ELECTROPHYSIOLOGICAL CORRELATES AND CONSEQUENCES OF SELECTIVE AUDITORY ATTENTION

by

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The sensory and perceptual mechanisms of the human brain can be reconfigured so as to optimize the processing of a selected type or class of information (i.e. frequency, location, etc.). A foundational goal of cognitive neuroscience is to pursue an understanding of the neural processes that underlie this reconfiguration. Auditory selective attention has been the topic of considerable investigation, principally by the use of event-related potential (ERP) techniques to record certain electrophysiological correlates of attentional selection. The large majority of this work has focused on a single paradigm, known as the sustained-attention paradigm, in which listeners continuously focus their attention at a particular location or on a particular frequency of sound. Only a very few previous studies have investigated the more realistic situation in which listeners continuously reorient their attention on a moment-by-moment basis. This thesis reports the systematic investigation of transient auditory attention. The ERP technique was used to address questions regarding the neural correlates and functional anatomy of auditory selective attention in a variety of situations in which attention was continuously reoriented in space. Following a brief introduction and review in Chapter One, Chapter Two reports the result of the first high-density (64-electrode) study of the ERP correlates of transient spatial auditory attention. This chapter concludes with the speculation that transient attention modulates neurons within a dedicated spatial processing or “where” pathway that projects posteriorly and dorsally from auditory cortex. Chapter Three checks the assumptions of this hypothesis by identifying an ERP correlate of spatial processing and localizing the generator of this correlate to a region of cortex believed to constitute part of this “where” pathway. Finally, Chapter Four reports
the results of several experiments that localized certain attention-related modulations of
the ERP to this putative "where" pathway. These experiments also demonstrated that
transient auditory attention involves a complex interaction between stimulus-driven and
goal-driven (bottom-up and top-down) processes that lead to distinctly different patterns
of ERP activity. The thesis concludes with a discussion of the advancements made,
relative to the state of previous knowledge, as a result of the work presented here.
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"'I am leaving, I am leaving', but the fighter still remains"

-Paul Simon

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CHAPTER ONE: SELECTIVE ATTENTION

The problem of information selection

The behavior of every organism is guided by information extracted from the environment. Information regarding the presence or absence, location, identity, direction of motion, etc. of things in the world may be detected and interpreted by an organism so as to optimize its behavior. However, as researchers and theorists (e.g., Berlyne, 1970; Broadbent, 1958) began to weave the ideas of Information Theory into a background of Behaviorism, it became evident that making use of information in the environment is not a simple matter of responding to it. When simultaneously presented with two stimuli demanding two incompatible behavioral responses, to which stimulus will an organism respond? If a single response is made to simultaneous stimuli and a reward is delivered, to which stimulus is that reward attributed for the purpose of learning. How is the appropriate behavior accomplished when a relevant stimulus occurs among a clutter of irrelevant distracting stimuli? These concerns were well summarized by Berlyne (1970): “The upshot of all these facts is that mutual interference among neural activities must be widespread, continuous, and potentially severe”.

The crux of these questions is captured in the results of early investigations of human information processing by Broadbent (1952a,b). Subjects were presented with a visual field divided into numbered sections. The subject could then be asked questions such as “Is there a cross in section two?”. Subjects had no difficulty when a single question was asked, but when two different questions were asked simultaneously, subjects encountered difficulty in answering. This observation highlights a fundamental characteristic of human information processing: there are limitations on capacity. No less
important was the subsequent observation that, when the questions came from two
different speakers and the subjects were instructed in advance as to which of the two
questions was to be answered, the difficulty in answering was greatly reduced. Here we
see a second fundamental characteristic of how humans deal with sensory information:
certain sources information can be preferentially selected, a phenomenon called selective
attention.

**Implementation of selective attention in sensory systems**

The mechanisms by which selective attention is implemented in human sensory
systems have been the subject of tremendous scrutiny. Selection was initially
categorical as a filter that “discards some part of the information reaching the ear”
(Broadbent, 1958), and a variety of theories were advanced regarding the “stage” at
which selection mechanisms might operate (eg. Broadbent, 1970; Treisman, 1969). Was
selective attention implemented early in the course of information processing? Does
most sensory information get in and then not get used or does the brain effectively shut
down the encoding of non-selected information. What parts of the brain might be
modulated by attention, and in what way? It became of interest to obtain
electrophysiological evidence that might help to answer these questions, and, among
others, the event-related potential (ERP) technique was applied in investigations of
selective attention.

ERP is the stimulus-locked average of the electroencephalogram (EEG). By
averaging the complex electrical activity following multiple presentations of an identical
stimulus under identical conditions, the electrical response attributable to that stimulus
can be isolated from activity unrelated to that stimulus. When used in studies of selective
attention, the ERP elicited by attended stimuli is compared with the ERP elicited by unattended stimuli, typically by subtracting one from the other, to reveal modulations attributable to selective attention.

The first clear evidence of modulation of neural activity due to selective attention was provided by Hillyard, Hink, Schwent, and Picton (1973) (earlier studies eg. Spong, Haider, & Lindsley, 1965, Wilkinson & Lee, 1972, although suggestive, had proved difficult to interpret because of methodological issues). In this study, subjects were presented with a stream of tone pips to each ear. Subjects were to attend to one of the two ears and detect the occurrence of a slightly higher pitched target tone in that ear. Thus the ERP elicited by non-target tones in the attended ear could be compared with the ERP elicited by non-target tones in the unattended ear. Two important differences were found, both of which appeared as a negative deflection of the ERP elicited by attended relative to unattended stimuli: the first beginning at latencies of about 100 ms post-stimulus onset (the so-called early negative difference or early Nd) and the second between 300 and 400 ms (the late Nd). Importantly, subsequent investigations found that the ERP modulation depended on the characteristics of the stimuli themselves. For example, the onset of the early Nd could be modulated by altering the inter-stimulus interval (ISI) between the tone pips. The early Nd appeared over the N1 component (an early negative deflection in the ERP that occurs at about 100 ms post-stimulus) only when tone pips were presented at a high stimulus rate with ISIs of about 250 ms or less (Näätänen & Michie, 1979). In contrast, the late Nd appeared to be unaffected by the stimulus rate.
Investigations of visual attention have likewise proved useful in developing our understanding of the neural mechanisms subserving attention. As with auditory attention, neural correlates of visual selection can be found using ERP. For example, Mangun, Hillyard, & Luck (1993) found that the amplitudes of the P1 and N1 ERP components evoked by visual targets at an attended location were larger than these same components elicited by targets at unattended locations. These and other modulations of the ERP waveform have been interpreted as electrophysiological consequences of attentional selection mechanisms (Näätänen & Mitchie, 1979; Hansen & Hillyard, 1984; Hillyard, Hink, Schwent, & Picton, 1973; Näätänen, 1992). At the most basic level, these differences in the electrical response of the brain tell us that sensory processing, and the neural mechanisms underlying it, are modified in some way by the focusing of attention. The studies presented in this thesis are part of a concerted effort across the field of cognitive neuroscience to refine that understanding by asking questions about how the auditory system handles information in general, which parts of the system are modulated by attention, and upon what factors this modulation depends.

ERP data provide two important types of evidence, "when" and "where", from which we may make inferences about underlying brain function: the latency of ERP modulations tells us something about the relative stage(s) of processing at which attention acts, and the topographic distribution of those modulations across the scalp provides hints about the underlying functional anatomy. From the results reported by Hillyard, et al. (1973) and a large body of subsequent literature (reviewed extensively by Näätänen, 1992) we thus find two important suggestions regarding the neural mechanisms subserving selective attention. First, by considering the latency of attention effects, we
see that attention can, under certain conditions, act at "early" stages of sensory processing. The early Nd onset latency corresponds roughly with that of the N1 component, provided that the stream of stimuli are presented with brief ISI. Since the N1 component is believed to be among the first responses generated by neurons in auditory cortex (Scherg, Vajsar, & Picton, 1989; Waldorff, et al., 1993), modulations of the ERP that co-occur with the N1 are thought to reflect differences in how auditory cortex handles attended and unattended stimuli at initial stages of processing. Hillyard, et al. (1973) took this result to be evidence of an early attentional filter that allows only stimuli from an attended "channel" into subsequent stages. Attention probably acts at later stages as well, since the ERP is also modulated at later latencies, which Hillyard et al. interpreted as reflecting an additional selection process associated with discriminating targets from non-targets.

Event-related potential studies also allow us to develop a functional map of human sensory systems. What parts of the brain represent various kinds of information and where are various cognitive operations accomplished? The scalp topography of attention-related ERP modulations offers some indication of where in the brain selective attention is acting. The neural modulation that causes the early Nd probably occurs in primary or secondary auditory cortex in Heschl's gyrus because it is maximal at central electrodes positioned above the supra-temporal plane. This has been supported by converging evidence using magnetoencephalography (MEG) (Waldorff, et al., 1993), which is the magnetic counterpart of electroencephalography, and functional Magnetic Resonance Imaging (fMRI) (Grady et al. 1997), which identifies the loci of task-related changes in cerebral blood flow. The late Nd is focused more frontally and is therefore
unlikely to be generated by the same set of neurons as the early Nd. Thus the
topography of the ERP suggests that selective auditory attention can modulate the
behavior of neurons in both primary auditory cortex and other cortical regions, possibly
including the frontal lobes. Chapter Two of this thesis considers whether this modulation
of primary auditory cortex is a general aspect of auditory selective attention. Does the
focusing of auditory attention always modulate the behavior of primary auditory cortex as
observed by Hillyard et al. (1973) or might it depend on the nature of the stimuli or task
engaged by the listener?

Our understanding of how selective attention in implemented in sensory systems
is predicated on an understanding of how information is handled in general. An
important general principle has emerged in this regard: sensory information is parsed so
that different aspects of the incoming information are represented by distinct populations
of neurons. For example, the visual system is thought to be divided into two independent
systems, one dedicated to the processing of object identity and one for the representation
of objects in space (eg. DeYoe & Van Essen, 1988; Ungerleider, & Mishkin, 1982).
Much less in known about how the auditory system encodes and processes different kinds
of information, and most of what is known is inferred from research with non-human
primates. One recent model suggests that the human auditory system, like the visual
system, contains anatomically distinct pathways to represent spatial ("where") and non-
spatial ("what") information (Rauschecker & Tian, 2000). This putative segregation of
auditory information is of considerable interest in any effort to identify the neural
mechanisms of selective attention. For example, the experiments in this thesis involve
the focusing of auditory attention in space (as opposed to focusing on a particular sound
frequency). Does this modulate the behavior of neurons in the putative auditory “where” pathway? There is some suggestion that this may be the case. For example, Woods & Alain (2001) found a negative deflection of the auditory ERP waveform for stimuli that shared a feature (frequency, location, or duration) with the target. The scalp distribution of this modulation depended on the shared feature, with frequency-related modulations more frontal than location-related modulations. However, no study has yet definitively reported ERP activity generated in the posterior “where” pathway. Thus, it is not entirely clear that the activity in this pathway can be differentiated from other components of the ERP.

The topographic scalp distribution of ERP modulations (known as a “topo map”) is difficult to interpret because it is a two-dimensional representation of the electric field generated by sources in a three-dimensional head. As an analogy, one might imagine trying to study the behavior of fish in a pond by examining ripples at the surface. A recently developed technique known as source analysis (Scherg et al., 1989) attempts to reconstruct the three-dimensional geometry of generators that underlie specific ERP modulations. Source analysis is a promising tool for mapping the functional anatomy of the human auditory system and the nature of attention-related modulations. For example, several studies (reviewed in Näätänen & Alho, 1995) have identified the electrical source(s) of the Mismatch Negativity (MMN), a well-known ERP response to unusual deviations in an ongoing pattern of acoustic stimuli. The MMN has been repeatedly observed to be fronto-central and maximal along the midline electrodes, suggesting bilateral generators on the supratemporal plane. For the situation in which the MMN is generated in response to deviations in non-spatial features such as pitch,
intensity, or duration, source analysis has identified dipole sources in Heschl's gyrus, just anterior to the generator of the N1. Chapter Three describes the results of a source analysis of the MMN generated in response to deviations in the spatial location of a sound. This study contributes to a functional map of the auditory system by demonstrating that neurons near the temporo-parietal junction (TPJ) and within the putative auditory "where" pathway engage in processing the auditory spatial information. This result tells us not only that such a pathway exists in humans, but also that at least a subset of the neural activity within this pathway can be imaged using the ERP technique. This observation makes it possible to attempt a more careful investigation of the neural correlates of spatial auditory attention.

The discussion in Chapters Two and Three comprise two parts of a bigger picture. Chapter Two considers the ERP correlates of spatial auditory attention; Chapter Three investigates the functional anatomy of auditory spatial processing in general. The third and final set of experiments, which appears in Chapter Four, brings these lines of questioning together by asking whether spatial auditory attention modulates behavior in a region or regions that are part of the putative spatial processing pathway of the auditory system. Chapter Four also investigates the behavior of this pathway under two different attention conditions: one in which attention is under top-down voluntary control, and one in which bottom-up processes are responsible for modulating the behavior of the auditory system. This investigation constitutes a preface to what will be an ongoing effort to carefully characterize the neural correlates and consequences of auditory selective attention.
Transient versus sustained attention

Although research to date has yielded important insights into how selective auditory attention might be implemented in the human cortex, it has made an important error of omission. The present discussion now turns to a more detailed consideration of what is known and what remains unknown regarding the cognitive neuroscience of auditory attention.

Until early in the 1990s, nearly every ERP investigation of selective auditory attention had employed a paradigm similar to the one originally used by Hillyard, et al. (1973). In this sustained attention paradigm, subjects focus their attention on one stream of information (e.g. high pitched tones, tones presented to the left ear, etc.) for durations on the order of several minutes. Although we do occasionally find ourselves listening to the same information source for long periods, this is not the only mode in which attention normally operates. Attention is also dynamic. It is rapidly oriented and reoriented both voluntarily according to the goals of the listener and reflexively in response to external events. An understanding of the neural mechanisms subserving sustained attention might not apply to the brain in other situations. Indeed, the original experiments carried out by Broadbent, towards which the work of Hillyard et al. was directed, employed a transient attention task. The to-be-attended speaker was indicated on a trial-by-trial basis by means of a visual cue.

It was originally thought that transient attention had no effect on behavioral performance (Posner, 1978), however, it is now well accepted that reorienting attention from trial to trial in response to an attentional cue can produce reliable changes in measures of performance such as accuracy and reaction time. For example, judgments of spatial localization (Rhodes, 1987; Ward, 1994) and discrimination (Spence & Driver,
(Mondor & Zattore, 1995) were facilitated when attention was transiently focused on the location or speaker from which an auditory target was presented.

Although previous ERP investigations of auditory selective attention have been limited to the sustained attention situation, much is known about the neural mechanisms subserving transient visual attention. In addition to the electrophysiological correlates of visual attention mentioned above, much is known about the neural circuitry that mediates the orienting of selective attention. The preponderance of evidence taken from studies of patients with brain lesions (e.g., Posner, Walker, Friedrich, & Rafal, 1984), Positron Emission Tomography (PET) (Corbetta, Meizin, Shulman, & Petersen, 1993), and functional Magnetic Resonance Imaging (e.g., Corbetta, et al., 2000; Hopfinger, Buonocor, & Mangun, 2000) supports a theory that a fronto-parietal network of brain regions, probably also involving the superior colliculus and pulvinar nucleus of the thalamus, is responsible for disengaging, shifting, and reengaging focused visual attention. The experiments presented in this thesis are part of an ongoing effort to bring our level of understanding of auditory attention into line with our understanding of visual attention by reaching beyond the sustained attention paradigm.

The suggestion that transient auditory attention might operate differently from sustained attention at a neuronal level could be gleaned from an investigation into the dynamics of the sustained attention Nd effects by Donald & Young (1982). They found that, whereas the later difference components were constant over time, the early Nd component emerged only after subjects had sustained their attention for about 30 seconds (see also Hansen & Hillyard, 1988). This result leads to the prediction that transient
attention, in which attention is reoriented on a moment-by-moment basis and never sustained for long periods of time, might involve a fundamentally different mechanism of operation – one that does not involve selection mechanisms operating at very early stages of sensory encoding.

Schroger (1993) and Schroger and Eimer (1993) reported the first ERP investigations of transiently oriented auditory attention using a Posner (1978) type cue-target task in which the to-be-attended speaker was indicated by a visual arrow. By subtracting the ERP to uncued stimuli from the ERP to cued stimuli, Schroger (1993) found two distinct negative difference components, which differed in latency and topography: the earlier component peaked at about 150 ms and was maximal at the PZ electrode site (parietal) whereas the later component peaked at about 300 ms and was maximal at FZ and CZ (frontal and central). Using a nearly identical paradigm, Schroger and Eimer (1993) found these same two components, but also distinguished a third component that was maximal at CZ but with a latency intermediate between the first and second, at around 200 ms. Some confusion has arisen regarding the occurrence and the naming of these components. Schroger (1993) referred to the earlier and later components as Nd1 and Nd2, respectively. Schroger and Eimer (1993) again used the term Nd1 for the early parietal component (at 150 ms), but applied the term Nd2 to the intermediate fronto-central component (at 200 ms) and the term Nd3 to the later fronto-central component (at 300 ms). A subsequent study by Schroger and Eimer (1997) identified only the two components described as the Nd1 (150 ms) and the Nd3 (300 ms) by Schroger & Eimer (1993). The intermediate component (200 ms) found by Schroger and Eimer (1993), although somewhat visible in the 1997 study, was not discussed.
This sort of confusion is expected and unavoidable in the early stages of investigation when a new paradigm is being employed and new ERP components are discovered. What is required now is to thoroughly characterize these components and obtain consensus among different investigators using different approaches, in order to differentiate those components that are characteristic of transient auditory attention in general from components that arise due to subtle variations in stimulus configuration and task instructions.

The experiments presented in this thesis contribute directly to this effort in two important ways. First, they take the investigations of Schröger and Eimer out of the realm of multi-modal stimulation. It is of considerable interest to know if the difference components observed by Schröger and Eimer can be reproduced under very different conditions. Thus, the stimuli employed in this thesis, with the exception of static visual fixation points, are entirely auditory. Second, an underlying goal of the experiments presented here was to clarify the precise topographic distribution of the transient attention difference components. The Schröger and Eimer studies reported both latency and topography differences between the ERP correlates of sustained and transient attention. For example, the earliest transient attention effect (the Nd1) emerged about 50 ms later than the earliest sustained attention effect (the early Nd). Since the early Nd found in sustained attention studies occurred only with high stimulus delivery rates (Naatanen & Michie, 1979), and the stimulus delivery rates used in transient attention experiments must be quite low to allow the subject enough time to orient his or her attention, it is perhaps not surprising that the Nd1 emerges later than the early Nd. What is truly interesting about the Nd1 is that it is maximal at parietal electrodes whereas the early Nd
is usually found to be maximal at the vertex. In this case, it is the topography rather than the latency that proves to be the crucial distinction between ERP correlates of sustained and transient attention. It is thus of the utmost importance to characterize the topography of these components with high spatial resolution. Unfortunately, Schröger and Eimer measured these components at only three electrodes sites (Fz, Cz, Pz). The present studies employ "high-density" ERP techniques using up to 63 different electrode sites to map difference components over the entire scalp. The study described in Chapter Two constitutes the first step in this effort by providing the first high-density investigation of the ERP correlates of transient auditory spatial attention. Chapter Three forms the basis of a functional anatomical approach to understanding these correlates by investigating auditory spatial processing pathway in human cortex. Finally, the analysis presented in Chapter Four takes yet another step beyond the existing low-density studies by employing source analysis to identify the probable anatomical structures in which these ERP correlates of auditory attention are manifested.

Chapter Four is comprised of three experiments aimed at investigating the differences between the goal-driven or "top-down" and the stimulus-driven or "bottom-up" configuration of attention. The experiment presented in Chapter Two makes it clear that the neural response to sensory stimulation can be configured in advance of stimulus onset. At issue in Chapter Four is the manner in which this configuration occurs. This might occur in two different ways. A previous stimulus might set up an "attentional trace" (Naatanen, 1990) that configures the brain to optimally handle subsequent stimuli from the same location. The brain might also be configured in a more abstract goal-driven way to deal with subsequent stimuli that are expected to be at a location other than
the previously stimulated one. In the study presented in Chapter Two, both of these modes of orienting attention could act in concert because no explicit attentional cue was presented to indicate a to-be-attended location. Chapter Four opens with an experiment juxtaposing the ERP evoked by targets when both bottom-up and top-down process can work in concert with the ERP evoked by identical targets in a situation in which top-down and bottom-up processes are contradictory.
CHAPTER TWO: TRANSIENT SPATIAL ATTENTION MODULATES DISTINCT COMPONENTS OF THE AUDITORY ERP

Preface

The experiment presented in Chapter Two has been published as Tata, Prime, McDonald, & Ward (2001). This study extended the previous work by Schröger (1993) and Schröger & Eimer (1993; 1997) in two important ways. First, we determined that the ERP correlates of transient attention identified in previous studies are not confined to the specific visual-cue/auditory target type of paradigm used previously. We used an auditory target-target paradigm in which participants simply performed a spatial discrimination on a series of randomly located targets. This paradigm differs from previous investigations in that all stimuli were auditory. The target-target paradigm also eliminated the need for an explicit cue and thus allowed us to demonstrate ERP modulations consistent with previous reports yet under substantially different conditions of attention orienting. Second, this study was the first to obtain high-density topographic data regarding the scalp distributions of these newly discovered ERP correlates of transient auditory attention. This is of particular interest given that the Nd1 modulation, which is the earliest ERP correlate in this transient attention situation, is differentiated from the earliest correlates of sustained attention primarily by its topographic distribution. To anticipate, we found that the Nd1 has a pronounced posterior focus, well posterior to the central focus of the early Nd typically found in sustained attention studies.

Introduction

The neural processes involved in selective attention have been studied by measuring scalp-recorded electrical activity (event-related potentials or ERPs) in
response to attended and unattended sounds. Many ERP studies employed the sustained-attention paradigm, in which participants continuously monitored sounds possessing a specific feature (e.g., at a particular location or of a particular frequency) and ignored sounds possessing other features (Hansen & Hillyard, 1980; Hillyard, Hink, Schwent, & Picton, 1973; Näätänen, Gaillard, & Mantysalo, 1978; Teder-Sälejärvi & Hillyard, 1998); for reviews see Hillyard, Vogel & Luck, 1999; Näätänen, 1992). Sounds possessing the to-be-attended feature generally gave rise to more negative ERP deflections than sounds lacking the to-be-attended feature. The earliest portion of this negative difference (Nd) overlapped the N1 component (100-130 ms) and was found to be maximal at central electrodes. A later portion of the Nd was observed in the 150-650 poststimulus time interval and was more frontally distributed. The early Nd appears to reflect neural activity in auditory cortex; whereas the late Nd appears to reflect neural activity in auditory cortex and modality-nonspecific areas of frontal cortex (Woldorff, et al. 1993).

Although we often need to sustain our attention on a single auditory feature for an extended period of time, we also need to re-orient our attention on a moment-by-moment basis in response to changes in the auditory environment. Investigators have found distinct effects of transiently oriented spatial attention on auditory ERPs using the spatial cueing paradigm (Schröger, 1993; Schröger & Eimer, 1993; 1997). On each of several trials, a symbolic cue (an arrow) indicated the to-be-attended ear or loudspeaker and was followed by a target tone at either the validly or invalidly cued location. A comparison of auditory ERPs elicited on valid and invalid trials revealed an Nd (Nd1) in the 140-180 ms latency range that was larger over the parietal scalp (Pz) than over central or frontal sites.
A later Nd (Nd2) was observed in the 200-350 ms latency range that was larger over frontocentral sites (Cz and Fz). The Nd1 appeared to be distinct from the more anteriorly-distributed early Nd that occurs in sustained-attention paradigms. Moreover, the Nd1 was found when participants attended to sounds at a particular location but not when they attended to sounds of a particular frequency (Schröger, 1994). Thus, the Nd1 could reflect an important characteristic of transiently oriented spatial attention.

Here, we investigated the effects of transiently oriented spatial attention on auditory ERPs using a paradigm that was different from the one used previously. In our study, participants responded to sequentially presented target tones in the absence of any instructions or cues to attend to a particular location. Unlike the visual system, the auditory system lacks a central fovea (Buchtel & Butter, 1988). Thus, we hypothesized that auditory attention might not automatically reorient to the point of visual fixation, but would instead be sustained at the location of a peripheral target until the occurrence of the next target. Indeed, prior studies indicated that attention is sustained at the location of an auditory target for over 500 ms (Mondor & Zatorre, 1995) unless a central reorienting event is used to summon attention away from the target location (McDonald & Ward, 1999; Spence & Driver, 1998). Thus, we predicted that participants would respond rapidly to targets appearing at the same location as the immediately preceding target (same-side trials), and more slowly to targets appearing on the opposite side of fixation (opposite-side trials). Importantly, we tested whether the Nd1 and Nd2 would be observed in this paradigm by comparing the ERPs on same-side trials to the ERPs on opposite-side trials. To obtain more precise information about the topography of any
resulting Nds, we recorded ERPs from a high-density electrode array (62 sites). Observations of Nd1 and Nd2 components similar to previous studies would indicate that the parietal Nd1 and fronto-central Nd2 are general phenomena of transient auditory attention, and not specific to the visual-cue/auditory-target paradigm used previously.

**Method**

Fifteen healthy right-handed adults (4 male) participated in the experiment after giving written informed consent. All participants reported normal hearing. Participants sat in a darkened sound-attenuating booth (background noise 35 dB SPL) facing 3 horizontally arranged speakers. The center speaker was located at a distance of 105 cm and the peripheral speakers were located at 33 deg laterally from center. A chin rest stabilized the head and prevented head movements toward peripheral stimuli. Participants were instructed to maintain visual fixation on an LED attached to the center speaker.

Trials began with a brief flicker of the central LED to alert the participant, followed by a random delay of 800-1300 ms. A tone (1kHz, 75 dB SPL, 50 ms duration, 2.5 ms rise/fall time) was then presented at random from one of the three speakers. The task was to press a button if this first tone (T₁) was presented from one of the peripheral speakers and to refrain from pressing the button if T₁ was presented from the central speaker. After a silent response-stimulus interval (620-1120 ms), a second tone (T₂), identical to the first, was then presented at random from one of the three speakers. Participants responded to T₂ as they did to T₁. Response times were measured using a custom I/O board with an interval timer chip. Trials with errors were re-run.

The electroencephalogram (EEG) was recorded from 62 Ag/AgCl electrodes
positioned at standard 10-10 scalp sites (American Electroencephalographic Society, 1994). The electrooculogram (EOG) was recorded bipolarly with electrodes placed beside and below the left eye. Electrode impedances were kept below 5 kΩ. EEG and EOG were amplified with a gain of 20,000 and a bandpass of 0.1-30 Hz (-12 dB/octave; 3 dB attenuation), digitized at a rate of 250 Hz, and stored on disk for off-line averaging. Scalp voltages were referenced to the right mastoid and subsequently digitally re-referenced to averaged mastoids. The University of British Columbia human subjects review committee approved all procedures.

For each participant, ERPs to T2 were averaged in 1,200 ms epochs (beginning 200 ms before stimulus onset) for all combinations of T2 location (left and right) and T1 location (same side and opposite side). The first block of trials served as practice and did not contribute to the averaged ERPs. Eye movement, muscle, and blocking artifact were minimized in the ERP waveform by applying automatic rejection criteria to the EEG for each trial (applied to the EOG channel for eye movements, posterior channels for muscle artifact, and all channels for blocking). The threshold (in A/D converter units) for rejecting artifacts was adjusted by visual inspection of the ERP waveforms. The amplitudes of the ERPs were measured as the differences between the mean voltage within a 100-ms pre-target baseline period and the mean voltage within the 140-200 and 220-260 ms time windows, respectively. These latency windows bracketed the first two peaks in the difference waves and corresponded in latency to the Nd1 and Nd2 found in previous transient spatial attention studies (Schröger, 1993; Schröger & Eimer, 1993; 1997). These mean amplitudes were entered into separate, repeated-measures multivariate analyses of variance (MANOVAs) with Electrode Location (FZ, CZ, POZ)
and $T_1$ Location (same-side, opposite-side) as factors. The data were normalized in order to assess topographical differences in the ERP amplitudes (McCarthy & Wood, 1985).

**Results**

Participants were significantly faster to respond to $T_2$ on same-location trials (425 ms) than on different-location trials (436 ms), one-tailed $t(14) = 2.006$, $p < .03$. Fig. 1 shows two prominent Nds. The first (Nd1) peaked at approximately 175 ms, and the second (Nd2) peaked at approximately 250 ms. The Nd1 was largest at POz, which led to a statistically significant interaction between electrode location and $T_1$ location in the 140-200 ms latency window, $F(2,28) = 6.00; p = .007$. The Nd2 was largest at Cz and Fz, which led to a significant interaction between electrode location and $T_1$ location in the 220-260 ms latency window $F(2,28) = 6.57; p = .004$. As shown in Fig 2, the Nd1 was distributed over the posterior scalp, whereas the Nd2 was distributed over the fronto-central scalp. Close inspection of the difference waves in Fig 1 reveals the possible contribution of a third component located more posteriorly and centered at 300 ms latency although no significant interaction between electrode location and $T_1$ location existed for the 280 – 320 ms latency interval $F(2,28) = 1.39; p = .27$. The entire dataset appears in Appendix A.
Figure 1. Grand-Averaged Waveforms and Difference Waves. A) Grand average ERP waveforms for fifteen participants for same-side (dashed) and opposite-side (solid) stimuli at three representative electrode sites. B) Grand average difference waves (same-side minus opposite-side) for the same participants with the Nd1 and Nd2 latency windows indicated.
Figure 1 Isopotential voltage maps of the topographic distributions A) for the Nd1 component during the 120-200 ms interval and B) for the Nd2 component during the 220-260 ms interval. These maps were generated by computing the mean amplitude of the difference wave at 62 sites.

**Discussion**

The main goals of this study were to investigate the effects of transient spatial attention on neural processing of sound and to determine whether observers momentarily sustain their attention at the location of a behaviorally relevant sound after responding to it. By recording ERPs using a high-density electrode array, we were able to study both the temporal and spatial characteristics of transient spatial attention effects in audition.

As in recent spatial cueing experiments (Schröger, 1993; Schröger & Eimer, 1993; 1997), we did not find any evidence for an early Nd over the fronto-central scalp. At CZ, the T2-
elicited ERPs on same-side and opposite-side trials progress in synchrony throughout the P1 and N1 deflections and begin to diverge only at the onset of the P2 component, approximately 175 ms after stimulus onset. The early modulations of the ERP due to sustained attention are thought to reflect an early selection process; thus the absence of a early, fronto-central Nd in this and other transient auditory attention studies indicates that the configuration of a low-level sensory filter (Hansen & Hillyard, 1980; Hillyard, et al. 1973; Hillyard, et al. 1999; Woldorff, et al. ) or attentional trace (Näätänen, et al. 1978; Näätänen, 1992) is relatively slow and requires more time than was provided by the brief interstimulus interval in our paradigm. This notion is consistent with reports that the early Nd is not apparent during the first 30–45 seconds of a block of sustained attention trials (Donald & Young, 1982; Hansen & Hillyard, 1988).

Transient auditory attention did produce clear modulations of the ERP waveforms in the present study. Despite substantial differences in methodology, the Nd waves found here closely resembled those found in earlier spatial cueing studies (Schröger, 1993; Schröger, 1994; Schröger & Eimer, 1993; 1997). Both approaches yielded a posterior Nd1 in the 120 to 200 ms latency window followed by a larger, fronto-central Nd2 in the 200 to 300 ms latency window. It is unlikely that these differences were due to refractoriness of sensory neurons given that more than 1000 ms elapsed between T1 and T2. This strongly suggests that these Nd components are representative of transient auditory attention in general and are not restricted to a specific paradigm or methodology.

Schröger and Eimer (1997) suggested that the Nd1 might represent an intermediate level of selection that involves processes concerned with the spatial location of stimuli. However, the functional significance of the Nd1 is still largely unknown. The
posterior distribution of this component suggests that it may result from the modulation of sensorineural activity in the parietal cortex. The parietal cortex, specifically the inferior parietal lobule, is thought to be involved in processing of spatial auditory information in humans (Weeks, et al., 1999). The Nd1 might be a consequence of the attentional modulation of spatially tuned auditory neurons in the inferior parietal lobule, neurons that are critical to localizing the target in space. If so, the Nd1 might be expected to become enhanced with repetitive stimulation (i.e. a target preceded by several targets at the same location). Alternatively, the Nd1 might reflect the modulation or recruitment of neurons in the parietal cortex that are involved in the reorienting of spatial auditory attention when the target occurs at an unattended location. This is consistent with the observation that the Nd1 arises principally on invalid trials rather than valid trials in spatial cueing experiments (Schröger & Eimer, 1997). It is also consistent with evidence that neurons in the Lateral Intraparietal Sulcus (area LIP) of macaques respond to auditory stimuli at a median latency of 155 ms (Mazzoni, et al., 1988), but only when that stimulus elicits an overt orienting response (Linden, Grunewald & Andersen, 1999). According to this view the Nd1 would not reflect a consequence of attentional selection, but instead would be a correlate of the selection mechanism itself.

In contrast to the differences found here between transient and sustained attention at short ERP latencies, the Nd2 was similar in latency and scalp distribution to the late Nd observed in sustained attention studies. This may represent a convergence of the neural processes underlying these two modes of attention. However, the later Nd observed here is likely to be comprised of multiple generators (both frontal and parietal). The functional correlates of these components remain to be investigated.
**Conclusion**

Selective attention influences the perception of and neural responses to auditory stimuli, whether it is sustained at one location or shifted between locations on a trial-by-trial basis. There are, however, substantial differences between the electrophysiological underpinnings of these two operating modes of attention, as evidenced by the differential effects on auditory ERPs. Here, we demonstrated that transiently oriented attention has a robust effect on auditory ERPs even in the absence of attentional instructions or cues. Of considerable interest to further explorations of transient auditory attention will be the involvement of parietal cortex, possibly playing a role in the orienting of spatial auditory attention.
CHAPTER THREE: AN AUDITORY “WHERE” PATHWAY FOR PROCESSING SPATIAL INFORMATION IN HUMAN CORTEX

Preface

In Chapter Two it was suggested that the Nd1 ERP modulation associated with transient spatial auditory attention probably arises in parietal rather than primary auditory cortex. This suggestion was based on two main points: First, the topographic distribution of the Nd1 was considerably more posterior than that of the early Nd associated with sustained attention, which is believed to arise in primary or adjacent auditory cortex. Second, previous investigations employing functional imaging techniques and single-unit studies of non-human primates have begun to characterize a network of brain structures posterior to the primary auditory cortex that seem to be engaged in spatial aspects of auditory perception. These investigations have converged on a model of the auditory system in which spatial and non-spatial information are segregated into dedicated “where” and “what” processing pathways. The topographic distribution of attention-related Nds will be taken up again in Chapter Four. Chapter Three, currently under editorial review (Tata & Ward, 2003a), takes a step back and asks whether there is sufficient evidence for a posterior “where” pathway in the human auditory system. To provide critical converging evidence on this point, we have taken the novel approach of applying source analysis in an event-related potential (ERP) investigation of the functional anatomy of the human auditory system. Specifically, we investigated whether an automatic spatial discrimination of incoming auditory information would generate an ERP component that could be reliably localized to this putative posterior “where” pathway. This finding, in addition to supporting the functional segregation model, would also demonstrate in principle that event-related
electrical activity within this pathway can be characterized using ERP techniques. It is upon the results presented here that Chapter Four bases an effort to localize the Nd1 correlates of spatial attention to spatially responsive regions of the auditory system.

**Introduction**

A foundational goal in the field of cognitive neuroscience is to understand how sensory information is represented and processed in the human brain. An important general principle is that different types of information are encoded and processed by distinct populations of neurons. For example, the visual system is known to encode spatial and figural information in anatomically distinct pathways (DeYoe & Van Essen, 1988; Zeki, 1983). This dissociation suggests a more general anatomical and functional segregation of spatial and non-spatial information into putative ventral “what” and dorsal “where” systems (Ungerleider & Mishkin, 1982); the former being specialized for identifying visual stimuli and the later being specialized for locating and/or interacting (Goodale & Milner, 1992) with objects in visual space.

Much less is known regarding the functional organization of the human auditory system and most of what is known has been inferred from electrophysiological recordings in non-human primates. In monkeys, several auditory areas on the supratemporal plane are organized tonotopically (Merzenich & Brugge, 1973; Rauschecker, Tian & Hauser, 1995), but other more caudal regions contain cells that are predominantly tuned to the location of a sound source (Leinonen, Hyvarinen & Sovijarvi, 1980; Tian, Reser, Durham, Kustov & Rauschecker, 2001). This differential representation of spectral and spatial information in separate regions of monkey auditory cortex suggests that, like the visual system, the auditory system is comprised of anatomically distinct anterior “what”
and posterior "where" pathways (Rauschecker & Tian, 2000). The existence of a "where" pathway specialized for processing auditory location, however, has been the subject of controversy (Belin & Zatorre, 2000).

The possibility that functional segregation might exist in humans is supported indirectly by the double-dissociation of localization and identification deficits following cortical lesions (Clarke, et al., 2002), and by functional imaging studies indicating increased blood flow in the parietal cortex, usually in the inferior parietal lobule (IPL), during auditory spatial localization tasks (Alain, Arnott, Hevenor, Graham, & Grady, 2001; Bushara, et al., 1999; Weeks, et al., 1999; Zatorre, Bouffard, Ahad, & Belin, 2002) and the perception of auditory motion (Griffiths, Green, Rees & Rees, 2000; Lewis, Beauchamp & De Yoe, 2000). These later imaging studies have been inconclusive however, since the implicated regions of parietal cortex are also putatively involved in the orienting of spatial attention (Corbetta, Miezin, Shulman & Petersen, 1993). Indeed, Zatorre and colleagues found no differential activation attributable solely to the encoding and processing of auditory location unless participants were actively engaged in a localization task.

Unlike functional brain-imaging techniques that measure cortical activity indirectly via changes in blood flow, electroencephalography (EEG) directly and non-invasively measures the electric field generated by cortical pyramidal neurons. The event-related potential (ERP) is a series of negative and positive deflections of the EEG that are time-locked to a sensory event, such as the onset of an acoustic stimulus. The modulation of the ERP by aspects of a participant's task such as memory retrieval or the focusing of attention often provides clues as to the behavior of the neural populations that
accomplish these operations. An initial indication that spatial and frequency information might be represented in "different cortical fields" in humans was provided in a study of differential modulation of the ERP due to focusing attention on spatial or frequency information in an ongoing auditory stream (Woods, Alho & Algazi, 1994). This study found that the distribution of ERP modulations across the scalp depended on the type of information to which the listener was attending. Unfortunately, because of spatial imprecision in simple topographic analysis of the ERP scalp distribution, it is difficult to identify the actual cortical structures that might have been differentially modulated by attention to spatial and non-spatial features. What is presently needed to extend the functional segregation hypothesis to human cortex is direct and spatially precise evidence of the encoding of spatial acoustic information in regions of the auditory system posterior to primary auditory cortex. Here we report the first observation of event-related electrical activity generated by neurons in this putative "where" auditory pathway in response to the spatial information content of an auditory stimulus. This observation is based on source analysis of the well-known component of the auditory ERP called the mismatch-negativity (MMN).

The MMN is elicited when an unusual stimulus (a deviant) occurs among repetitive (standard) stimuli (see Näätänen, 1992 and Picton, Alain, Otten, Ritter, and Achim, 2000 for a review). It usually consists of a single peak that is maximal at fronto-central electrodes although some evidence suggests multiple peaks (Giard, Perrin, Pernier & Bouchet, 1990) and a right hemisphere predominance (Paavilainen, Alho, Reinikainen, Sams & Näätänen, 1991). For several reasons, this ERP component offers an ideal tool to investigate the functional layout of the human auditory system. First, the MMN is
automatically generated in response to deviant stimuli and is largely independent of any task the listener may be performing (Giard, et al. 1990; Näätänen, 1992). Second, the underlying neural processes that generate the MMN to *non-spatial* deviants (i.e. pitch, duration, intensity, etc.) have been well studied (Hari, et al. 1984; Lavänen, Hari, McEvoy & Sams, 1993; Sams, Kaukoranta, Hämäläinen & Näätänen, 1991). These studies have used the source of the negative-going N1 ERP component as a landmark since it is believed to be generated by primary or adjacent auditory cortex (Scherg, Vajsar & Picton, 1989) during the early stages of response to acoustic stimuli. Each of these studies found generators of the MMNs elicited by non-spatial deviants on the supratemporal plane *anterior* to the N1 source. The predominant view is that the MMN reflects a mismatch between the features of the most recent stimulus and the encoded features of previous stimuli (Giard, et al. 1990; Näätänen, 1988). Thus the MMN is thought to be generated by regions of the cortex that encode the deviant feature (i.e. pitch, duration, etc.). The localization of the non-spatial MMN anterior to primary auditory cortex is therefore consistent with the hypothesis of an anterior pathway specialized for non-spatial information, however this important evidence has, to our knowledge, gone unnoticed in the literature. It follows that, whereas the MMN responses to pitch, duration, or intensity deviants are generated in the “what” pathway anterior to the generator of the N1, the MMN elicited by a deviant that differs from the standards purely in its spatial location should be generated in the putative “where” pathway, *posterior* to the generator of the N1.
**Methods**

**Participants**

Fifteen undergraduate students (2 left-handed, 6 males) at the University of British Columbia were paid to participate in the study after giving informed consent. All listeners reported normal hearing. Data from one listener was rejected because of excessive eye movement during EEG recording. All procedures were approved by the University of British Columbia Human Subjects Ethics Review Committee.

**Stimuli and Procedure**

Listeners sat in a darkened sound-attenuating booth (background noise about 35 dB SPL) facing 3 horizontally arranged speakers, marked by steady LEDs. The center speaker was located at a distance of 105 cm and the peripheral speakers were located at 35 deg laterally from center. Three types of stimuli were possible: targets, standards, and deviants. Targets consisted of two 30 ms bursts of broad-band noise (63 dBA SPL) separated in time by either a 20 ms or a 50 ms gap of silence. The listener’s task was to indicate the duration of the silent gap by pressing one of two buttons. The target always occurred at the center speaker and listeners were encouraged to ignore peripheral stimuli.

Two 40-target practice blocks in which no data were collected acquainted the listeners with this task. Standards and deviants consisted of 20 ms tone pips (1000 Hz, 70 dBA SPL, 5 ms rise/fall time) presented from the peripheral speakers. Within a block, standards were always presented from one side and deviants from the opposite side, and the side of presentation of standards and deviants was randomized across blocks.

Listeners completed 15 blocks of trials; 8 listeners completed 7 left-deviant blocks and 8 right-deviant blocks, and 6 listeners completed 8 right-deviant blocks and 7 left-deviant blocks.
Each block progressed as a stream of standards, deviants, and targets with a random (rectangular distribution) inter-stimulus interval (ISI) of 400 – 800 ms. So that no unusually long gaps of silence occurred during the period following a target but prior to a response, additional standards were presented during this period with the same 400 – 800 ms ISI. Each block contained 20 deviants and 40 targets, but a variable number of standards (minimum 180) depending on the time taken to respond to targets (typically between 40 and 80 extra standards per block). Thus the probability of a standard was at least .75 and the probability of a deviant was at most .08. Blocks took approximately 2.5 minutes and were separated by brief rest breaks.

**Electrophysiological Recording**

The electroencephalogram (EEG) was recorded at 63 scalp sites with Ag/AgCl electrodes (59 electrodes in the standard 10-10 system plus the left mastoid (A1) and three electrodes (S11, S1Z, S12) placed inferior to the inion) (American Encephalographic Society). Voltages were referenced to the right mastoid (A2) during recording and digitally re-referenced to averaged mastoids for statistical analysis. The electrooculogram was recorded with electrodes placed beside and below the left eye and referenced to each other. Electrode impedances were kept below 30 kΩ. The EEG was amplified with a gain of 20,000, bandpass filtered (0.1 – 100 Hz; -12 dB/octave; 3 dB attenuation), and digitized at 250 Hz. The EOG was recorded likewise but with a bandpass filter of 0.1 – 30 Hz. The event-related potential (ERP) was computed separately for each listener by averaging the voltages (time-locked to the onset of the stimulus of interest) during a 3000 ms interval (1500 ms pre-stimulus period) using a 200 ms pre-stimulus baseline. This extended interval was used so that adjacent events could
be observed if necessary. Before averaging, an automated artifact rejection protocol discarded any stimulus event accompanied by an eye movement, blink, or muscle artifact during the 3000 ms ERP window. Data from one listener were rejected entirely because more than 50% of stimuli in at least one condition had been rejected. ERPs elicited by left and right standards and deviants were computed independently. For topographic and dipole analysis the mismatch negativity (MMN) was computed by subtracting the ERP elicited by standards from the ERP elicited by deviants. Components of the MMN were taken to be topographic foci at or near the peaks of the resulting difference wave during the latency window spanning 100 to 200 ms post-stimulus. ERPs to standards and deviants for each listener were entered into a 2 electrode (FC3, FC4) x 2 Field of Presentation (left, right) x 2 Condition (standard, deviant) repeated measures Analysis of Variance (ANOVA).

**Topographic and Dipole Source Analysis**

The underlying neural generator of the target-stimulus N1 and the early and late peaks of the MMN were modeled as equivalent dipole sources using the Advanced Source Analysis software package (ANT Software BV, Enschede, The Netherlands). This software models equivalent dipoles in a realistic head model based on the Montreal Neurological Institute (MNI) representative brain. The software projects electrodes (a subset of 55) onto this head model by matching each to the closest corresponding point on the scalp. Isopotential contour maps were computed for left-deviant and right-deviant MMNs as well as the N1 at each sample in the voltage time series between 100 and 200 ms by fitting a spline interpolation. The N1 peak was identified at 116 ms post-stimulus latency. Two subcomponents of the MMN were identified: an early contralateral peak
(160 ms for left deviants, 156 ms for right deviants) and a later fronto-central peak (196 ms for both left and right deviants). Dipoles were fitted separately within a time window spanning one sample (4 ms) on either side of these peaks.

For the early phase of the MMN, a single dipole was “seeded” in the auditory cortex (Heschl’s gyrus) (Rademach, et al., 2001; Talairach & Tournoux, 1988) contralateral to the stimuli (Talairach coordinates +/- 42, 21, 11) and allowed to fit with no constraints. The central distribution of the late phase of the MMN and the target-stimulus N1 required bilaterally symmetric dipoles with spatial constraints (Scherg et al., 1989). Our main interest was in the relative anterior – posterior position of each dipole. Thus these peaks were fitted by constraining initial seeds in Heschl’s gyrus to be fixed on the medial – lateral axis (x axis) and symmetric about the sagittal plane.

**Behavioral Analysis**

Response time and accuracy data were collected during the ERP sessions described above and during a second behavioral experiment. Responses were measured only on artifact-free trials. Differences in performance between targets preceded by standards and targets preceded by deviants were assessed with paired-sample t-tests. In the second behavioral experiment, thirty-six listeners participated in this experiment after giving informed consent. None had participated in the previous ERP session. The EOG was recorded as described above so that the same artifact rejection could be applied. Six participants were excluded due to excessive artifacts. Listeners completed 21 blocks as described above including a practice block. The interstimulus intervals were randomly either 100 ms, 400 ms, or 800 ms. Response time and accuracy data were analyzed with a 3 (100, 400, 800 ms ISI) x 2 (standard, deviant) repeated measures ANOVA.
**Results**

The MMN is typically identified as a negative deflection of the deviant stimulus ERP relative to the standard stimulus ERP in the 100 to 200 ms post-stimulus latency range. ERPs elicited by standards and deviants at selected electrodes are presented separately for left and right stimuli in Fig. 3, along with the ERP elicited by the central target. Isopotential voltage maps (Fig. 3) and equivalent source dipoles (Fig. 4) were computed for the MMN and N1 components. We observed a robust MMN contralateral to the deviant between 100 and 200 ms post-stimulus [electrode (FC3, FC4) x stimulus side (left, right) x condition (standard, deviant) interaction: F1,13 = 14.5; p = 0.002]. As is typically found with the MMN, the polarity reversed (became positive) at inferior temporal sites near the mastoid. The MMN was clearly biphasic with a strongly lateralized early phase peaking at 160 ms for left deviants and 156 ms for right deviants followed by a later fronto-central phase peaking at 196 ms for deviants from either side. The entire dataset appears in Appendix B.
Figure 1.

Figure 3. Comparison of mismatch negativities (MMN) for left and right deviants. (A) Event-related potential (ERP) waveforms elicited by left and right standards (red) and spatial deviants (blue) at selected electrode sites. (B) Isopotential voltage maps indicating the contralateral scalp distribution of the early phase of the MMN for left and right stimuli (maximal at 160 ms and 156 ms, respectively). The MMN is computed by separately subtracting the ERP elicited by standards from the ERP elicited by deviants at each electrode. In each pair of heads, the outermost models are oriented facing out of the page and the inner models face into the page at about 45 deg to the left or right (C) Isopotential voltage map of the late phase of the MMN (maximal at 196 ms for both left and right stimuli). (D) ERP elicited by the central target stimulus as recorded at the vertex (CZ) and the corresponding isopotential voltage map of the N1 component at 116 ms post-stimulus latency.
To identify the cortical areas most likely to have generated these components, we fitted equivalent source dipoles separately for the early and late phases of the MMN as well as for the robust N1 generated by target stimuli. Since the early-phase MMN was clearly focused over the hemisphere contralateral to the stimuli, we seeded the dipole analysis procedure with a single dipole in contralateral Heschl’s gyrus (Rademach, et al., 2001; Talairach & Tournoux, 1988). For left and right deviants, we found dipoles medial and posterior to the initial seed explaining 94.7% and 96.4% of the variability in the scalp distribution, respectively (Talairach coordinates for left deviants: 26, -48, 15; right deviants: -36, -43, 5) (Fig. 4). The central distribution of the late-phase MMN suggests bilateral generators and thus required a more complex fitting procedure (see Methods). Bilaterally-symmetric dipoles of similar magnitude located near Heschl’s gyrus (Talairach coordinates: +/- 42, 9,10 for left stimuli and +/- 42, 9, 31 for right stimuli) accounted for 92.8% and 86.9% of the late-phase MMN scalp distributions for left and right deviants, respectively.

The stereotactic coordinates of the early-phase MMN generators suggest a source in posterior temporal cortex near the temporo-parietal junction (TPJ). The spatial precision of these fits, however, depends on the co-registration between the ERP dataset and the realistic head model used by the source analysis software. To identify a landmark intrinsic to the ERP dataset itself, we fitted dipoles to the target-stimulus N1 peak. Like the late-phase MMN, the N1 was best fitted (94.4%) by bilaterally symmetric dipoles near Heschl’s gyrus (Talairach coordinates +/- 42, 0, 17).
Figure 4 Relative dipole locations for left and right deviants. (A) Relative positions of the equivalent source dipoles that generated the early phase (red) and late phase (blue) of the MMN, superimposed on the Montreal Neurological Institute representative brain. As a landmark, the generator of the N1 component (green) in auditory cortex has also been plotted. Each arrow represents the location and orientation of an equivalent dipole. This axial structural MRI is portrayed at the plane of the early-phase MMN generator. (B) The same dipoles plotted on the corresponding saggital slice. (C) The same dipoles rendered within the realistic head model used by the software. Note that a single contralateral generator sufficiently explained the early phase of the MMN whereas bilaterally symmetric generators explained the N1 and the late phase of the MMN. The ipsilateral counterparts of these bilateral dipoles are not visible in these figures. Contours represent isopotential voltage lines for the early phase of the MMN as in Fig. 1 (B).
The principal difficulty in interpreting recent studies of auditory spatial processing has been a confounding of spatial processing with the orienting of spatial attention. Our study eliminated this confound by including central auditory targets to which listeners were instructed to attended. Listeners performed a non-spatial (duration) discrimination. Our behavioral data suggest that listeners did maintain their attention at the center and did not orient to the location of the deviants. Listeners were not significantly slower or less accurate in responding to targets preceded by deviants (840 ms mean response time (RT) and 86% mean accuracy) than to targets preceded by standards (832 ms mean RT and 88 % mean accuracy) [difference in RT: t(13) = -0.773, p = 0.46; difference in accuracy: t(13) = 1.4, p = 0.18]. Since the 400 to 800 ms ISI between deviants and targets might have allowed listeners to reflexively orient to the peripheral deviant and then voluntarily orient back to the central speaker before the target occurred, we conducted an additional behavioral experiment with 100, 400, or 800 ms ISIs and found no effect of the preceding stimulus (standard or deviant) and no interaction between the preceding stimulus and the ISI for either the RT or accuracy [p > 0.1 in all cases].

Discussion
In contrast to the anterior pitch, duration, and intensity MMN generators identified by previous studies, the generators of the early-phase of the spatial MMN were approximately 4.8 and 4.3 cm posterior to the N1 generator, for left and right deviants respectively. Ideally, it would be possible to apply a statistical test to assess the reliability of this difference in location. One approach might be to model and compare the N1 and the MMN separately on a subject-by-subject basis. This approach requires very low
within-subject variability, however, and was not possible with the present data. Thus the area of cortex most likely to be responsible for generating this early phase of the MMN was posterior to primary auditory cortex and at or near the TPJ. Since standards and deviants differed solely in their spatial location, we conclude that this early-phase MMN represents activity in a putative “where” pathway dedicated to processing auditory spatial information. It is worth noting here that lesions to the TPJ have been shown to reduce the amplitude of the MMN elicited by a frequency deviant when that deviant was contralateral to the lesion (Alain, Woods, & Knight, 1998). Further investigation will be necessary to determine the role of this region in generating a mismatch response to other features.

Our findings are consistent with proposals that the MMN is comprised of an early modality-specific component followed by a later modality-independent component (Giard, et al., 1990; Näätänen & Michie, 1979). Direct support of that theory, however, has been difficult to obtain using non-spatial deviants, possibly because of spatial and/or temporal overlap of the constituent generators (Giard et al.). Presumably both phases of the MMN to such deviants are generated near each other, slightly anterior to primary auditory cortex (Hari, et al., 1984; Levänen, et al., 1993; Sams, et al., 1991) and are therefore difficult to distinguish. The fact that in this study the early-phase spatial MMN generators are approximately 5.7 and 5.2 cm posterior to the late-phase spatial MMN generators for left and right deviants, respectively, probably accounts for the clear differences we found in the scalp distributions of the early and late phases in this study. These two phases can be differentiated also by the fact that the earlier phase is strongly lateralized and can be accounted for by a single contralateral dipole, whereas the later
phase is less lateralized and requires bilaterally symmetric dipoles to obtain a plausible fit. Furthermore, it is possible that previous failures to differentiate two separate phases of the non-spatial MMN were due to temporal overlap of these components. It may be necessary to use the fine-grained (sample-by-sample) analysis of the dataset that we employed in the present study in order to differentiate these nearly simultaneous components. This may explain why a previous investigation of the spatial MMN (Takegata, Huotilainen, Rinne, Näätänen & Winkler, 2001) identified only a single bilateral source anterior to the N1 component.

The MMN has been interpreted as reflecting pre-attentional processing in a “change detection” system (Giard et al., 1990; Näätänen, 1988). More specifically, Giard and colleagues suggested that the early phase of the MMN might represent a “call” to an attention orienting mechanism that is followed by an orienting response reflected in the later frontal phase of the MMN. This hypothesis predicts that targets following deviants should be responded to more slowly and less accurately than targets following standards, since attention is presumably briefly oriented away from the target source. Since we observed a robust later frontal phase of the MMN without concomitant behavioral effects of distraction, we suggest the alternative hypothesis that the early MMN represents a trigger for a reflexive attentional shift, while the later frontal phase represents an active process that cancels or suppresses that shift. It is possible however that spatial deviants might cause a reflexive reconfiguration of the neural mechanisms within a system dedicated to spatial processing without affecting the non-spatial duration discrimination that the listeners were performing in this study. Further investigation of the neural correlates of reflexive attention will elucidate the cognitive operations reflected by the
separate components of the spatial MMN. It is also possible that, despite instructions to focus at the center, listeners were compelled to attend to the location of standard stimuli. If true, one would expect a reduced amplitude of target-elicited ERP at early latencies. However, the N1 elicited by the target exceeded both the N1 elicited by the standard and the N1 elicited by deviants. There is consequently both behavioral and electrophysiological evidence indicating that listeners were maintaining attention at the center speaker.

In addition to providing evidence for an auditory pathway in human cortex dedicated to processing spatial information, the present results provide clear evidence for lateralization of auditory processing under free-field listening conditions. Previous studies have found stronger contralateral magnetic responses using magnetoencephalography (MEG) to stimuli presented monaurally through headphones (Woldorff, et al. 1999), but no clear pattern of lateralization was found when stimuli were delivered via external speakers. The very low residual variance of the dipole fits for the early-phase MMN suggests that a single contralateral dipole generated this ERP component (although we cannot rule out the secondary contribution of an ipsilateral dipole). The evidence therefore suggests that the human auditory system contains an anatomically distinct pathway specialized for the processing of spatial information. Furthermore, it is probable that, as in the visual system, this pathway is organized to represent spatial information in the hemisphere contralateral to the stimulus itself. Future investigations will determine how this specialized pathway interacts with the putative anterior non-spatial auditory pathway (and probably sub-cortical structures) to generate the seamless percept of an extrinsically localized and identifiable sound.
CHAPTER FOUR: TOP-DOWN AND BOTTOM-UP ATTENTION DIFFERENTIALLY MODULATE A POSTERIOR AUDITORY "WHERE" PATHWAY

Preface

The investigations reported in Chapter Two and Chapter Three were motivated by two lines of questioning: what is the functional anatomy underlying transient spatial auditory attention, and are the associated ERP modulations concomitants of spatial auditory attention in general or are they specific to the nature of the task in which the listener is engaged? In Chapter Two it was demonstrated that two pronounced negative deflections, the Nd1 and Nd2, accompanied behavioral facilitation in an auditory target-target orienting paradigm. Although the scalp distribution of the Nd1 was clearly differentiable from that of the sustained-attention early Nd, it was possible only to speculate that the underlying generator might be among dedicated spatially responsive auditory areas. A more careful source analysis was called for in order to step beyond that speculation. Chapter Three provided the basis for that source analysis by corroborating the existence of a putative spatial processing pathway and demonstrating the possibility of recording ERP signals from that pathway. The present chapter, currently under editorial review (Tata & Ward, 2003b), tests the hypothesis that the Nd1 is generated within the putative “where” pathway by undertaking the first source analysis of this ERP modulation.

The experiment reported in Chapter Two demonstrated that predictable attention-related negative ERP modulations arose outside of the visual-cue/auditory-target paradigm used previously by Schröger (1993) and Schröger & Eimer (1993; 1997). The study did not, however, consider the relationship between the way in which attention was
oriented and the subsequent ERP correlates. Since the first target in a pair was
unpredictive of the location of the second target, and since listeners were given no
explicit instructions as to where they should orient their attention, we cannot know
whether the negative deflections observed were a consequence of voluntarily maintaining
attentional focus at the location of the first target, or whether they reflect a bottom-up
reconfiguration of the auditory system as a response to the previous target. This
observation highlights an assumption that has been implicit in the several studies of
transient auditory attention: the assumption that attention acts like an indivisible
“spotlight” that enhances processing at the selected location to the detriment of
information at other locations. In the present chapter we consider whether such a
spotlight metaphor describes the behavior of auditory spatial attention and whether the
Nd modulations previously thought to be invariable concomitants of focused attention are
indeed tightly linked to the locus of voluntarily focused attention.

**Introduction**

All organisms use sensory information to guide behavior. Humans, like other
organisms, have evolved mechanisms to select important information from a noisy
background of stimulation – mechanisms to which we ascribe the umbrella term *selective
attention*. A wealth of psychological investigation has revealed that, regardless of
sensory modality, attended and unattended information is handled differently – attended
information is typically responded to more quickly and accurately (eg. Broadbent, 1958;
Posner, 1978), is unaffected by interference from concurrent competing information (Di
Lollo, Enns & Rensink, 2000; Tata, 2002), and is more likely to be included in
consciousness (Mack & Rock, 1998; Rensink, Regan, & Clark, 1997). Evidently a
reconfiguration of perceptual and/or cognitive systems leads to enhanced processing in a selected information channel. The “spotlight of attention” is a popular metaphor used to describe enhanced processing of visual information from an attended spatial location, although “directional microphone” is more appropriate for auditory spatial attention, with which this article is concerned. Regardless of the modality in which attention acts, however, elucidation of its underlying neural mechanisms remains a foundational goal of cognitive neuroscience.

Modulation of cortical processes by auditory spatial attention already has been demonstrated in converging paradigms. For example, selective listening to one of two spatially distinct streams of sounds increased firing rates of cells in monkey auditory cortex as measured by single-unit recording (Benson & Hienz, 1978), enhanced regional cerebral blood flow in human auditory and frontal cortices as measured by positron emission tomography (Alho, et al. 1999), and modulated the response of pyramidal cells to attended versus unattended sounds in humans as measured by electroencephalography (EEG) (Hillyard, Hink, Schwent, & Picton, 1973; Näätänen, 1982).

Of the several approaches employed to investigate the neural correlates of selective attention, the human EEG has been investigated in the greatest detail, typically by comparing event-related potentials (ERPs) – stimulus-locked averages of the EEG – elicited by attended and unattended sounds. Sustained focusing of attention at one location or frequency facilitates behavioral responses to attended sounds relative to unattended sounds. Furthermore, this sustained selection generates deflections of the ERP elicited by attended stimuli beginning as early as 20 to 50 ms post-stimulus (Woldorff, Hansen, & Hillyard, 1987), with a pronounced negative-going deflection at
about the same latency as the N1 component (about 100 ms post-stimulus latency) (Hillyard, Hink, Schwent, & Picton, 1973; Näätänen, 1982). This ERP modulation, termed the “early negative difference” (early Nd) or “processing negativity”, is typically maximal at central electrodes (near CZ) and is thought to be generated in auditory cortex on the supratemporal plane, lateral to Heschl’s gyrus (Woldorff, et al. 1993). The early Nd modulation associated with sustained focusing of attention has been interpreted as reflecting a consequence of low-level control of sensory gain or attentional filtering at initial stages of processing (eg Hillyard, Vogel, & Luck, 1999; Woldorff et al. 1993; for a review see Näätänen, 1992).

More recent studies (Schröger, 1993; Schröger & Eimer, 1993, 1997; McDonald, Teder-Salejärvi, Heraldez & Hillyard, 2001; Tata, Prime, McDonald & Ward, 2001) have investigated ERP consequences of orienting auditory attention in space on a moment-to-moment basis. Using common cue-target or target-target paradigms in which attention is oriented according to a symbolic cue or the location of a previous stimulus, these studies revealed at least two, but probably three, prominent negative modulations of the ERP elicited by attended relative to unattended sounds. These modulations can be distinguished by their post-stimulus latencies and their distribution across the scalp: a posterior component (the Nd1) arises between 120 and 200 ms post-stimulus, a more central component (the Nd2) is maximal at about 200 ms post-stimulus, and a fronto-central component (the Nd3) arises between 250 and 350 ms. Importantly, the earliest ERP modulation due to transient attention (the Nd1) differs from the early Nd that arises in sustained attention paradigms in both its latency and its distribution across the scalp.
Whereas the early Nd arises at about 100 ms and is maximal at central scalp sites, the Nd1 typically occurs several tens of milliseconds later and is maximal at posterior sites.

The Nd1 modulation is thought to reflect the modified behavior of spatially tuned auditory neurons (Schröger & Eimer, 1997; Tata, Prime, McDonald & Ward, 2001). Furthermore, based on the result of a high-density mapping of the Nd1 scalp distribution, Tata et al. proposed that, unlike the sustained-attention early Nd, the Nd1 probably arises in parietal rather than primary auditory cortex. The temporo-parietal junction (TPJ) and Inferior Parietal Lobule (IPL) are regions of particular interest, because any such modulation of cortical activity in these regions due to the focusing of spatial auditory attention would contribute to the nascent effort to dissociate anterior “what” and posterior “where” processing streams in the human auditory system (Rauschecker & Tian, 2000; Romanski, et al., 1999). There is mounting evidence that spatial auditory information is processed in regions of the supratemporal plane posterior to primary auditory cortex (Leinonen, Hyvarinen & Sovijarvi, 1980; Tian, Reser, Durham, Kustov & Rauschecker, 2001) and in the posterior-parietal cortex (PPC), especially in the IPL (Alain, Arnott, Hevenor, Graham, & Grady, 2001; Bushara, et al., 1999, Griffiths, Green, Rees, & Rees, 2000; Lewis, Beauchamp, & DeYoe, 2000; Weeks, et al., 1999, Zatorre, Bouffard, Ahad, & Belin, 2002). In addition, we have recently demonstrated that the well-known ERP component known as the mismatch negativity (MMN) is generated posterior to primary auditory cortex at or near the TPJ, when a mismatch occurs in the spatial locations of repetitive acoustic stimuli (Tata & Ward, 2003). The principle goal of the present study was to precisely characterize the spatial and temporal parameters of the Nd1, Nd2, and Nd3 attention-related modulations with specific emphasis on the Nd1. We sought to test
whether the Nd1 reflects modulation of equivalent source dipoles in specific regions known to be involved in auditory spatial processing. In particular, since the generator of the spatial MMN has been shown to be near the TPJ, we hypothesized that the Nd1 might be a modulation of a generator at or near the same location. If so, this finding would provide further evidence for the existence of a posterior “where” pathway for processing spatial auditory information.

Reconfiguration of perceptual and/or cognitive mechanisms can be implemented by at least two different modes of attending (e.g. Posner & Petersen, 1990). Attention can be oriented by endogenous, or top-down, mechanisms that configure perceptual/cognitive systems according to the explicit expectations and goals of the perceiver. We refer to this as goal-driven attention. Alternatively, perceptual/cognitive systems can be reconfigured in an exogenous or bottom-up manner, as an adjustment to immediately preceding stimuli. Since this bottom-up reconfiguration could in principle include tuning of sensory mechanisms by non-attentional processes (e.g., priming; Posner 1978), we refer to this process inclusively as stimulus-driven reconfiguration. Important differences between these two modes of reconfiguration, potentially related to dissociable “what” and “where” auditory pathways, are evident in previous work (McDonald & Ward, 1999; Spence & Driver, 1994). A valid spatially-informative cue, which causes the listener to voluntarily orient to the cued location, improves performance on spatial tasks such as localization, but also on non-spatial tasks such as pitch discrimination. If the spatial relationship between a cue and a target is random however, so that only stimulus-driven mechanisms are engaged, there is a benefit only for spatial tasks. Stimulus-driven spatial orienting does not improve performance on non-spatial tasks. It
therefore seems likely that goal-driven and stimulus-driven reconfiguration also have different neural correlates, yet no investigation has systematically addressed this question. For example, stimulus-driven processes might influence the subsequent behavior of "where" pathway neurons independent of goal-driven processes. Goal-driven attention on the other hand, might involve more complex "between-stream" reconfiguration. This view predicts that goal-driven and stimulus-driven reconfiguration would have overlapping behavioral and ERP effects when they were aligned to the same location, but dissociable effects when engaged at different locations.

The "spotlight of attention" analogy has proven to be a useful first approximation of the operation of visual attention (Posner, 1980; see also Treisman, 1964; Eriksen & Yeh, 1985 for examples of alternative models). This conceptualization has also been implicit in investigations of spatial auditory attention. In this view, the behavioral facilitation and concomitant ERP modulations (such as the early Nd in sustained-attention paradigms and the Nd1, Nd2, and Nd3 in transient-attention paradigms) are linked to the location at which the spotlight is engaged. Put another way, the focusing of attention improves responses to stimuli occurring at the attended location and the ERPs elicited by those stimuli reflect the neural correlates of that facilitation. The strong interpretation implicit in this view is that the ERP correlates and the behavioral consequences are causally related. This simple model predicts that ERP correlates and behavioral consequences should always be linked to the locus of the spotlight and should not depend on whether the spotlight was oriented in a goal-driven or stimulus-driven process. This is in contrast with the notion that goal-driven and stimulus-driven orienting should have at least partially independent manifestations; a view that, in some sense,
implies two independent "spotlights". A second goal of the present study was to consider whether or not a simple spotlight model is an appropriate analogy for spatial auditory attention, and whether it is tenable to hold that the Nd1, Nd2, and Nd3 ERP modulations are causally related to behavioral facilitation arising from the transient focusing of auditory attention. To anticipate, we show not only that the auditory system is reconfigured by goal-driven and stimulus-driven processes independently and at different stages, but also that the Nd1, Nd2, and Nd3 ERP modulations are not invariable correlates of behavioral facilitation and thus cannot be reconciled with a simple attention spotlight model.

**Methods**

**Participants**

Twenty-two right-handed undergraduate students (6 males) at the University of British Columbia were paid to participate after giving informed consent. All participants reported normal hearing. All procedures were approved by the university’s human subjects ethics review process.

**Behavioral Task and Procedure**

Listeners were instructed to maintain visual fixation on an LED attached to a center speaker (Figure 5) and were encouraged to blink only as often as required to remain comfortable. Each trial began with 250 ms of silence followed by a central white noise burst to orient the listener to the center speaker and another 800 to 1200 ms of silence (randomly selected from a rectangular distribution). A spatially-informative auditory cue (70 ms white noise burst at 63 dBA SPL) was then delivered from a speaker either to the right or left of center (each 35 deg from center and marked with a steady
LED). Following a cue-target interval of 800 – 1200 ms (“jitter” interval randomly selected from a rectangular distribution to eliminate artifact-generating cue-target ERP overlap), an auditory target consisting of two 30 ms tone pips (1000 Hz, 70 dB SPL) separated in time by either a 30 ms or a 60 ms gap of silence was presented at one of the peripheral speakers. On each trial, listeners indicated which gap duration had occurred with a button press.

Figure 5. Cue and target stimuli. Listeners faced a horizontal array of speakers and maintained fixation on a central LED. On direct-cue trials the cue occurred at the location of the upcoming target on 75% of trials and at the opposite location on 25% of trials. In the counter-cue condition, the cue occurred at the speaker opposite the location of the upcoming target on 75% of trials and at the same location on 25% of trials. The situation depicted here would be an invalid-direct-cue trial or a valid-counter-cue trial.

Each listener performed two different attention orienting tasks in separate sets of blocks, but within the same two hour recording session. In the direct-cue condition, the cue indicated that the listener should expect the target to occur at the same speaker as the cue on 75% of trials (valid trials) but at the opposite side on 25% of trials (invalid trials). In the counter-cue condition, the cue indicated that the listener should expect the target to occur at the opposite side on 75% of trials (valid trials) and at the cued speaker on 25% of
trials (invalid trials). Thus the cue was always valid on 75% of trials, however listeners focused their attention where the cue had occurred in the direct-cue condition and where the cue had not occurred in the counter-cue condition.

Following at least one practice block in which no data were recorded, each listener completed ten contiguous 32-trial blocks of either direct-cue trials or counter-cue trials separated by a brief rest break. They then completed ten contiguous blocks of the other cue condition. The order of conditions (direct cue or counter cue) alternated across subjects. The experimental blocks were preceded by a passive listening condition in which 75 repetitions of the cue and short and long targets were presented at 1.5 s intervals from the central speaker.

**Electroencephalographic Recording**

The electroencephalogram (EEG) was recorded at 63 scalp sites including 59 electrodes in the standard 10-10 system, three electrodes (SI1, SIZ, SI2) located inferior to the inion, and the left mastoid (A1) (American Encephalographic Society, 1984). Data from FC1 and FC3 were rejected because of occasional channel failures. Voltages were referenced to the right mastoid (A2) during recording and subsequently digitally re-referenced to averaged mastoids. The electrooculogram was recorded with electrodes placed beside and below the left eye and referenced to each other. Electrode impedances were below 30 kΩ and the input impedance of the EEG amplifier (SA Instruments, San Diego, CA) was 2 GΩ. The EEG was amplified with a gain of 20,000, bandpass filtered (0.1 – 100 Hz; -12 dB/octave; 3 dB attenuation), and digitized at 250 Hz. The EOG was recorded likewise but with a bandpass filter of 0.1 – 30 Hz.
Event-Related Potentials (ERPs) were computed for a 3000-ms window (beginning 1,500 ms pre-stimulus) separately for each type of stimulus following automated rejection of blink or eye-movement contaminated trials. ERP and behavioral data were collapsed across short-gap and long-gap targets. Each ERP waveform was digitally filtered with a Gaussian finite impulse function (3 dB at 30 Hz). Response time and accuracy to discriminate the target gap were computed for artifact-free trials. The selection of latency windows for further analysis was guided by the latencies of the Nd1, Nd2, and Nd3 reported previously (Schröger, 1993; Schröger & Eimer 1993, 1997; McDonald et al. 2001; Tata et al. 2001). The Nd1 was measured as the mean voltage difference between attention conditions at three posterior sites (PO3, POZ, PO4) between 140 ms and 200 ms post-stimulus, the Nd2 at three central sites (C3, CZ, C4) between 175 ms and 225 ms, and the Nd3 at three frontal sites (F3, FZ, F4) between 275 ms and 350 ms. The unanticipated Late Positive Difference (LPd - see Results) was measured as the mean voltage at C3, CZ, and C4 in a 500 to 700 ms latency window. We analyzed ERPs elicited by left and right targets separately so as to capture any hemispheric lateralization with respect to the side of stimulation. Isopotential voltage maps were created by spline interpolation of the mean voltage differences at each electrode. Mean amplitudes of the ERP modulation within these latency windows were analyzed with ANOVA and the Huynh-Feldt adjustment of the degrees of freedom for sphericity violations was employed where appropriate (unadjusted degrees of freedom are reported).

Source Analysis

Electrical source analysis was accomplished with Advanced Source Analysis software (ANT Software BV, Enschede, The Netherlands). This procedure models
underlying neural activity as “equivalent source dipoles” and iteratively seeks (subject to constraints) the configuration of one or more such dipoles that best predicts the observed pattern of electrical activity at the scalp. A subset of 55 electrodes was projected onto a realistic head model generated from the Montreal Neurological Institute’s (MNI) representative brain. Thus our ERP dataset was coregistered with the MNI representative brain so that our dipole analysis could be carried out in standard stereotactic coordinates. The dipole fitting process iteratively modifies the orientation, magnitude, and location (from an initial “seed” location) of an equivalent dipole or set of dipoles and predicts the resultant pattern of electrical activity at the scalp. The iterative adjustment of dipole parameters proceeds until a “best-fit” is achieved between the predicted and observed data. The quality of this fit is described as the percentage of voltage variance across the scalp that can be explained by the model.

The emphasis of the present study was on the Ndl modulation occurring in the 140 to 200 ms latency range. We identified the peak of the Ndl to be at 148 ms for both left and right targets (Figure 4) and applied source analysis on a latency range spanning one four-millisecond sample on either side of this peak. Unless otherwise indicated, the fitting procedure was “seeded” in Heschl’s gyrus of the appropriate left or right temporal lobe at Talairach coordinates +/- 42, -21, 11 as described below.

Validation of Stereotactic Coregistration

The goal of source analysis is to identify the location(s) in three-dimensional space of a configuration of one or more dipoles that most likely underlies the observed ERP modulation of interest. The reliability of this localization in our study was potentially compromised by imprecision in the coregistration between our ERP dataset
and the MNI representative brain. To evaluate the reliability of this coregistration, we performed a source analysis on the well-known N1 component. The generators of this obligatory negative-going deflection of the ERP at about 100 ms post-stimulus are thought to be bilateral, oriented perpendicular to the supratemporal plane, and located in primary or adjacent auditory cortex in Heschl’s gyrus (e.g. Scherg, Vajsar, & Picton, 1989; Woldorff et al. 1993). The N1 thus provides a landmark intrinsic to the ERP dataset itself that can provide a first approximation of the reliability of the stereotactic coordinates generated in the source analysis.

We examined the N1 elicited by attended left and right targets in the direct cue condition as these stimuli yielded the most robust N1 components in our ERP dataset. The N1 was maximal at fronto-central sites at 112 ms and 108 ms for left and right targets, respectively. We initiated the fitting procedure with bilaterally symmetric dipole “seeds” at stereotactic coordinates (+/- 42, -21, 11) near the center of Heschl’s gyrus (Penhune, Zatorre, MacDonald, & Evans, 1996; Rademacher, et al., 2001; Talairach & Tournoux, 1988). Bilaterally symmetric dipoles oriented orthogonal to the supratemporal plane present a unique challenge in source analysis because the absence of electrodes on the ventral surface of the brain prevents measurement of much of the electric field generated around such sources. As a consequence, any configuration of sources with different orientations on the medial – lateral (x) axis can yield nearly equivalent patterns at the scalp. Thus we further constrained the fitting procedure by fixing the medial-lateral coordinate (x) of each dipole to +/- 42, and requiring that the anterior-posterior (y) and dorsal-ventral (z) coordinates be mirror symmetric. Despite such constraints, these bilaterally-symmetric dipoles accounted for 99.3% and 99.1% of the distribution of the
N1 for left and right stimuli, respectively, and were oriented orthogonal to the supratemporal plane of the MNI representative brain. Furthermore, the best-fit locations of these dipoles was at +/-42, -21, 12 (1 mm from the seed) and +/- 42, -21, 9 (2 mm from the seed) for left and right stimuli, respectively. The low residual variance, orientation, and location of these fits demonstrates that the coregistration between our ERP dataset and the MNI representative brain is reliable and suggests that the stereotactic coordinates of dipoles localized in this study are reliable. It should be kept in mind, however, that the familiar limitations on the spatial resolution of ERP (ie. volume conduction, between-subject variability, etc.) apply also to electrical source analysis. Thus, we also provide the N1 dipoles as landmarks intrinsic to the ERP dataset itself so that other dipole sources identified here may be localized purely in relation to the N1 generator.

**Direct-cue condition**

**Results**

Listeners were faster (723 ms vs. 802 ms; t\_17 = -3.265, p\_\text{(one-tailed)} = 0.002) and slightly more accurate ( 86% vs. 84%; t\_17 = 1.361, p\_\text{(one-tailed)} = 0.096) on valid-cue relative to invalid-cue trials. There were no statistically significant differences in response times or accuracy rates for left-field and right-field targets. As expected, attentional enhancement of performance was accompanied by a posterior Nd1, a central Nd2, and a frontal Nd3 (Figures 6, 6, and 8A). A contralateral distribution of the Nd1 was confirmed by an ANOVA showing a significant electrode (PO3, POZ, PO4) x target side (left, right) x validity (valid, invalid) interaction (F\_2,34 = 4.218, p = .037). Likewise, the tight focus of the Nd2 at CZ regardless of the target side was reflected in an electrode
(C3, CZ, C4) x validity (valid, invalid) interaction ($F_{2.34} = 5.988, p = .006$). The Nd3 had a broad focus spanning much of the frontal scalp and reflected in a main effect of validity ($F_{1.17} = 7.602, p = .014$). In addition to these negative deflections, a positive deflection (marginal main effect of Validity; $F_{1.17} = 3.983, p = .062$) was observed between 500 and 700 ms that we refer to here as the Late Positive difference (LPd). The entire dataset for this condition appears in Appendix C.

Figure 6. Comparison of ERPs to validly-cued and invalidly-cued targets at selected sites in the direct-cue condition. The Nd1, Nd2, Nd3, and LPd differences between ERPs to validly-cued and invalidly-cued targets are highlighted. Waveforms for left and right targets are compared separately.
Figure 7. Comparison of the scalp distributions of the Nd1, Nd2, Nd3, and LPd (valid-cue-trial minus invalid-cue-trial voltage difference) in the direct-cue condition. (a) The contralateral distribution of the Nd1. (b) The focus of the Nd2 at CZ. (c) The distributed frontal Nd3. (d) The parieto-central LPd. Note that only the Nd1 distribution is contralateral with respect to the target.
Figure 8. Topographic and Source Analysis of the Direct-Cue condition. (a) The scalp distributions for left-target and right-target Nd1 modulations at 148 ms. The isopotential voltage map is projected onto the realistic head model based on the MNI representative brain. In each pair, the more outside head is oriented facing into the page and the more central head is oriented facing towards the middle of the page. (b) Unconstrained equivalent source dipoles for the Nd1 distribution (red arrows) are shown superimposed on the MNI representative brain (both axial and sagittal slices are through the Nd1 generator). The N1 generators (green arrows) in Heschl’s gyrus are included as landmarks. For reference, the generator of the spatial MMN (blue arrow) elicited by left or right deviants (Tata & Ward, 2003) has been depicted as described in the text. Note the similarities between this generator and that of the Nd1 for left-field stimuli. (c) The same generators rendered within the head model used for the source analysis.
We next sought to test whether these attention-related modulations might reflect differential activity in brain regions known to be active during auditory spatial processing. Left- and right-target Nd1 modulations were fitted separately, first with a single dipole in the hemisphere contralateral to the target. Initial seeds were placed in Heschl's gyrus and both their orientation and their location were unconstrained in the fitting procedure. For left targets, a single dipole (standard stereotactic coordinates: 25,-46,19) located 2.5 cm posterior to the left-target N1 generator accounted for 94.4% of the left-target Nd1 scalp distribution (Figure 8). Furthermore, this dipole was located near the TPJ, within millimeters of the generator of the MMN elicited by left-field spatial deviants (26, -48, 15) as identified in a previous study (Tata & Ward, 2003).

A single dipole was less successful in explaining the scalp distribution of the right-target Nd1 (86.9%) and the location of this dipole in parietal cortex (-33,-71,31) did not match the location of the right-deviant spatial MMN reported previously (Figure 4). A single dipole fixed at the coordinates (-36,-43,5) and orientation (0.71,0.12,0.69) of the right-deviant spatial MMN generator accounted for only 62.9% of this Nd1 distribution. Consequently, we considered whether a more complex configuration of dipoles could better explain the right-target Nd1 distribution. In particular, we asked whether additional sources at coordinates in IPL might have contributed to the Nd1 distribution for right-field targets. We used the coordinates of activation foci in right and left IPL published in a recent investigation of auditory spatial processing (Alain, Arnott, Hevenor, Graham, & Grady, 2001). Dipoles fixed at the left hemisphere spatial MMN generator and in left IPL (25,-45,39) accounted for 81.9% of the right-target Nd1. The same two dipoles in conjunction with a third fixed in right IPL (25,-45,39) accounted for
88.4% of this Nd1 distribution. Note that this configuration of three dipoles did not include the location of the single unconstrained dipole that accounted for 86.9%.

**Discussion**

As predicted, the focusing of auditory attention at a location in space yielded both behavioral and electrophysiological consequences. Responses were faster and more accurate for attended targets and the ERPs elicited by these targets exhibited the anticipated Nd1, Nd2, and Nd3 modulations. The contralateral focus of the Nd1 with respect to the target stimulus is consistent with the results of a PET study that showed increased regional cerebral blood flow in auditory cortex contralateral to an attended auditory stream (Alho, et al. 1999). However, these findings are in contrast to a previous report (McDonald, et al. 2001), that the Nd1 generated in a cross-modal paradigm was focused ipsilateral to the target. This discrepancy may be due to differences in the orientation of the underlying ERP generators rather than a true difference in laterality. Small differences in the orientation of a deep generator can produce substantial topographic differences at the scalp.

For both left- and right-field targets, the Nd1 modulation was best fitted by dipole sources posterior to the N1 generator. These dipoles are likely to be located in areas of cortex that comprise the putative “where” pathway in the human auditory system (Alain, Arnott, Hevenor, Graham, & Grady, 2001; Rauschecker & Tian, 2000; Tata & Ward, 2003; Zatorre, Bouffard, Ahad, & Belin, 2002). Indeed, in the case of the left-target Nd1, the best-fitting dipole was located only millimeters away (in standard stereotactic space) from the recently identified generator of the spatial MMN. Thus the present result suggests that, unlike sustained auditory attention, which is thought to operate on early
stages of processing including primary and/or secondary auditory cortex (Grady, et al. 1997; Hillyard et al. 1973, Woldorff et al. 1993), the mechanisms of transient spatial auditory attention operate at later stages and in cortical areas that are involved in representing auditory space. The possibility that transient spatial attention acts at earlier stages should not be ruled out, however, since the ERP technique detects only a subset of electrical activity in the brain (for example, it is probably largely insensitive to changes in the behavior of cortical interneurons and subcortical structures).

Tata & Ward (2003) argued that the spatial MMN is generated within a region of cortex dedicated to processing the location of acoustic stimuli. It is therefore worth considering the relationship between the spatial MMN and the Nd1 with an interpretation that differs somewhat from the traditional view that attention-related ERP modulations reflect an augmenting of neural activity for attended stimuli. In addition to their similar coordinates, these two generators have similar latencies (148 ms for the Nd1 and 160 ms for the MMN). Furthermore, their orientations were almost precisely 180 degrees opposite to each other. The spatial MMN is an ERP component that is elicited when the location of an acoustic stimulus deviates from the location of repetitive “standard” stimuli. One widely-held interpretation of the MMN is that it reflects a mismatch between a current stimulus and a “template” or sensory trace that has been established for previous repetitive stimuli (Näätänen, 1992). The MMN is traditionally measured by subtracting the ERP elicited by standards from the ERP elicited by deviants. The Nd1 can be thought of as an ERP component elicited when the location of a target did not match the location at which it was expected. Consistent with this notion, Schröger & Eimer (1997) argued that the Nd1 principally reflects a “cost” on invalid trials rather than
a "benefit" on valid trials. In this sense, the spatial MMN and the Nd1 are generated under similar conditions: both occur when an acoustic stimulus does not come from the expected location. Unlike the MMN however, the Nd1 is traditionally measured by subtracting the ERP elicited by stimuli at the unexpected location (invalidly-cued targets) from the ERP elicited by stimuli at the expected location (validly-cued targets). Consequently, the two components have opposite polarities. When this is taken into account, it becomes clear that the MMN elicited by deviants in left hemispace and the Nd1 elicited by targets in left hemispace bear a strong similarity and might reflect activity of an identical population of neurons (Figure 8).

Whereas a single dipole accounting for the Nd1 elicited by left-field targets resembled, in location and orientation, the generator of the MMN elicited by left-field deviants, no simple configuration of dipoles compellingly explained the Nd1 elicited by right-field targets. The fact that a dipole fixed at the location of the right-deviant MMN, along with dipoles in left and right IPL achieved an 88.4% fit suggests that the right-target Nd1 might involve dipoles at or near these locations, however this cannot be determined with certainty on the basis of the present data. It is not surprising that the ERP elicited by right-field stimuli should be more complex than that elicited by left-field stimuli. This is consistent with the observation that right parietal cortex is of disproportionate importance in spatial processing,(Griffiths et al. 2000; Posner, Walker, Friedrich & Rafal, 1984; Zatorre et al. 2002) and deals with both left and right hemispace, whereas left parietal cortex deals with only right hemispace. Thus, at least at early stages of processing, right-field targets might engage multiple regions on both sides of the brain whereas left-field targets might only engage regions of the right hemisphere.
Importantly, Tata & Ward (2003) found no clear pattern of right hemisphere predominance in the generation of the spatial MMN. Thus, although the Nd1 and spatial MMN bear similarities and might involve the same ensembles of neurons, they probably do not represent electrophysiological correlates of the same cognitive operation(s). One interpretation is that the Nd1 modulation reflects a superposition of several generators, particularly in the case of right-field targets, that probably includes the generator of the spatial MMN.

The distinct Nd2 and Nd3 components observed in this study shed light on discrepancies in the recent literature. Using a symbolic (arrow) cue to orient their participant’s auditory attention, Schröger & Eimer (1993) found three distinct modulations of the auditory ERP: a posterior Nd1 between 125 and 175 ms, a central Nd2 between 205 and 255 ms, and a frontal Nd3 between 285 and 335 ms. Subsequent studies employing somewhat different methodology (Schröger, 1993; Schröger & Eimer, 1997; Tata et al. 2001) reported only two modulations: the posterior Nd1 and a component that these studies referred to as “Nd2”. The latencies of these Nd2 components spanned the range of 220 to 350 ms, consistent more with the Nd3 than the Nd2 as reported originally by Schröger & Eimer (1993). Close inspection of the waveforms reported in these studies reveals the possible contribution of an earlier, more central component, presumably the one that was originally referred to as the Nd2 by Schröger & Eimer (1993). In the present study, we have replicated Schröger & Eimer’s (1993) result in that we have obtained clear evidence for an earlier central Nd2 maximal at about 200 ms and a later more frontal Nd3 maximal around 300 ms. We have also
identified a later positive deflection, the LPd, maximal at parieto-central sites and ranging from 500 to 700 ms post-stimulus.

The functional significance of the Nd2, Nd3, and LPd modulations is not known, however an important physiological difference between these later modulations and the Nd1 is worth noting. Only the Nd1 is distributed contralaterally with respect to the target. The later components are focused at the midline, suggesting bilateral generators. Tata & Ward (2003) concluded that the auditory “where” pathway is organized to represent spatial information in the hemisphere contralateral to the hemispace in which it occurred. We thus speculate that the Nd2, Nd3, and LPd modulations do not reflect an aspect of sensory processing that is linked directly to the spatial location of the target. The frontal and central distributions of these later modulations are similar to the later negative deflections commonly observed in sustained attention paradigms (eg. Hillyard, et al. 1973) and may reflect a convergence between the mechanisms of transient and sustained attention. The LPd observed between 500 and 700 ms represents an as yet unreported attentional modulation, the significance of which is unclear. The fact that the LPd occurs less than 300 ms before response to the target suggests that it might reflect attention-induced differences in the ERP correlates of response selection or motor planning processes.

**Counter-cue condition**

One of the goals of the present study was to consider whether a simple single "spotlight" model adequately describes the correlates and consequences of spatial auditory attention. This conceptualization holds that the behavioral and electrophysiological correlates of attention should be linked to each other and, in a cue-
target situation, should depend only on whether the target stimulus occurred at a validly- or invalidly-cued location. One would thus predict that negative deflections (Nd1, Nd2, and Nd3 modulations) in the ERP elicited by validly-cued targets should always accompany enhanced behavioral responses to such targets. This result should be obtained even when the spotlight of attention is oriented by a counter cue that does not occur at the to-be-attended location. On the other hand, if performance enhancement in a counter-cue situation is unaccompanied by negative ERP deflections, or is accompanied by an as yet unobserved pattern of deflections, we would conclude that a simple spotlight model is not tenable for spatial auditory attention. We tested this hypothesis using the same procedure as above, but with a counter cue rather than a direct cue.

**Results**

Listeners were faster (733 ms vs. 790 ms; \( t_{17} = -2.39, p_{\text{one-tailed}} = 0.02 \)) but not significantly more accurate (83\% vs. 82\%; \( t_{17} = .62, p_{\text{one-tailed}} = 0.27 \)) on valid counter-cued trials (target was opposite the cue) relative to invalid counter-cued trials (target was on the same side as the cue). Unlike the direct-cue condition however, no negative deflections were evident in the ERP waveforms (Figure 9). Instead, robust positive deflections were generated by the validly-cued relative to the invalidly-cued targets. The entire dataset for this condition appears in Appendix D.
Figure 9. ERP waveforms in the counter-cue condition. For clarity, the waveforms have been collapsed across electrodes at the frontal, central and posterior sites and across the side of target presentation. Note the positive deflection of the validly-cued target ERP relative to the invalidly-cued target.

Discussion

The results of the direct-cue condition, in which attention was voluntarily directed to the location of the cue, painted a familiar picture of the consequences of selective auditory attention: a series of negative ERP modulations that presumably reflected attentional reconfiguration of the auditory system and the resultant performance
advantage for validly-cued targets. In the counter-cue condition, valid cues did yield a performance advantage relative to invalid cues, however positive rather than negative deflections of the ERP were observed. It is clear that a simple spotlight model does not adequately describe the behavior of auditory spatial attention. A more sophisticated model is necessary to understand the behavior of auditory attention; a model in which goal-driven and stimulus-driven processes can act independently.

**Between-conditions analysis**

In the direct-cue condition, the cueing stimulus presumably oriented attention both in a goal-driven manner, because it was explicitly informative of target location, and in a stimulus-driven manner, because it was a suddenly occurring and thus highly salient peripheral stimulus. In the counter-cue condition, attention was directed in a goal-driven manner to a location that was not stimulated. Stimulus-driven reconfiguration, however, could occur only for the location at which the cuing stimulus occurred, but not at the cued location. Thus goal-driven and stimulus-driven processes were engaged at different locations and the consequences of these modes of orienting could act independently. Since validly-cued targets occurred at an attended but unstimulated location, we reasoned that both behavioral and electrophysiological responses to these targets captured correlates of goal-driven but not stimulus-driven reconfiguration. Likewise, since invalidly-cued targets occurred at the location of the cue itself, but not at the locus of goal-driven attention, the behavioral and ERP responses to these targets would reflect stimulus-driven but not goal-driven reconfiguration. It is thus inappropriate to use either of these types of targets as a baseline for the other.
In the direct-cue condition we used the ERP to invalidly-cued targets as a baseline against which to compare the impact of attention on validly-cued targets. That approach fails in the counter-cue condition, since validly- and invalidly-cued targets are affected by different modes of reconfiguration. Instead we again used the ERP to invalidly-cued targets from the direct-cue condition as a baseline for both validly and invalidly-cued targets in the counter-cue condition, since these invalid direct-cue targets occurred at a location that was engaged by neither goal-driven nor stimulus-driven processes. We were therefore able to independently observe behavioral and electrophysiological correlates of goal-driven and stimulus-driven reconfiguration.

**Results**

Goal-driven reconfiguration enhanced performance on the discrimination task. Listeners were faster (733 ms vs. 802 ms; $t_{17} = 2.488, p_{(one-tailed)} = .011$) and equally accurate (83% vs. 84%; $t_{17} = .376, p_{(one-tailed)} = .356$) in discriminating validly-cued targets in the counter-cue condition relative to invalidly-cued targets in the direct-cue condition. However stimulus-driven reconfiguration did not significantly speed reaction time (790 ms vs. 802 ms; $t_{17} = .923, p_{(one-tailed)} = .184$) nor did it significantly improve accuracy (82% vs. 84%; $t_{17} = .858, p_{(one-tailed)} = .201$). There were no statistically significant differences in response times or accuracy rates for left-field and right-field targets. ERP modulations arising from goal-driven and stimulus-driven reconfiguration are compared in Figure 10, and the corresponding isopotential maps are compared in Figure 11. Stimulus-driven reconfiguration generated pronounced Nd1 (electrode x field x validity interaction; $F_{2,34} = 5.399, p = .017$) and Nd2 (significant main effect of validity; $F_{1,17} = 6.428, p = .021$) modulations as well as unfocused negative modulations in the Nd3
latency window (marginally significant electrode x field x validity interaction; $F_{2,34} = 2.813, p = .07$). The stimulus-driven LPd did not reach significance. Goal-driven attention produced a weak Nd1 that did not reach significance (electrode x field x validity interaction; $F_{2,34} = 1.964, p = .118$) and no discernable Nd2. It is clear in Figure 12, however, that the scalp distributions of the peaks of the goal-driven and stimulus-driven Nd1 modulations closely match the Nd1 observed in the direct-cue condition. It is thus likely that the goal-driven situation does result in an attenuated but nevertheless real Nd1 modulation. As in the stimulus-driven case, goal-driven attention generated unfocused negative differences in the Nd3 window (electrode x field x validity interaction; $F_{2,34} = 3.470, p = .043$) and the LPd did not reach significance. The entire datasets for the stimulus-driven and goal-driven comparisons appear in Appendices E and F, respectively.

To further relate stimulus-driven and goal-driven ERP correlates to those observed in the direct-cue condition, we considered whether similar dipole sources could explain the Nd1 modulations observed in these conditions. In the stimulus-driven case, a single unconstrained dipole seeded in right auditory cortex as described above fit 97.1% of the stimulus-driven left-target Nd1 distribution. This dipole was located at 22,-47,6, near the direct-cue Nd1 generator for left targets (25,-46,19), and was similarly oriented. Indeed, a dipole fixed at the direct-cue left-target Nd1 generator accounted for a similar 96.6% of the stimulus-driven left-target Nd1. As in the direct-cue case, no single dipole adequately accounted for the stimulus-driven right-target Nd1 modulation. Furthermore, the combination of dipoles near the left TPJ and in right and left IPL that fit 88.4% of the direct-cue right-target Nd1 accounted for only 52% of the stimulus-driven right-target
Nd1. In the goal-driven case, no single dipole or configuration of dipoles could explain greater than 85% of the Nd1 distribution for left or right targets.

Figure 10. Comparison of ERPs in stimulus-driven and goal-driven comparisons. For clarity, waveforms were collapsed across electrodes at the frontal, central, and posterior sites and across the side of target presentation. (a) ERPs to invalidly-counter-cued targets and invalidly-direct-cued targets. Since the only difference between these targets was whether or not they had been preceded by a stimulus at the same location, differences between these waveforms reflect the consequences of stimulus-driven processes. (b) ERPs to validly-counter-cued targets and invalidly-direct-cued targets. Since the only difference between these targets was whether or not they came from a voluntarily selected location, differences between these waveforms reflect the consequences of goal-driven processes. Note the presence of an Nd1 and Nd2 in (a) but not in (b), the presence of weak Nd3 in both (a) and (b), and the presence of a weak LPD in (b).
Figure 11. Scalp distributions of stimulus-driven and goal-driven modulations. Robust Nd1 (a) and Nd2 (b) modulations were generated by stimulus-driven but not goal-driven reconfiguration. (c) Both goal-driven and stimulus-driven reconfiguration led to weak and unfocused Nd3 modulations. (d). A weak LPd is evident in both conditions but is larger in the goal-driven condition; however, this modulation did not reach significance in either case.
Figure 12. Scalp distribution of the Nd1 at 148 ms for the direct-cue, stimulus-driven, and goal-driven situations. Note the similar contralateral distribution of the modulation in each case. The voltage scale has been unconstrained to highlight similarities in the scalp distribution rather than differences in the absolute amplitude of the modulations.
Discussion

The results of the between-conditions comparison suggest that stimulus-driven and goal-driven attention give rise to (at least) partially independent behavioral and ERP correlates. Goal-driven, but not stimulus-driven processes, led to robust behavioral enhancement. In contrast, stimulus-driven, but not goal-driven, reconfiguration generated robust Nd1 and Nd2 modulations. These early modulations are therefore neither necessary nor sufficient correlates of the performance benefit attributable to the focusing of attention at a location in auditory space. Although goal-driven processes might subtly affect early responses of neurons in the auditory system, including in a posterior “where” pathway, as evidenced by the attenuated Nd1 in the goal-driven situation, they did not override the consequences of stimulus-driven reconfiguration. Instead, the Nd1 and Nd2 modulations depended more on the location of the previous stimulus than on the locus of goal-driven attention. Thus, stimulus-driven processes seem to dominate the configuration of early processing stages of the auditory system.

Given the similarity of the Nd1 in the direct-cue, stimulus-driven, and goal-driven situations, it is reasonable to ask: what is the same about these three conditions? One similarity is that each of these conditions used the invalidly cued targets in the direct-cue condition as a baseline. It is therefore worth revisiting the suggestion that the Nd1 might reflect the detection of a mismatch between the actual and expected locations of the target. We suggest that the brain may set up a transient template, similar in function to the template involved in generation of the MMN. Stimuli that do not match this template require a reorienting of either goal-driven or stimulus-driven mechanisms, or both, and thus trigger a mismatch response, presumably in the region(s) of cortex that encode the
deviant feature. In the case of spatial attention, stimuli at an unexpected location would generate a mismatch response within the putative “where” pathway. This would account for the close alignment between the MMN generators reported by Tata & Ward (2003) and the Nd1 generators reported here. Interestingly, the results of the between-conditions analysis, in conjunction with the work of Schröger & Eimer, suggests that a stimulus-driven process is very effective at establishing such a template, but that goal-driven attention oriented in response to a symbolic cue can also set up a spatial template. Future investigations may bridge the conceptual gap between the cue-target and MMN paradigms.

The between-conditions analysis also clarifies a question regarding the possible involvement of Inhibition of Return (IOR) in the counter-cue condition. IOR is a behavioral phenomenon in which responses to visual (Posner & Cohen, 1984) or auditory (McDonald & Ward, 1999) targets occurring at previously cued locations are, under certain circumstances, found to be slower than responses at uncued locations (see Klein, 2000 for review). One theory used to explain this result suggests that attention is inhibited in returning to a previously attended location (Posner, Rafal, Choate, Vaughan, & 1985). In the counter-cue paradigm employed in this study, attention was presumably first directed to the location of the cue and then directed to the opposite side. Thus the slower response to targets at the invalid (stimulated) location might reflect the involvement of IOR. Although it is unclear how IOR might contribute among the several factors potentially influencing behavioral responses in this counter-cue condition, it is unlikely that it played a dominant role for two reasons: First, if IOR were acting to inhibit responses at the invalidly cued location then one would predict that responses to
targets occurring at this location would have been slower than responses to targets at the unstimulated and unattended location in the invalid direct-cue condition. In fact, listeners were faster (though non-significantly) on invalid counter-cue trials than on invalid direct-cue trials (790 ms vs. 802 ms). Thus there is no behavioral evidence for IOR. Second, although the neural correlates of auditory IOR are not well understood, Prime, Tata & Ward (2003) have argued that the Nd1 is eliminated in a target-target situation in which auditory IOR occurs. Since a robust Nd1 was generated in comparing ERPs elicited by invalid counter-cue targets with ERPs elicited by invalid direct-cue targets, the electrophysiological data are inconsistent with the involvement of an IOR-like process.

It is also not clear how stimulus-driven and goal-driven processes interact to influence the later Nd3 and LPd modulations. Neither generated clear Nd3 patterns, however an LPd-like pattern is evident in both the stimulus-driven and goal-driven situations in Figure 11d. It may be that the robust Nd3 and LPd modulations observed in the direct-cue condition occur only when both stimulus-driven and goal-driven processes are aligned to the same location.

Conclusions

Our principle goal was to further characterize the negative ERP deflections typically observed in conjunction with the transient focusing of auditory attention in space. In the direct-cue condition we observed the anticipated negative deflections (Nd1, Nd2, and Nd3 modulations). The observation of distinct Nd2 and Nd3 components

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1 In a similar study also employing a counter-cue paradigm, we included targets presented at a central unstimulated/unattended location. In this study a cue occurred either on the left or the right side, but never at the central location. Targets occurred at the opposite side (valid trials) on 60%, at the same side (invalid trials) on 20%, and at the central unstimulated/unattended location on 20% of trials. Listeners were faster on valid relative to invalid trials (715ms vs 732ms) and were also slightly faster (732 ms vs. 734ms) on invalid trials relative to targets at the unattended/unstimulated location. We therefore conclude that IOR did not substantially influence the outcome in this counter-cue paradigm.
resolves some controversy by demonstrating that the central Nd2 reported by Schröger & Eimer (1993) is a legitimate correlate of transient auditory attention, despite subsequent failures to distinguish it from the later and more frontal Nd3.

Tata et al. (2001) suggested that the Nd1 modulation in particular might represent either the recruitment or modulation of spatially-tuned auditory neurons in the putative auditory "where" pathway. The result of the source analysis here lends support to this hypothesis. The equivalent source dipoles most likely to account for the Nd1 modulation were found to be posterior to primary or secondary auditory cortex as indicated by the generator of the N1. Indeed, the Nd1 modulations seem to have been generated by neurons at or near the TPJ, a region previously identified as being a component of this putative "where" pathway. Further investigations will determine whether non-spatial attention (i.e. focusing on stimuli of a specified pitch) distinctly modifies behavior of neurons in an anterior "what" pathway.

It seems likely that spatial auditory attention acts, at least in part, by modifying the behavior of neurons in this putative "where" pathway. Two hypothesis regarding the nature of this modification can be advanced here: the Nd1 might reflect an enhancement of sensory gain for neurons that encode stimuli at the attended location, a notion similar to that proposed to explain the early Nd found in sustained attention paradigms (eg Hillyard, Hink, Schwent, and Picton, 1973). We have also considered here the possibility that the Nd1, like the MMN, reflects the detection of a mismatch between the location of a target stimulus and the expected location of that stimulus. In this case it would be more accurate to conceptualize the Nd1 as a positive deflection of the ERP elicited by stimuli
at unexpected locations rather than a negative deflection of the ERP elicited by stimuli at an attended location.

The juxtaposition between these two views of the Nd1 highlights a difficulty that arises when differences between two ERP waveforms are named according to their signs (positive or negative) as in the “negative difference 1” or the “mismatch negativity”. It is usually impossible to unambiguously determine whether an ERP modulation resulted from a positive deflection of one waveform or a negative deflection of the other. Furthermore, due to the dipolar nature of electrical sources, the Nd1 as it has been defined in the literature is in fact positive when measured at frontal electrodes. We suggest that, as high-density electrode arrays and source analysis become more accurate, reliable, and widespread, the field of ERP research should shift towards descriptions of ERP modulations in terms of the geometry of the underlying dipole sources rather than voltage differences measured at a few scalp electrodes. For example, the similarities between the generators of the Nd1 (a posterior negative difference) and the spatial MMN (an anterior negative difference) would not have been suspected upon inspection of only a few waveforms.

Our second goal was to attempt to assess the validity of a simple single-spotlight model for auditory attention. Such a model would have accurately predicted the behavioral results in both direct- and counter-cue conditions: better performance (as measured by RT) on validly-cued relative to invalidly-cued trials. This simple model, however, would fail to predict the ERP data. Whereas behavioral responses to targets at the locus of the hypothetical spotlight were faster relative to targets at the unattended location, in the counter-cue situation this performance enhancement was accompanied by
positive rather than negative deflections of the ERP. The behavioral and ERP correlates of attention were in part dissociable, with the behavioral correlates depending on the locus of goal-driven attention and the ERP correlates depending principally on the location of the previous stimulus. We conclude that a simple spotlight conceptualization must be replaced by a more complex model in which a single location may be selected in a goal-driven manner, while stimulus-driven reconfiguration might act at other locations independent of the locus of a goal-driven attentional spotlight.

One of the strongest assumptions that can be made in ERP research is that modulations of the ERP reflect differences in cortical activity that cause subsequent differences in behavior. We conclude here that the Nd1 and Nd2 modulations are not in this strict sense causative correlates of attention-related performance enhancement. This is a compelling demonstration of the care that must be taken in interpreting ERP data. The course of sensory encoding and perception, encoding and retrieval in memory, response selection and preparation of that response involves many interrelated factors, each of which might give rise to a modulation in the corresponding electroencephalogram. The outcome we observe, however, is often a single action, such as the press of a button, which may or may not capture the intricacies of the neural mechanisms that gave rise to it.

Given the present data, the dissociation between behavioral and ERP correlates of attention holds only in the specific situation in which stimulus-driven affects linger after a goal-driven "spotlight" has been oriented away from the stimulated location. This situation is arguably uncharacteristic of the real-world behavior of auditory attention. Presumably under most conditions, the location at which a sound occurred is also the
location with the most behavioral relevance regarding that sound. It should therefore be emphasized that goal-driven and stimulus-driven processes are typically aligned at the same location and each of the several ERP modulations observed in the direct-cue condition might play a significant role in accomplishing the performance enhancement afforded to attended information in that situation. It is also important to note that the Nd1 modulation can be elicited in situations in which the interval between the cue and target is quite brief, on the order of 100 to 300 milliseconds (McDonald et al. 2001). In vision, stimulus-driven and goal-driven orienting have been shown to operate on different time-scales (Nakayama & Mackeben, 1989), with stimulus-driven attention operating over a brief period spanning only a few hundred milliseconds after a cue. Several studies have reported performance enhancements for auditory discrimination tasks following similarly brief cue-target intervals (McDonald & Ward, 1999; Mondor & Zatorre, 1995; Spence & Driver, 1994; Ward, 1994). Since the cue-target interval in the present study spanned 800 to 1200 ms, it is possible that the Nd1 and Nd2 modulations observed here reflect the lingering electrophysiological consequences of a brief stimulus-driven effect, the behavioral consequences of which were simply no longer manifested after a cue-target interval of many hundreds of milliseconds.

The differential effects of stimulus-driven and goal-driven processes on the Nd1 seem to reflect differential modulation of a posterior “where” pathway. We suggest an alternative to a simple spotlight model that distinguishes “within-stream” from “between-stream” reconfiguration. We propose that stimulus-driven processes mediate a reflexive “within-stream” reconfiguration that prepares the auditory system for subsequent stimuli at the same location. Adjusting this pathway to the spatial properties of an upcoming
stimulus, however, has no impact on behavioral tasks based on features, such as pitch or
duration, that are processed outside of the “where” pathway. On the other hand, goal-
driven attention mediates a “between-stream” reconfiguration so that voluntarily focusing
of attention in space improves performance on both spatial and non-spatial tasks, perhaps
by filtering out information at other locations. This hypothesis is consistent with
previous studies (McDonald & Ward, 1999; Spence & Driver, 1994) that found
behavioral facilitation on non-spatial tasks only when spatial attention was oriented in a
goal-driven manner. This view predicts that the Nd1 is invariably correlated with
behavioral facilitation when the listener's task is spatial in nature, but not when the task is
non-spatial, as in the present study.

Since the cues used in this study were broad-band noise bursts, it is likely that we
isolated the correlates of spatial mechanisms from non-spatial mechanisms. It is unclear
whether the same dissociation between goal-driven and stimulus-driven processes will
hold for frequency-based reconfiguration of the “what” pathway dedicated to processing
non-spatial information. Given that auditory information is encoded initially in a
frequency-based (tonotopic) format, there may be an asymmetry between spatial and non-
spatial attention. Stimulus-driven orienting to a cued frequency, for example, may
facilitate discrimination of the location of sounds of the same frequency. Convergence of
the present findings with other approaches will be necessary to fully elucidate the
mechanisms by which various auditory pathways are reconfigured by different attentional
factors.
CHAPTER 5: CONCLUSIONS

A substantial body of literature has been dedicated to the investigation of ERP correlates of sustained auditory attention. Prior to the studies reported here, however, little was known about the characteristics of the ERP under conditions of transient auditory attention. The several studies reported by Schröger and Eimer described above had used a cross-modal visual-cue/auditory-target paradigm and, more importantly, had employed a relatively sparse array of electrodes. Here I review some questions that were unresolved or uninvestigated in the previous literature and indicate progress toward their resolution that has been accomplished by the present studies.

Previous ERP studies of transient auditory attention considered only the specific situation in which auditory attention was oriented in response to a symbolic visual cue. These studies therefore did not demonstrate whether or not the observed ERP correlates were correlates of transient auditory attention in general. For example, the posterior Nd1 might have arisen in visual cortices as a consequence of the visual cue. These correlates might also have arisen only with the goal-driven orienting associated with a symbolic cue. In retrospect, it was perhaps premature for Schröger & Eimer (1997) to conclude that transient auditory attention did not modulate "early" stages of processing in a manner similar to sustained attention, since other paradigms might have yielded modulations of the ERP at earlier latencies. The study reported in Chapter Two demonstrated Nd1 and Nd2 modulations in an exclusively auditory paradigm and in a situation unlike that used by previous studies. Importantly, this study also found no modulation of the ERP earlier than the Nd1 component. As such it supported the extension of previous results to
transient auditory attention in general. The study reported in Chapter Four went further by showing pronounced Nd modulations, precisely consistent with the original study by Schröger & Eimer (1993), yet in an auditory cue-target paradigm unlike any previous study. In addition, Chapter Four demonstrated an important distinction between the early correlates of goal-driven and stimulus-driven attentional mechanisms which had gone unnoticed in previous work. This result dispelled the notion, implicit in previous studies, that a tight and causal link might exist between early-latency ERP correlates and behavioral facilitation.

None of the studies reported by Schröger & Eimer employed more than five electrodes. These studies thus provided a sparse view of the topographic distribution of the Nd modulations. Since the principle distinction between the earliest correlates of transient and sustained attention (the Nd1 and early Nd, respectively) lay specifically in their topography, it was critical to obtain a better understanding of the scalp distribution of these components. Indeed, the results of the high-density topographic analysis in Chapter Two showed that the Nd1 modulation, maximal over the PO3, POZ, and PO4 electrodes was considerably more posterior than reported in previous studies. More importantly, in Chapter Four it was reported that the Nd1 arose over the hemisphere contralateral to the target stimulus. This demonstrated an important aspect of the functional anatomy of the auditory system that could not have been identified by the previous low-density studies.

Chapter Two concluded with the speculation that transient spatial auditory attention might modulate the behavior of neurons in a dedicated spatial processing pathway in posterior parietal cortex. This speculation made two important assumptions:
first, that such a pathway exists in human cortex, and second, that the electrical behavior
of neurons in this pathway is reflected in the auditory event-related potential. The first
assumption follows unremarkably from functional imaging and non-human primate
research. The second assumption, however, was somewhat more speculative, since no
previous study had reported ERP components arising from these structures. The results
reported in Chapter Three supported both of those assumptions. It was shown that the
early phase of the spatial MMN is generated posterior to primary auditory cortex, near
the temporo-parietal junction, and within part of the putative “where” auditory pathway.
Since this ERP component was elicited in response to the detection of a difference in the
spatial location of stimuli, it is likely that it reflected the electrical activity of neurons
engaged in processing spatial information, thereby supporting the theory that posterior
auditory areas engage in spatial processing. Furthermore, the identification of this
component offers proof-in-principle that at least a subset of the electrical activity in this
pathway can be observed with the ERP technique.

With the groundwork in place following the study reported in Chapter Two, it
remained only to test the hypothesis that the Nd1 modulation was generated within areas
considered part of the auditory “where” pathway. To this end, the study reported in
Chapter Four employed a careful dipole source analysis, including a check of the
precision of the source analysis procedure, to identify the probable generator(s) of the
Nd1. Although the source analysis revealed a predictable asymmetry between left- and
right- field targets, it strongly supported the engagement of posterior dipoles at or near
the TPJ with the probable involvement of dipoles in other parts of parietal cortex. In the
case of left-field targets, the most likely Nd1 generator bore a striking resemblance to the
generator of early-phase spatial MMN elicited by left-field deviants, thus providing
evidence that the Nd1 does indeed reflect the modulation of neurons within a spatial
processing pathway as suggested in Chapter Two.

Prior to the studies described here, the state of knowledge of the ERP correlates
of transient auditory attention was based on three 4- and 5-electrode investigations that
employed identical visual-cue/auditory-target paradigms. Our current understanding is
informed by high-density studies and dipole source analysis, under a variety of
attentional manipulations, and cast in the context of an emerging functional mapping of
the human auditory system.

The first chapter in the story of cognitive neuroscience opened with investigators
such as Stephen Hillyard and Risto Näätänen recording messy ERP waveforms from a
handful of electrodes. The studies described in this thesis are part of the beginning of the
second chapter. From here we will begin to make tight associations between specific
cognitive operations and precise and replicable dipole mappings. We will functionally
map the sensory pathways with a temporal resolution of milliseconds. We will
investigate the inter-relatedness of visual, auditory, and cross-modal attentional
mechanisms, identifying commonalities and differences. We will develop an
understanding of the neural mechanisms by which information is extracted, encoded,
identified and acted upon by human brains.
REFERENCES


pitch changes in a sequence of tone pips: neuromagnetic recordings in man.  


Appendix A. 64-channel dataset for target-target study (Chapter Two).
Appendix B. 64-channel dataset for left-field and right-field in spatial MMN study (Chapter Three)

**Left Stimuli**
Right Stimuli

[Graph of EEG waveforms showing responses to right stimuli]
Appendix C. 64-channel dataset for Direct-Cue condition (Chapter Four)

Left Targets
Right Targets
Appendix D. 64-channel dataset for counter-cue condition (Chapter Four)

Left Targets
Right Targets

2 uV

+ 700 ms

Valid

Invalid
Appendix E. 64-channel dataset for stimulus-driven condition (invalid counter-cue targets vs. invalid direct-cue targets)
Right Targets
Appendix F. 64-channel dataset for goal-driven condition (valid counter-cue targets vs. invalid direct-cue targets)

Left Targets

- 2 μV
- 700 ms

Validly Counter-Cued
Invalidly Direct-Cued
Right Targets

Validly Counter-Cued
Invalidly Direct-Cued