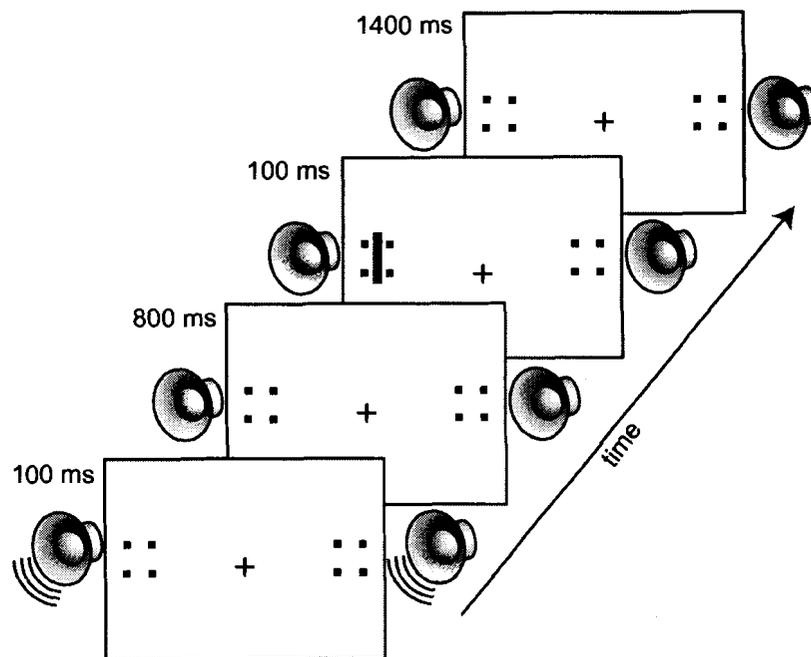


Figure 4-1. Illustration of events occurring on a target (nonprobe) trial in Experiment 3.

#### 4.1.4 Electrophysiological recording

All electrophysiological recording procedures were identical to those used in Experiment 1.

#### 4.1.5 Data Analyses

All data analysis procedures were performed in an identical manner to those used in Experiment 1.

### 4.2 Results and Discussion

#### 4.2.1 Behavioural measures

Participants performed well on the probe task (mean hit rate on valid trials = 96%; mean false alarm rate on invalid trials = 7%), which indicates that they attended to the location indicated by the cues. The median RTs for valid and invalid trials differed statistically,  $F(1,13) = 4.55$ ,  $p = .05$ , with a shorter RT on valid trials (595 ms) than on

invalid trials (628 ms). This 33-ms cueing effect indicates that participants shifted their attention to the cued location and that processing of targets appearing there was facilitated. There was no evidence of a speed-accuracy trade off (Error rates: valid = 4%, invalid = 4%,  $F(1,13) = .42$ ,  $p = .53$ ).

#### 4.2.2 Target-elicited ERPs

Figure 4-2 shows the ERP waveforms elicited by validly and invalidly cued targets at midline frontal, parietal, and lateral occipital sites (Fz, Pz, and PO7/8 respectively), along with difference waves that were created by subtracting the invalidly cued target ERP from the validly cued target ERP. The posterior P1 and N1 components were observed over lateral occipital scalp sites in the waveforms for validly and invalidly cued targets. The P1 peaked ipsilateral to the target about 140 ms after target onset, and the posterior N1 peaked contralateral to the target about 180 ms after the target onset. An earlier anterior N1 peaked over the frontal scalp about 130 ms after the target onset. There was no effect of validity on the P1,  $F(1,13) = .87$ ,  $p = .37$ , but the posterior N1 was larger on valid trials than on invalid trials,  $F(1,13) = 28.43$ ,  $p = .005$ . The N1 validity effect was larger for electrodes ipsilateral to the target location,  $F(1,13) = 16.62$ ,  $p = .001$ , but the main effect of target location and all the interactions were not significant (all  $p$ 's < .15). This N1 effect appears to be related to the more anterior Nd1, however, which began 30 ms earlier. This conclusion is bolstered by the topography of the valid-invalid difference in the N1/Nd1 time range, which clearly showed a negative peak over the parietal scalp rather than the occipital scalp (Figure 4-3). Thus, it appears that voluntary shifts of attention elicited by auditory cues have no effect on the occipital ERP components.

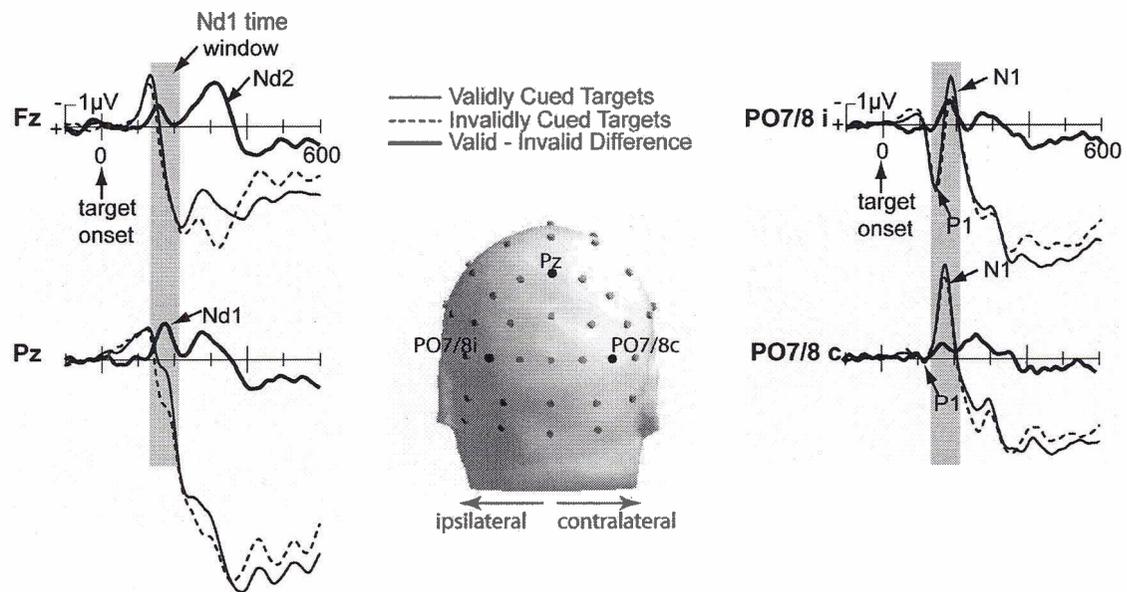
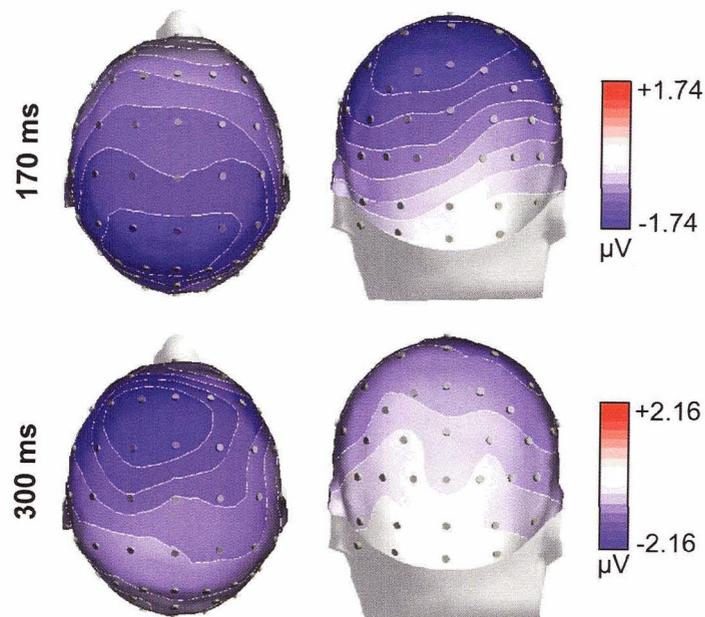


Figure 4-2. Grand-average ERP waveforms elicited by visual target stimuli in Experiment 3.

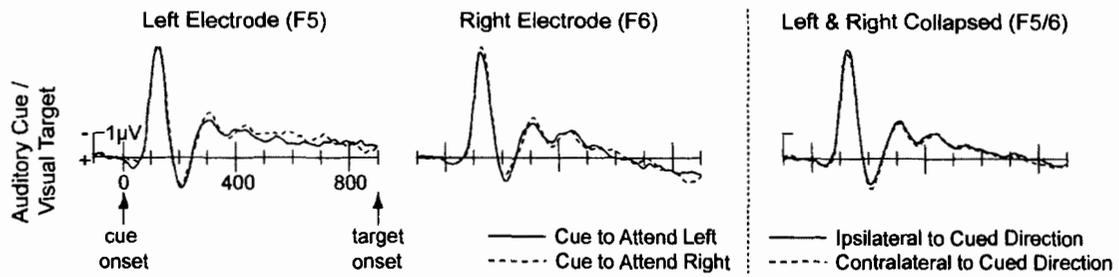
The Nd1 and Nd2 can be seen clearly as negative peaks in the valid-invalid difference waves. The Nd1 peaked at 160-180 ms and was larger over the parietal scalp than the frontal scalp, whereas the Nd2 peaked at 290-330 ms and was larger over the frontal scalp than the parietal scalp. These peaks are displayed in the topographic voltage maps in Figure 4-3, showing a clear parietal peak for the Nd1, and distinct fronto-central and parietal peaks during the time of the Nd2. The Nd1 was significant at Pz,  $F(1,13) = 15.09$ ,  $p = .002$ , and the Nd2 was significant at Fz,  $F(1,13) = 9.64$ ,  $p = .008$ , and at Pz,  $F(1,13) = 10.05$ ,  $p = .007$ . Neither the main effect of target location nor the location X validity interaction was significant for the Nd1 or Nd2 at either electrode (all  $p$ 's > .14).



**Figure 4-3.** Topographical voltage maps of the Nd1 and Nd2 elicited by visual target stimuli in Experiment 3.

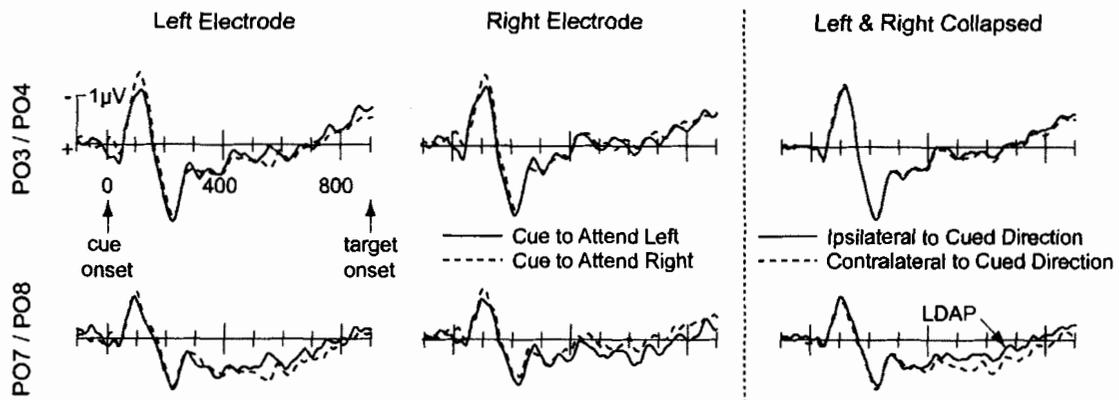
### 4.2.3 Cue-elicited ERPs

As can be seen in Figure 4-4, a contralateral negativity was not apparent in the ERP waveforms at frontal electrode sites. All main effects and interactions were not significant (all  $p$ 's > .15), which indicates that the ADAN was not present in the auditory cue-elicited ERPs, even when attention was directed in preparation for a visual target. This suggests that the modality of the cue stimulus may play a more important role in eliciting the ADAN component than the modality of the target stimulus that attention is being shifted towards.



**Figure 4-4. Grand-average ERP waveforms elicited by attention-directing cues recorded at anterior electrodes F5 and F6.**

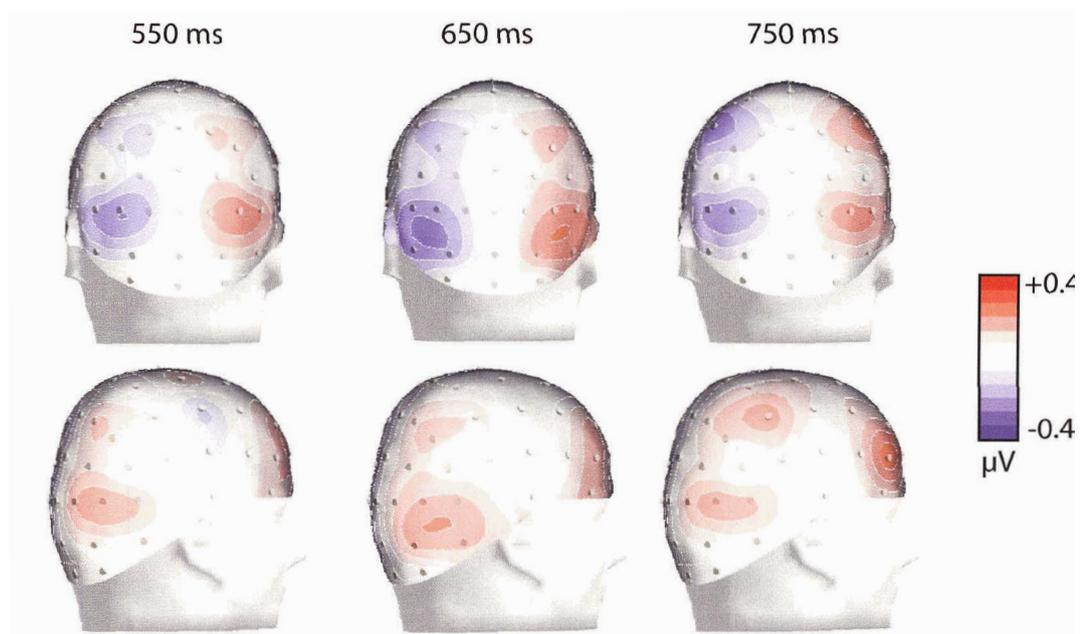
The LDAP was elicited by the auditory cues, however, and the ERPs observed at posterior electrodes PO3/PO4 and PO7/PO8 can be seen in Figure 4-5. The main effect of electrode location was significant,  $F(3,39) = 11.07, p = .001$ , as was the interaction between electrode lateralization and electrode location,  $F(3,39) = 14.53, p = .002$ , which indicates a difference in the LDAP at the tested electrode pairs. To examine the differences between the electrode pairs,  $t$  tests comparing ipsilateral and contralateral waveforms were performed separately for each electrode pair. The LDAP was significant at P3/4,  $t(12) = 4.30, p = .001$ , CP5/6,  $t(12) = 3.74, p = .002$ , and PO7/8,  $t(12) = 3.00, p = .01$ , but not at PO3/4,  $t(12) = 0.51, p = .66$ .



**Figure 4-5. Grand-average ERP waveforms elicited by attention-directing cues recorded at posterior electrodes PO3 and PO4 (top row) and PO7 and PO8 (bottom row).**

Similar to the LDAP observed in Experiment 1, the LDAP here shows a ventral occipital source. Unlike in Experiment 1, however, the LDAP was significant at parietal

electrode sites, and a clear, distinct parietal source can be seen in the topographical voltage maps in Figure 4-6. This pattern of results suggests that the generator of the LDAP is partially dependent on the modality of the impending target stimulus, likely reflecting preparation in sensory specific areas that will be processing the target. There also appears to be a distinct parietal source, which could reflect a supramodal attention shifting mechanism.

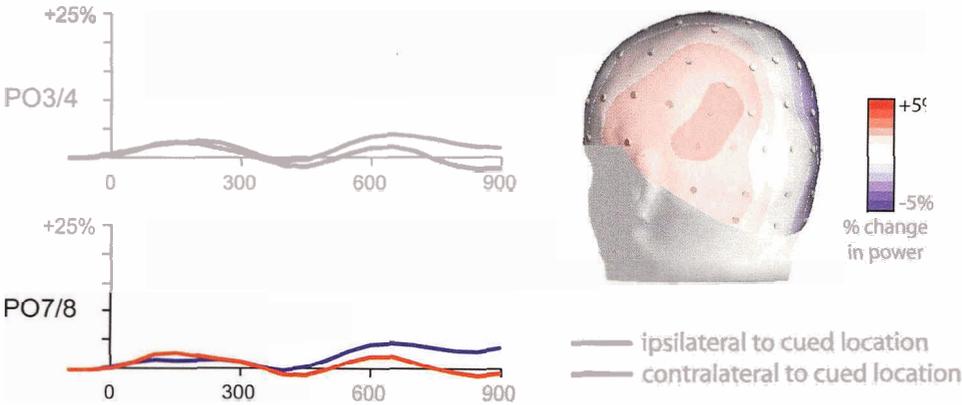


**Figure 4-6.** Topographical voltage maps of the LDAP elicited by auditory cue stimuli in Experiment 3 at 550 ms (left), 650 ms (middle), and 750 ms (right) following the cue.

#### 4.2.4 Cue-elicited oscillatory activity

The alpha activity induced by the auditory cues in this experiment at posterior electrodes PO3/PO4 and PO7/PO8 can be seen in Figure 4-7. The main effect of electrode lateralization was significant,  $F(1,13) = 5.08$ ,  $p = .04$ , but all other main effects and interactions were not significant (all  $p$ 's  $> .12$ ). This suggests that the alpha

modulation was not significantly different at the electrode pairs tested. As indicated by the lack of differences between the electrode sites and can be seen in the topographical map of the TSE waveforms, the alpha modulation observed here was less focused than that observed in Experiment 1. The presence of alpha modulation in this experiment rules out the possibility that a visual cue is necessary for eliciting changes in alpha-band activity, although it is still possible that spatially specific changes in alpha only occur during preparation for a visual target stimulus.



**Figure 4-7. Grand-average TSE waveforms of alpha (8-14 Hz) activity induced by attention-directing cues at posterior electrode PO3/4 and PO7/8. Topographical map displays the distribution of the contralateral-ipsilateral difference wave from 500-800 ms post-cue.**

## 5 EXPERIMENT 4 – VISUAL CUES AND AUDITORY TARGETS

In order to confirm that the presence of the ADAN is dependant on the use of a visual cue stimulus, Experiment 4 utilized visual cues to direct attention in preparation for an upcoming auditory stimulus. As the LDAP was observed in the three previous experiments it is likely that the LDAP will also be present in this experiment. In addition, if the LDAP reflects, in part, a modality specific generator that is dependant on the sensory modality of the target being prepared for, then the scalp topography of the LDAP in this experiment should be similar to that observed during intramodal auditory shifts of attention (Experiment 2) even though visual cues were used to direct attention. Based on the similarities observed in the target-elicited negative differences in the first three experiments it is expected that similar Nd's will be observed in this experiment as well.

Modulations of alpha activity in the cue-target interval were only observed in Experiments 1 and 3, when attention was shifted in preparation for a visual target stimulus. If the modality of the target stimulus determines the presence of changes in alpha then no modulations should be observed here, prior to an auditory target. However, it is possible that the presence visual information, in the form of a cue or target, is sufficient for these spatially specific changes to be observed. If this is the case, then similar modulations of alpha activity should be observed in this experiment when visual cues are used to direct attention.

## **5.1 Method**

### **5.1.1 Participants**

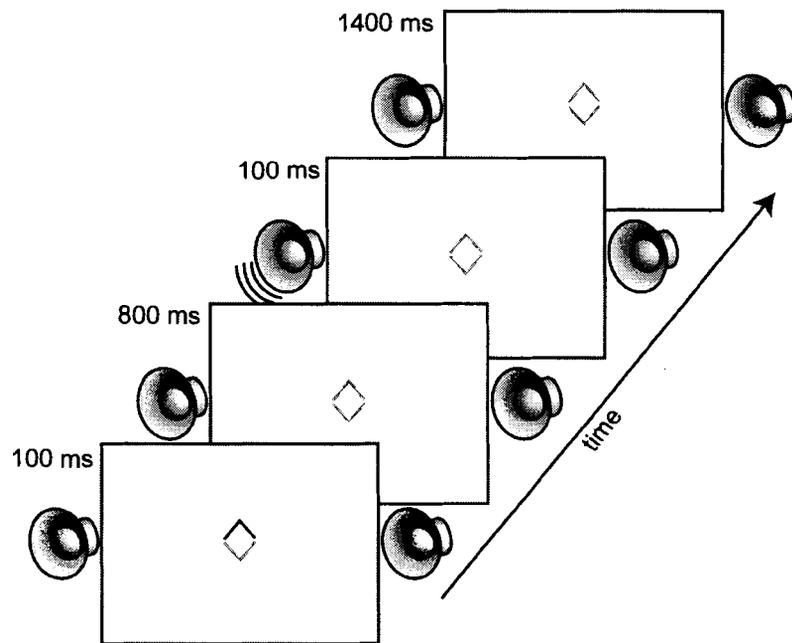
Fifteen volunteers participated in this experiment after giving informed consent and were either paid for their participation or received course credit. Data from two participants were excluded from the analyses as more than 30-percent of trials were rejected due to blinking. Of the remaining 13 participants (10 females; ages 18 - 41 years, mean = 23.2 years), all reported normal hearing and normal or corrected-to-normal vision, and all reported being right-handed.

### **5.1.2 Stimuli and apparatus**

The visual cue stimuli were identical to those used in Experiment 1, and the auditory target and probe stimuli were identical to those used in Experiment 2.

### **5.1.3 Procedure**

As depicted in Figure 5-1, the experimental procedures were identical to those used in Experiments 3, with the exception that the cue and target modalities were reversed.



**Figure 5-1.** Illustration of events occurring on a target (nonprobe) trial in Experiment 4.

#### **5.1.4 Electrophysiological recording**

All electrophysiological recording procedures were identical to those used in Experiment 1.

#### **5.1.5 Data Analyses**

All data analysis procedures were performed in an identical manner to those used in the first three experiments.

### **5.2 Results and Discussion**

#### **5.2.1 Behavioural measures**

Participants performed well on the probe task (mean hit rate on valid trials = 87%; mean false alarm rate on invalid trials = 7%), which indicates that they attended to the location indicated by the cues. The median RTs for valid and invalid trials differed

statistically,  $F(1,12) = 4.87, p = .048$ , with a shorter RT on valid trials (702 ms) than on invalid trials (733 ms). This 31-ms cueing effect indicates that participants shifted their attention to the cued location and that processing of targets appearing there was facilitated. There was no evidence of a speed-accuracy trade off (Error rates: valid = 9%, invalid = 10%,  $F(1,12) = 1.96, p = .19$ ).

### 5.2.2 Target-elicited ERPs

Figure 5-2 shows the ERP waveforms elicited by validly and invalidly cued targets at midline frontal and parietal sites (Fz and Pz, respectively), along with difference waves that were created by subtracting the invalidly cued target ERP from the validly cued target ERP. Over the frontal scalp, the ERPs for both validly and invalidly cued targets consisted of a large negative peak (N1) at about 115 ms, followed by a large positive peak (P2) at about 210 ms. The Nd1 and Nd2 can be seen clearly as negative peaks in the valid-invalid difference waves. The Nd1 peaked at 140-160 ms and was larger over the parietal scalp than the frontal scalp, whereas the Nd2 peaked at 280-320 ms and was larger over the frontal scalp than the parietal scalp. These peaks are displayed in the topographic voltage maps in Figure 5-3, showing a clear parietal peak for the Nd1, and distinct fronto-central and parietal peaks during the time of the Nd2. The Nd1 was significant at Pz,  $F(1,12) = 4.79, p = .049$ , whereas the Nd2 was significant at Fz,  $F(1,12) = 4.69, p = .05$ , and marginally significant at Pz,  $F(1,12) = 3.90, p = .07$ . Neither the main effect of target location nor the location X validity interaction was significant for the Nd1 or Nd2 at either electrode (all  $p$ 's > .34).

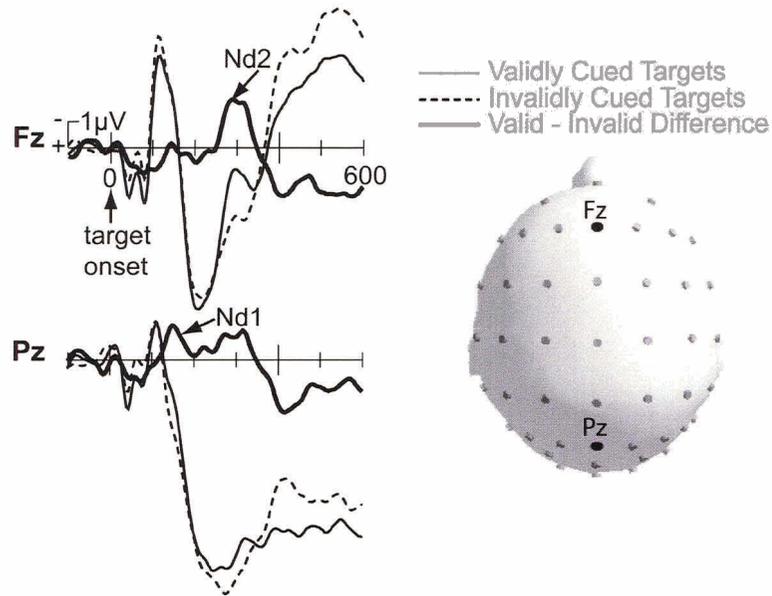


Figure 5-2. Grand-average ERP waveforms elicited by auditory target stimuli in Experiment 4.

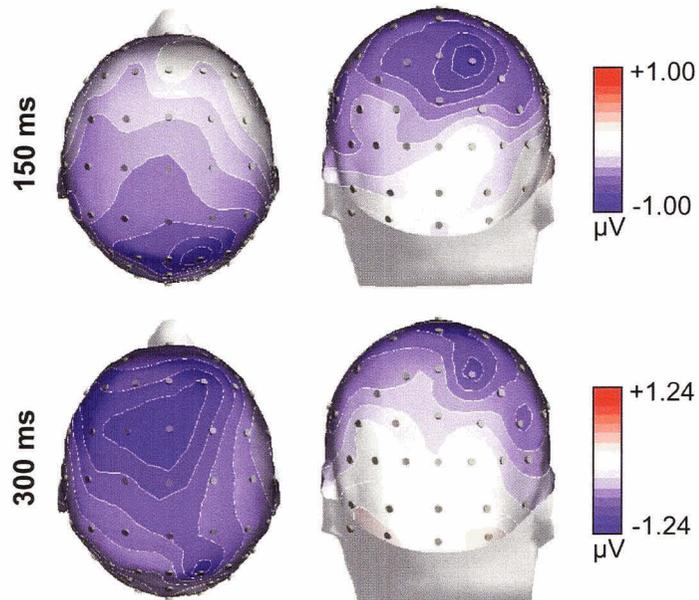
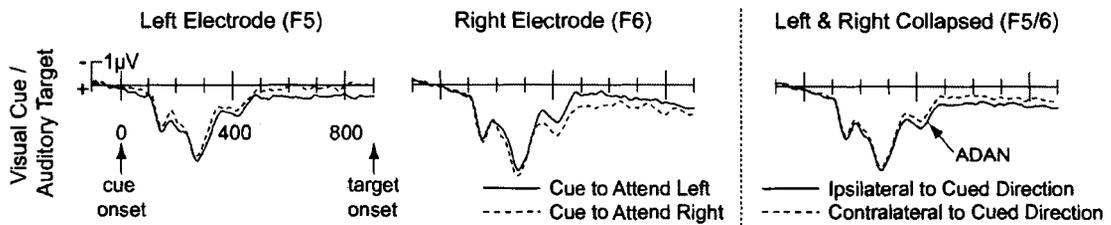


Figure 5-3. Topographical voltage maps of the Nd1 and Nd2 elicited by auditory target stimuli in Experiment 4.

### 5.2.3 Cue-elicited ERPs

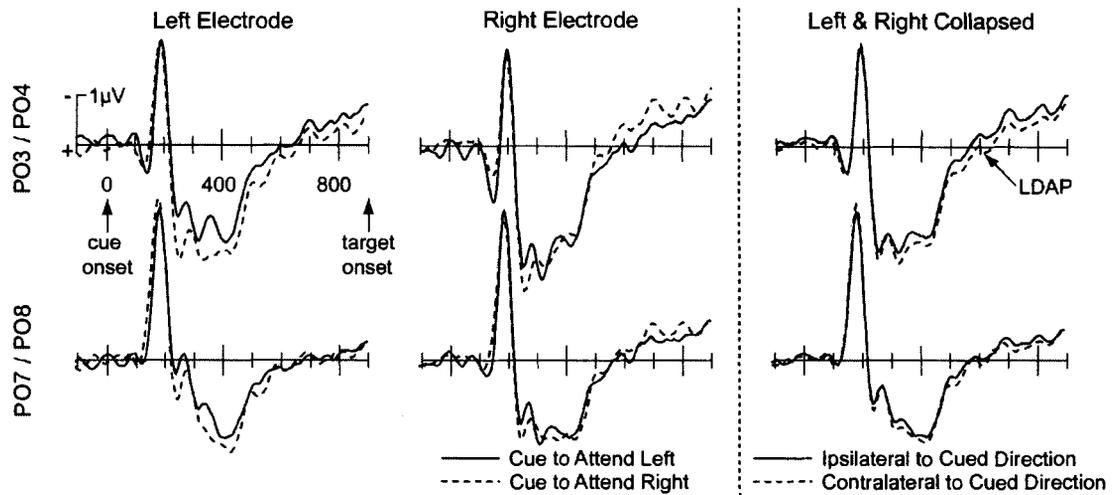
As can be seen in Figure 5-4, a contralateral negativity was apparent in the ERP waveforms at frontal electrode sites, beginning about 320 ms after cue onset and lasting until target onset. The main effect of electrode location was significant,  $F(3,36) = 4.22$ ,  $p = .05$ , as was the interaction between electrode location and electrode lateralization,  $F(3,36) = 4.90$ ,  $p = .047$ , which indicates a difference in the ADAN at the four electrode pairs tested. In addition, the ADAN was also larger over the right hemisphere than the left, as indicated by a significant cued side x electrode lateralization interaction,  $F(1,12) = 10.15$ ,  $p = .0002$ . None of the other main effects or interactions were significant (all  $p$ 's > .27). To examine the differences between the electrode pairs,  $t$  tests comparing ipsilateral and contralateral waveforms were performed separately for each electrode pair. The ADAN was significant at F5/6,  $t(11) = 2.61$ ,  $p = .03$ , and FC5/6,  $t(11) = 2.15$ ,  $p = .05$ , but not at F3/4,  $t(11) = 1.37$ ,  $p = .19$ , or F7/8,  $t(11) = 1.99$ ,  $p = .07$ .

An unplanned ANOVA on the mean ERP amplitudes in the later 500–800-ms interval indicated that the late ADAN was also significant,  $F(1,12) = 9.09$ ,  $p = .01$ , but unlike in the earlier interval, it was significant at all four electrode pairs, as indicated by a nonsignificant electrode location x electrode lateralization interaction,  $F(3,36) = 1.38$ ,  $p = .27$ , and was larger over the left hemisphere than the right as indicated by a significant cued side x electrode lateralization interaction,  $F(1,12) = 18.18$ ,  $p = .001$ . These results indicate that different neural processes may underlie the anterior negativity observed during the conventional ADAN interval and the anterior negativity observed later in the cue-target interval.



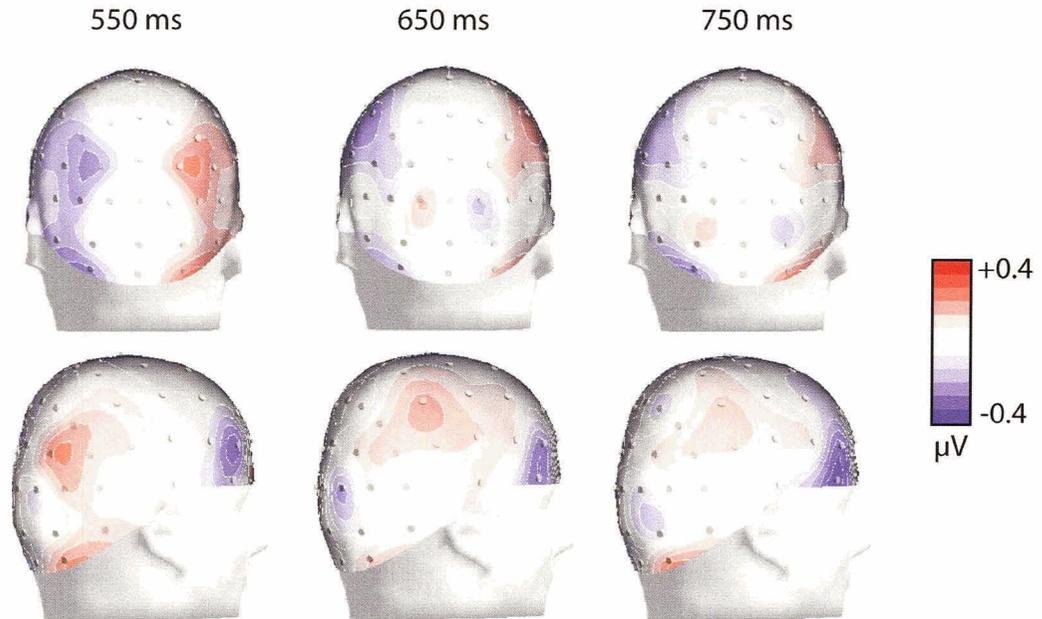
**Figure 5-4. Grand-average ERP waveforms elicited by attention-directing cues recorded at anterior electrodes F5 and F6.**

The LDAP elicited by the auditory cues in this experiment at posterior electrodes PO3/PO4 and PO7/PO8 can be seen in Figure 4-5. The main effect of electrode location was significant,  $F(3,36) = 6.17, p = .02$ , as was the interaction between electrode lateralization and electrode location,  $F(3,36) = 9.63, p = .001$ , which indicates a difference in the LDAP at the tested electrode pairs. None of the other main effects or interactions were significant (all  $p$ 's > .27). To examine the differences between the electrode pairs,  $t$  tests comparing ipsilateral and contralateral waveforms were performed separately for each electrode pair. The LDAP was significant at P3/4,  $t(11) = 2.47, p = .03$ , PO3/4,  $t(11) = 2.18, p = .05$ , and CP5/6,  $t(11) = 2.99, p = .01$ , but not at PO7/8,  $t(11) = 0.74, p = .47$ . This pattern of results indicates that the LDAP was present in this experiment but was focused more dorsally than in prior visual cueing experiments.



**Figure 5-5. Grand-average ERP waveforms elicited by attention-directing cues recorded at posterior electrodes PO3 and PO4 (top row) and PO7 and PO8 (bottom row).**

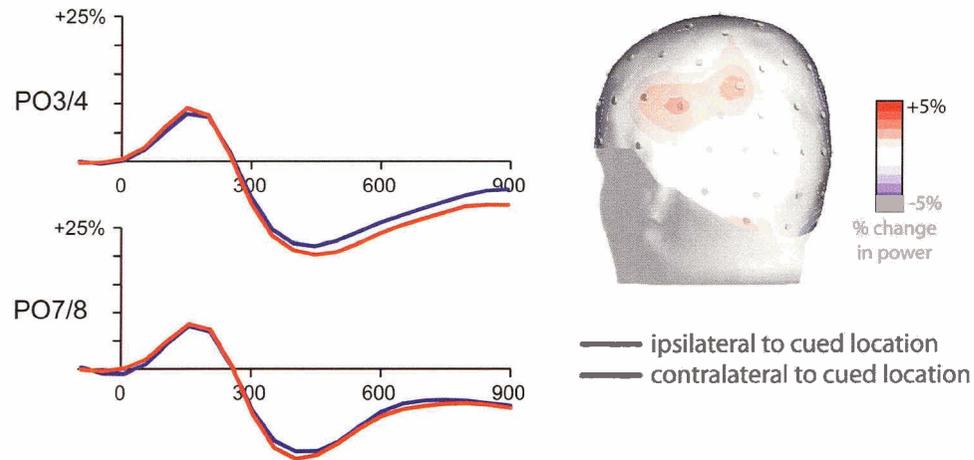
Similar to the LDAP observed in Experiment 2, the LDAP here shows a more dorsal parietal source, as can be seen in the topographical maps in Figure 5-6, and in the later time interval (650 and 750 ms) appears to be located over auditory cortex. This more dorsal activity could reflect preparatory activity in auditory areas, consistent with the finding of a more dorsally distributed LDAP in Experiment 2 as well.



**Figure 5-6.** Topographical voltage maps of the LDAP elicited by visual cue stimuli in Experiment 4 at 550 ms (left), 650 ms (middle), and 750 ms (right) following the cue.

#### 5.2.4 Cue-elicited oscillatory activity

The alpha activity induced by the visual cues in this experiment at posterior electrodes PO3/PO4 and PO7/PO8 can be seen in Figure 5-7. The interaction between electrode location and electrode lateralization was significant,  $F(3,36) = 5.77$ ,  $p = .03$ , but all other main effects and interactions were not significant (all  $p$ 's  $> .29$ ). This suggests that the alpha modulation was significantly different between the electrode pairs tested. To examine the differences between the electrode pairs,  $t$  tests comparing ipsilateral and contralateral waveforms were performed separately for each electrode pair. Difference in alpha activity were significant at P3/4,  $t(11) = 2.52$ ,  $p = .03$ , and CP5/6,  $t(11) = 2.31$ ,  $p = .04$ , but not at PO7/8,  $t(11) = 1.65$ ,  $p = .13$ , or PO3/4,  $t(11) = 1.72$ ,  $p = .11$ .



**Figure 5-7. Grand-average TSE waveforms of alpha (8-14 Hz) activity induced by attention-directing cues at posterior electrode PO3/4 and PO7/8. Topographical map displays the distribution of the contralateral-ipsilateral difference wave from 500-800 ms post-cue.**

As can be seen in the topographical map of the TSE waveforms, the foci of the alpha modulations appear consistent with changes in parietal and auditory generators in a similar manner as the LDAP observed during the same time period. The presence of alpha modulation in this experiment and its more dorsal focus suggests that spatially specific changes in alpha activity can occur prior to an auditory target, and that this activity occurs in distinct areas from the alpha modulations observed prior to visual targets (Experiments 1 and 3). It is interesting to speculate that alpha rhythms in the cue-target interval may index anticipatory changes in sensory specific cortical areas in preparation for the impending target stimulus. However, the results of Experiment 2 showed that unimodal auditory shifts of attention did not induce changes in alpha activity. It is possible that changes in alpha rhythms are specific to the visual modality and that auditory anticipatory activity occurs within a different frequency band. It is possible that when visual information is present during crossmodal shifts of attention (i.e. a visual cue which indicates the to-be-attended location or a visual target to be prepared for), a modality specific visuospatial attention system is activated in addition to auditory attention mechanisms such that changes in alpha can be observed.

## 6 GENERAL DISCUSSION

The present study investigated the electrophysiological activity elicited by attention-directing cues and subsequent targets in intramodal visual and auditory cueing as well as two audiovisual cueing conditions. Consistent with prior behavioural work (e.g., Mondor & Amirault, 1998; Spence & Driver, 1996), cueing facilitated responses to same and different-modality targets appearing at the to-be-attended location. Additionally, cueing modulated the neural processing of the targets, as indexed by the target-elicited ERPs, in a similar manner regardless of the modalities of the cues and targets. Specifically, in both the intramodal and crossmodal conditions, symbolic spatial cueing caused the ERPs to validly cued targets to be more negative than the ERPs to invalidly cued targets over a broad time range. Two distinct negative peaks could be observed in the valid-invalid difference waves, corresponding to the Nd1 and Nd2 components that have been observed in prior studies of intramodal auditory attention and some prior studies of intramodal visual attention (Eimer, 1994; Schroger & Eimer, 1993, 1997). Topographical mapping showed that the Nd1 was maximal over the posterior parietal scalp sites contralateral to the target, whereas the Nd2 was maximal over the fronto-central scalp in all four experiments. The posterior N1 was also larger on valid trials than on invalid trials in Experiments 1 and 3, but the topography of the valid-invalid difference wave in the time interval of the N1/Nd1 in Experiment 3 indicated that this enhanced negativity was related to the Nd1 rather than to an effect of cueing on the visual N1 component.

The lack of a cue validity effect on the visual P1 in both the intramodal visual and crossmodal cueing experiments is somewhat surprising given the results of prior symbolic visual cueing studies (e.g. Mangun & Hillyard, 1991). One possibility is that

participants failed to orient attention quickly enough to influence early cortical processing of the target. This seems unlikely given that cueing resulted in similar effects on behavioural performance and also on subsequent portions of the ERP waveforms (i.e. N1 effects and Nd's). It is more likely that a P1 cueing effect was not observed because attention typically modulates the P1 and N1 over the contralateral scalp (Di Russo, Martinez, & Hillyard, 2003; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2001), and in the present study there was little or no contralateral P1. Another possibility is that no P1 cueing effect was observed here because participants responded to both validly cued and invalidly cued targets, which has been shown to produce smaller cueing effects on early sensory ERP components than when only the targets at the validly cued location are response relevant (Eimer, 1994).

The similarity of the Nd1 and Nd2 components of the target-elicited waveforms regardless of the cue or target modalities is consistent with the hypothesis that voluntary shifts of spatial attention are mediated by a single supramodal system. Prior studies have suggested that the ADAN and LDAP components of the cue-elicited ERP reflect the workings of such a system. The results of the present study challenge the hypothesis that these ERP components reflect activity of a purely supramodal attentional control system. Here, the ADAN was present when visual cues were used to indicate the location of a visual or auditory target (Experiments 1 and 3) but not when auditory cues were used to indicate the location of a visual or auditory target (Experiments 2 and 4). Similarly, in a related intramodal cueing study, the ADAN was present when visual cues were followed by visual targets but was absent when auditory cues were followed by auditory targets (Green et al., 2005). The differences across the current experiments were not tested statistically because a within-participant design was not feasible. Nonetheless, on the basis of the emerging pattern of results, one can speculate that the

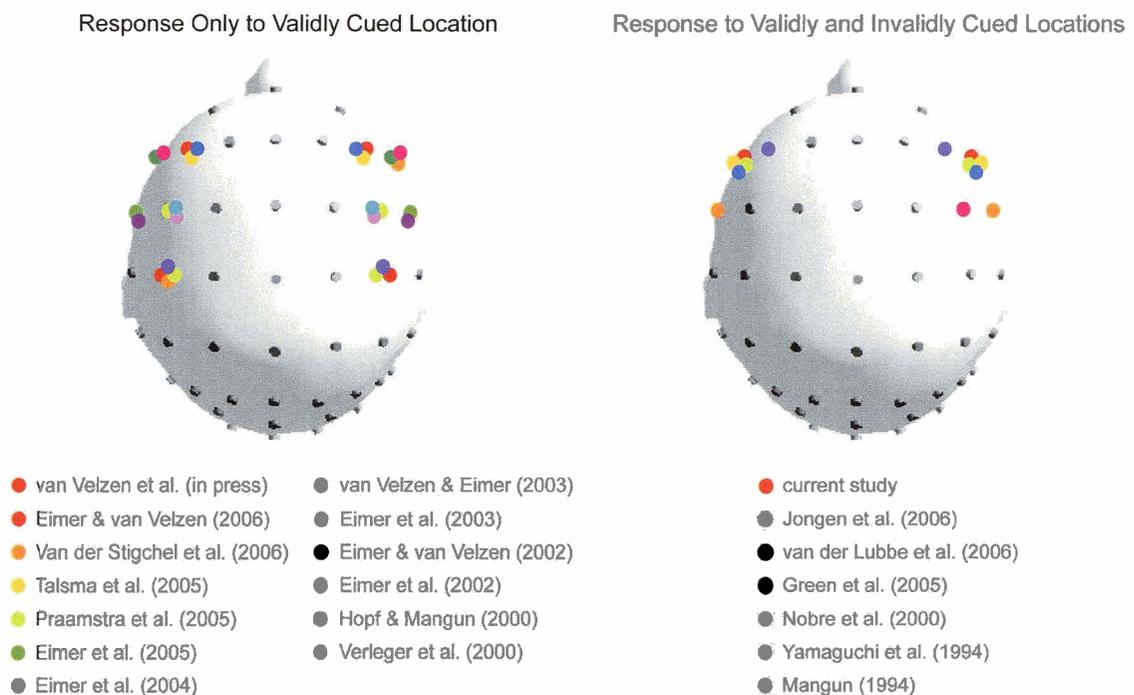
ADAN elicited by visual cues in this paradigm is neither supramodal nor an electrophysiological correlate of an executive-control process that is necessary for shifts of attention to take place.

Although auditory cues did not elicit the ADAN in these experiments, auditory cues have been found to elicit the ADAN prior to visual or tactile stimuli in previous experiments by Eimer and colleagues (Eimer & van Velzen, 2002; Eimer et al., 2003). The discrepancy between the current findings and those of Eimer and colleagues may be due to differences in the cueing procedures or task demands. In each case, the cue was non-predictive of the impending stimulus location, but in Eimer's paradigm all stimuli at the uncued location were task irrelevant and only infrequent deviant stimuli at the cued location were relevant. In our paradigm, a probe stimulus was used to ensure that participants shifted attention to the cued location and participants responded to targets appearing at invalidly cued locations as well as validly cued locations. Based on these methodological differences, it could be argued that auditory cues failed to elicit the ADAN in our studies because participants may have divided their attention between both potential target locations. Such an explanation is insufficient to explain the present results for three reasons. First, visual cues did elicit the ADAN, which confirms that the paradigm and methods were adequate for observing this frontal negativity. Second, auditory and visual cues produced comparable effects on RTs and target ERPs, thereby minimizing the possibility that participants shifted attention more strongly in response to the visual cues than the auditory cues. Third, if the ADAN reflected supramodal attentional control, then no attentional effects on RTs or target ERPs should be observed in the absence of the frontal negativity. The fact that cue validity effects were observed in the absence of the ADAN demonstrates that the processes underlying the ADAN are not necessary for attention to shift from one location to another.

Although the ADAN does not appear to be necessary for shifting attention, and the ADAN elicited by visual cues in the current study does not appear to reflect supramodal processes, the ADAN observed in previous studies may reflect other processes that are potentially supramodal. It is possible that the anterior negativity referred to as the ADAN is the result of multiple processes, such as interpreting the visual cue stimulus (Verleger et al., 2000), suppressing a saccade to the cued location (van der Lubbe et al., 2006), and holding the cued location in working memory. The finding that the earlier portion of the anterior negativity observed in Experiment 3 (300-500 ms) was larger over the right hemisphere whereas the later portion of the anterior negativity (500-800 ms) was larger over the left hemisphere provides support for the hypothesis that multiple processes are involved in generating this activity. The discrepancies between our findings and Eimer's findings might therefore be caused by differential involvement of these hypothetical ADAN sub-components. In our task, attention-directing cues may elicit frontal lobe processes specific to the visual modality, whereas other tasks might elicit other frontal lobe processes that are not specific to visual cues.

Although purely speculative, it is possible that the scalp distribution of the anterior negativity is different depending on the processes necessary for the task. The scalp distribution of the anterior negativity has not been directly compared between different experimental paradigms, however a comparison of the electrode sites at which the ADAN was maximal in previous studies is suggestive of topographical differences depending on the task participants are required to perform (Figure 6-1). When the participants were required only to respond to the validly cued location the ADAN appears more likely to be maximal at central and fronto-central scalp sites, whereas when the participants were required to respond to both the validly and invalidly cued locations the

ADAN appears more likely to be maximal at frontal scalp sites. This suggests that different processes are activated depending on the response requirements of the task in addition to any differences in processing for cue and target stimuli in modalities other than vision. Given the wide variety of executive functions ascribed to the frontal lobes it is plausible that the anterior negativities being observed in a variety of experimental tasks are indexing different processes. Hopefully future studies directly comparing the scalp distributions and neural generators of the ADAN elicited in different tasks will help clear up this discrepancy.



**Figure 6-1.** Comparison of electrode sites where ADAN was maximal between studies requiring responses only to the validly cued location and studies requiring responses to both validly and invalidly cued locations.

Although it appears that the ADAN component is not necessary for shifting attention, and may actually reflect task-dependant processes, one caveat is that the ADAN is operationalized as a lateralized difference between the activities elicited by

cues directing attention to the left and right of space. Any activity reflecting attentional control processes that are not lateralized depending on the to-be-attended location will not be identified in traditional left-cue versus right-cue comparisons. Some of the activity of frontal-lobe attentional control mechanisms may be non-lateralized, and the frontal-lobe attentional control activity may be less lateralized for cues presented in the auditory modality, particularly when the cues are not predictive of the target locations and uncued locations are still response relevant as in the current experiment. Future research is needed to investigate such non-lateralized activity related to the control of attention.

In contrast to the ADAN, the LDAP was observed in the present study during intramodal visual, auditory, and crossmodal shifts of attention. Other recent studies have found the LDAP to be present in intramodal visual cueing tasks (Green et al., 2005; Hopf & Mangun, 2000), intramodal auditory cueing tasks (Green et al., 2005), and in crossmodal cueing tasks involving visual, auditory, and tactile stimuli (Eimer et al., 2002, 2003; van Velzen et al., 2002). This emerging pattern of results suggests that the LDAP reflects supramodal processes involved in shifting attention in space. However, there is a caveat to this interpretation: The scalp topography of the LDAP appears to vary depending on the modalities of the cues and targets. In the present study, the LDAP was found more ventrally over the lateral occipital scalp when attention was directed in preparation for visual targets and more dorsally over the temporo-parietal scalp when attention was directed in preparation for auditory targets, regardless of the sensory modality of the cue stimulus. The LDAP in all four experiments appeared to have a parietal source, which may reflect activity of a supramodal system for shifting attention in space. The LDAP also appeared to have one or more modality-specific sources, which may reflect spatially specific excitation in sensory areas involved in processing the target. Based on the scalp topographies of the contralateral minus ipsilateral difference

waves, it can be speculated that the LDAP is partially generated in modality-specific visual areas in the occipital lobe prior to visual targets and in modality-specific auditory areas in the temporal lobe prior to auditory targets.

In addition to differences in scalp topographies of the LDAPs suggesting that it does not just reflect supramodal activity, there have been studies that did not report an LDAP during the cue-target interval even though other attention effects were observed (Nobre et al., 2000; Talsma et al., 2005; Yamaguchi et al., 1994), further suggesting that the LDAP may reflect consequential activity caused by an attention mechanism but is not the mechanism itself. A handful of visual cueing studies have failed to observe the LDAP, and one commonality between these studies is that all had varying SOAs between the cue and the target. It is possible that the preparatory portion of the activity seen in the LDAP is dependant on the temporal predictability of the target onset, and that attention is being directed both spatially and temporally during cueing tasks with a invariant cue-target interval (Coull, Frith, Büchel, & Nobre, 2000; Coull & Nobre, 1998; Miniussi, Wilding, Coull, & Nobre, 1999).

The LDAP was also not observed in a recent study of crossmodal auditory-tactile cueing using blind participants and sighted participants run in dark conditions, but was observed in sighted participants run in illuminated conditions (Eimer, van Velzen, Gherri, & Press, in press). This led the authors to conclude that the presence and magnitude of the LDAP is dependant on the presence of visual information. However, upon closer examination of the ERPs elicited by the auditory cues used in that study, the negativity referred to as the ADAN was sustained until target onset and was present at widely distributed electrode sites including parietal electrode sites. It is possible that this sustained activity reflects preparatory activity in somatosensory areas, and when no visual information is present the occipital activity is not observed. This activity was likely

not interpreted in this fashion by the authors because it appeared as a contralateral negativity rather than the contralateral positivity traditionally associated with the LDAP. A few other researchers have observed a negativity rather than a positivity during the LDAP interval (Van der Stigchel et al., in press; Worden et al., 2000) and my own as yet unpublished data suggests that even within the visual modality the polarity of this posterior effect can flip depending on the spatial location of the targets being prepared for (Green, Weeks, & McDonald, 2005). Thus, modality-specific preparatory activity may play a large part in generating the LDAP component, but activation of visuospatial attention mechanisms and visual preparation may also contribute to the LDAP when visual information is available. The visual modality has the highest spatial acuity and thus would be most efficient in spatial tasks to use any visual information that was available (e.g. Ward, 1994).

The alpha-band oscillatory activity during the cue-target interval showed a similar pattern of results to the LDAP in the three experiments that contained visual stimuli. In Experiments 1 and 4, when attention was directed in anticipation of a visual target, spatially specific modulations of alpha activity were observed over ventral occipital scalp sites, whereas in Experiment 3, when attention was directed in anticipation of an auditory target, alpha modulation was observed more dorsally. Given that low frequency activity in the alpha-band is dominant in both averaged ERPs and unaveraged EEG (Makeig et al., 2002), it is plausible that alpha activity and ERP activity occurring in anticipation of a target stimulus are indexing similar processes. In particular, the alpha modulation observed in the present study seems most likely related to the sensory-specific portion of the LDAP, as similar topographical differences were seen when attention was shifted in preparation for visual and auditory targets.

One way that the changes in alpha activity could be influencing neural responses to an attended target is through neural circuits involving reciprocal thalamocortical connections. These local circuits are hypothesized to be specialized for the type of task being performed, such as a circuit for coding the form or shape of an object in inferior temporal cortex (LaBerge, 2001) and a circuit for coding the location of an object in posterior parietal cortex (LaBerge, 2005). Within these circuits, post-synaptic potentials in the apical dendrites of pyramidal neurons increase the depolarization of the neuron, but the oscillatory pattern keeps this depolarization below the level necessary for the neuron to fire. When the target stimulus is presented at the end of the delay the neuron finally receives enough excitatory input to fire. It is thought that during the delay period of a task where the participant is anticipating the target the increase in excitatory post-synaptic potentials primes the neuron in preparation for the target, increasing the efficiency in firing in response to the target (LaBerge, 2005).

In addition to these local thalamocortical circuits that implement a function, there is also thought to be a global circuit that includes reciprocal connections between the prefrontal cortex, the thalamus, and posterior brain areas. The connections between the thalamus and posterior brain areas provide the basis of the changes in response to the target stimuli after the delay, but throughout the delay the activity in this local circuit is maintained and modulated by input from the prefrontal cortex. The thalamocortical connections between both task-specialized posterior locations and prefrontal areas that provide top-down influences produce oscillatory patterns of post-synaptic potentials that, when induced over a large enough number of neurons can be picked up by the scalp recorded EEG (LaBerge, 2005; Mazaheri & Picton, 2005). Further research examining changes in oscillations in other frequency bands during the cue-target interval may be

able to demonstrate the involvement of the prefrontal and parietal lobes in attentional control.

One potential problem with linking the LDAP to changes in alpha activity is the lack of alpha modulation during intramodal auditory shifts of attention in Experiment 2 even though an LDAP was elicited. Since auditory cues induced changes in alpha prior to visual targets in Experiment 3, and visual cues induced changes in alpha prior to auditory targets in Experiment 4, it is unlikely that attention must be directed by a visual cue or shifted in preparation for a visual target to induce spatially specific changes in alpha activity. One possible explanation is that the modulation of alpha rhythms is a purely visual phenomenon, and that the presence of any relevant visual stimulation, either attention-directing cues or response relevant targets, induces visuospatial shifts of attention. In addition, preparatory changes in oscillatory activity in the auditory modality may be difficult to observe at the scalp with EEG or may occur in outside the alpha frequencies tested here. A thorough exploration of the induced oscillatory changes in the cue-target interval of unimodal auditory shifts of attention, particularly using MEG as it is capable of picking up temporal lobe generated alpha activity (Hari et al., 1997), may help to determine if similar attentional modulations of alpha occur in auditory cortex or if different frequency bands are linked to anticipatory activity in different sensory modalities.

Although the effects of voluntarily attending to a location in space on the processing of stimuli that occur there initially suggests that supramodal mechanisms underlie shifts of attention, the activity observed in the cue-target interval suggests that multiple modality specific mechanisms may play a role. In the current trial-by-trial cueing paradigm only visual cue stimuli elicit the ADAN component, regardless of the modality of the target stimuli, which indicates that this activity is not only unnecessary for

controlling shifts of attention but also that it does not reflect supramodal processes. The LDAP was observed in all cue-target modality pairings, but the scalp distribution appeared to be dependant on the modality of the target, suggesting that, at least in part, the LDAP reflects modality specific activity in preparation for the target. The modulation of alpha activity in the TSE waveforms is also suggestive of modality specific processes. Although more research needs to be done, the alpha modulation appears linked to the the presence of visual information and may indicate that whenever relevant visual information is present visuospatial attention mechanisms are activated. This is not to say that a supramodal attention system does not exist. In fact, a distinct parietal source was observed in the topographies of the LDAP for all four experiments that may be part of a modality unspecific attentional system. However, at present it seems unlikely that if a supramodal system does exist that the ADAN, LDAP, or alpha-band oscillations are reliable markers of activity in this system.

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