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Spatial attention modulates activity in a posterior "where" auditory pathway

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Abstract

Selectively listening to a single location in space modulates both the behavioral and electrophysiological responses to auditory stimuli presented at that location. Transient attention oriented in cue–target or target–target paradigms results in several modulations of the auditory event-related potential known as the Nd1, Nd2, and Nd3. By employing electrical source analysis we tested the hypothesis that the earliest component (the Nd1) reflects modulation of neurons in parietal rather than auditory cortex. It was found that the most likely sources of the Nd1 modulation were posterior to primary auditory cortex within or near the temporo-parietal junction (TPJ). This location is within the putative auditory "where" pathway.
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1. Introduction

Humans, like all 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 information and unattended information are handled differently by the brain. This is usually manifested as faster response times and greater accuracy for attended stimuli in perceptual tasks. Evidently, a reconfiguration of perceptual and/or cognitive systems causes attended sensory information to be processed in an enhanced or extended way. Elucidation of the neural mechanisms underlying this reconfiguration remains a foundational goal of cognitive neuroscience.

Of the several approaches employed to investigate the neural correlates of selective attention in the auditory domain, the human electroencephalogram (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 (over a span of tens of seconds) at one location or frequency facilitates behavioral responses to attended sounds relative to unattended sounds. This behavioral facilitation is accompanied by modulations of the ERP elicited by attended stimuli beginning as early as 20–50 ms post-stimulus (Woldorff, Hansen, & Hillyard, 1987), with a pronounced negative-going deflection beginning 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 supra-temporal plane, lateral to Heschl's gyrus (Woldorff et al., 1993). The early modulations of the ERP associated with sustained focusing of attention are thought to reflect a consequence of sensory gain or attentional filtering at initial stages of processing (Hillyard, Vogel, & Luck, 1999; Woldorff et al., 1993; for a review see Näätänen, 1992).

More recent studies (Golob, Pratt, & Star, 2002; Hugdahl & Nordby, 1994; McDonald, Teder-Salejarvi, Haraldez, & Hillyard, 2001; Schröger, 1993, 1994; Schröger & Eimer,

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1993, 1996, 1997; Tata, Prime, McDonald, & Ward, 2001; Widmann & Schröger, 1999) have investigated ERP consequences of orienting auditory attention in space on a moment-by-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, several of 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 distributions 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 associated with 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 sustained-attention 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 pronounced differences between the Nd1 associated with transient attention and the early-latency sustained attention modulations (i.e. the early Nd), have led investigators to further explore the functional attributes of the Nd1. Importantly, the auditory Nd1 is similar in latency and scalp topography to an analogous negative deflection of the ERP elicited by attended relative to unattended visual stimuli (Eimer, 1994). Of particular interest is the finding that both the auditory (Schröger, 1994) and visual (Eimer, 1995) Nd1 modulations arise when subjects focus attention on spatial locations, but not when they attend to non-spatial features such as pitch or color. Furthermore, the Nd1 seems to be associated principally with "costs" on invalid trials rather than "benefits" on valid trials (Eimer, 1996; Schröger, 1994; Schröger & Eimer, 1997). In light of these similarities, the Nd1 modulation has been suggested to be a modality non-specific correlate of expectation linked to a specific spatial location (Eimer, 1998).

Little is known, however, about the cortical activity that underlies the Nd1 modulation. Since it is a correlate of spatial but not non-spatial attention, the auditory Nd1 is thought to reflect the modulated behavior of spatially-tuned auditory neurons (Schröger & Eimer, 1997; Tata et al., 2001), however the region or regions of cortex that generate the underlying electrical activity of the Nd1 have not been localized. The functional and topological similarities between the auditory and visual Nd1 modulations led Eimer (1998) to propose that these effects might arise from modulations of a polysensory area, possibly in the posterior parietal cortex (PPC). A recent high-density (64-channel) EEG study has advanced this theory by showing that the auditory Nd1 is focused over parieto-occipital scalp (Tata et al., 2001).

The role of the parietal cortex in auditory processing, especially of the temporo-parietal junction (TPJ) and inferior parietal lobule (IPL), has been of considerable interest as the functional anatomy of the auditory pathways in human cortex becomes increasingly well understood. A prominent model currently under investigation holds that the auditory system, like the visual system, is comprised of functionally segregated pathways: a "what" pathway dedicated to processing complex features of sounds, which projects anteriorly from primary auditory cortex, and a "where" pathway dedicated to processing the spatial location of sounds, which projects posteriorly into parietal cortex (Rauschecker & Tian, 2000; Romanski et al., 1999). Several lines of converging evidence suggest the existence of a posterior "where" pathway. First, neurons in regions of the supratemporal plane posterior to primary auditory cortex in non-human primates are tuned to the locations of auditory stimuli (Leinonen, Hyvarinen, & Sovijarvi, 1980; Tian, Reser, Durham, Kustov, & Rauschecker, 2001). Second, fMRI investigations of spatial localization and motion processing within the auditory modality have revealed activation of the PPC, especially 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) and planum temporale (PT) (Hart, Palmer, & Hall, 2004; Warren, Zielinski, Breen, Rauschecker, & Griffiths, 2002). Finally, one fMRI study also reported dissociations between regions activated by sound recognition and those modulated by sound localization (Maeder et al., 2001).

If the Nd1, an ERP correlate of the focusing of spatial attention, is indeed a modulation of electrical activity in the TPJ or IPL, it would be of interest for two principle reasons: first, this would contribute evidence supporting the existence of the putative posterior "where" auditory pathway. Second, it would advance an important principle regarding the mechanisms of attentional selection within auditory pathways: that focusing attention on a specific attribute of a stimulus (in this case location) modulates regions of the brain that are tuned to represent that kind of information. Some evidence for this type of selective modulation on the basis of attentional factors has already been demonstrated in regard to language processing (Hashimoto, Homae, Hakjima, Miyashita, & Sakai, 2000; Hugdahl, Thomsen, Ersland, Rimol, & Niemi, 2003) and spatial versus non-spatial working memory tasks (Anourova et al., 2001).

The goal of the present study was to investigate the spatial and temporal parameters of the Nd1, with a secondary interest in the later Nd2, and Nd3 attention-related modulations. We sought to test the hypothesis that the Nd1 might be a modulation of a generator within the putative "where" auditory pathway.

2. Methods

2.1. Participants and procedure

Twenty-two undergraduate students at the University of British Columbia were paid to participate after giving in-

formed consent. All participants reported normal hearing and were right-handed. All procedures were approved by the university's human subjects ethics review process.

We employed a cue–target paradigm in which listeners sat in a sound-attenuated booth (∼35 dBA background noise) and faced three horizontally-arranged wall-mounted speakers. Listeners were instructed to maintain visual fixation on an LED attached to the center speaker 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 broadband noise burst to orient the listener to the center speaker and then by another 800–1200 ms of silence (randomly selected from a rectangular distribution to reduce ERP overlap of consecutive stimuli). A direct spatially-informative (75% valid) auditory cue (70 ms broadband noise burst at 63 dBA SPL) was then delivered from a speaker either to the right or left of center (each 35° from center and marked with a steady LED). Following a cue–target interval of 800–1200 ms 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 by pressing the "up" arrow for short targets and the "down" arrow for long targets with their dominant (right) hand.

Following at least one practice block in which no data were recorded, each listener completed 10 contiguous 32-trial blocks of the discrimination task. For all participants, the recording session also included a counter-cue condition, the results of which are reported elsewhere (Tata, 2003). 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.

2.2. Electroencephalographic recording and source analysis

The electroencephalogram 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 Electroencephalographic Society, 1994). 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 (EOG) was recorded with electrodes placed beside and below the left eye and referenced to each other. Electrode impedances were below 30 kΩ (0.000015% of amplifier input impedance). The EEG was amplified (SA Instruments, San Diego, CA) 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 were computed for a 3000 ms window (beginning 1500 ms pre-stimulus) separately for each type of stimulus following automated rejection of blink or eye-movement contaminated trials. Data from four subjects were rejected entirely due to excessive eye movements. ERP and behavioral data were collapsed across short- and long-gap targets as the ERP waveforms were morphologically similar and, because of counterbalancing, no systematic bias would be introduced into subsequent analysis by pooling these data. 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 (McDonald et al., 2001; Schröger, 1993; Schröger & Eimer, 1993, 1997; 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 and 200 ms post-stimulus, the Nd2 at three central sites (C3, CZ, C4) between 175 and 225 ms, and the Nd3 at three frontal sites (F3, FZ, F4) between 275 and 350 ms. The unanticipated late positive difference (LPd, see Section 3) was measured as the mean voltage difference at C3, CZ, and C4 in a 500–700 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 a spherical spline interpolation of the mean voltage differences at each electrode. Mean amplitudes of the ERP modulations 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).

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 (Scherg, Vajsar & Picton, 1989). We co-registered our ERP dataset with a realistic head model based on a structural MRI scan of the Montreal Neurological Institute (MNI) Representative Brain by projecting electrode locations from a spherical coordinate system to the closest point on the scalp. Dipoles were superimposed onto this structural MRI and stereotactic coordinates are reported with respect to the MNI/SPM99 template.

Source analysis was applied to two ERP components: the Nd1 and the N1. We identified the peak of the Nd1 to be at 148 ms for both left and right targets and applied source analysis on a latency range spanning one 4 ms sample on either side of this peak. Unless otherwise indicated, all analyses were "seeded" in Heschl's gyrus of the appropriate left or right temporal lobe (or both) at standard stereotactic coordinates ±42, −21, 11. The N1 was maximal at fronto-central sites at 112 ms for left and 108 ms for right targets, respec-
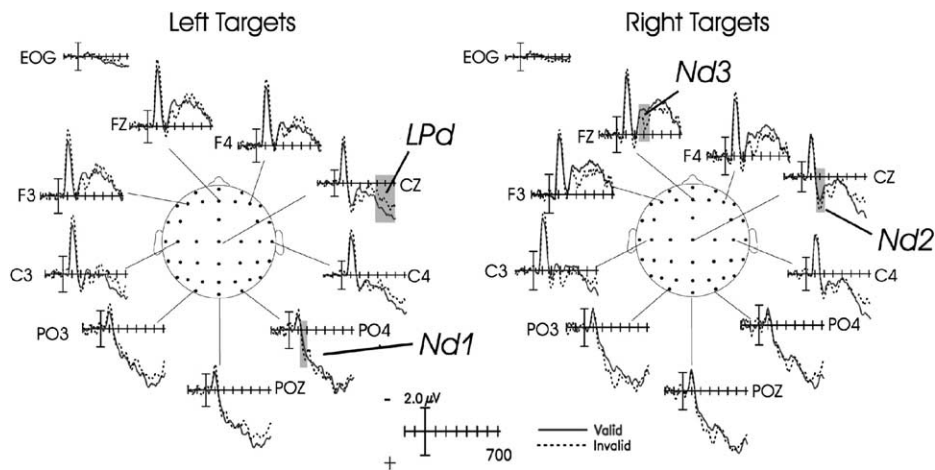
Fig. 1. Comparison of ERPs to validly- and invalidly-cued targets at selected sites. The Nd1, Nd2, Nd3, and LPd differences between ERPs to validly- and invalidly-cued targets are highlighted. Waveforms for left and right targets are compared separately.

tively, and source analysis was applied to these peaks as with the Nd1. The N1 was fitted with bilaterally symmetric dipoles fixed in the medial–lateral (x) dimension.

3. Results

Listeners were faster (723 ms versus 802 ms; $t_{17} = -3.265$, $P_{(one-tailed)} = 0.002$) and slightly more accurate (86% versus 84%; $t_{17} = 1.361$, $P_{(one-tailed)} = 0.096$) on valid-cue relative to invalid-cue trials. There were no statistically significant differences between response times or accuracy rates for left-field versus right-field targets.

As expected, attentional enhancement of performance was accompanied by a posterior Nd1, a central Nd2, and a frontal Nd3 (Figs. 1 and 2). A contralateral distribution of the Nd1 was confirmed by an ANOVA showing a significant electrode (PO3, POZ, PO4) × target side (left, right) × validity (valid, invalid) interaction ($F_{2,34} = 4.218$, $P = 0.037$). Furthermore, post-hoc paired-comparisons using Tukey's LSD revealed significant differences between validly- and invalidly-cued target ERPs at contralateral and midline electrodes, but not at ipsilateral electrodes (right-side targets at PO3: $P = 0.010$; right-side targets at POZ: $P = 0.030$; right-side targets at PO4: $P = 0.782$; left-side targets at PO3: $P = 0.826$; left-side targets at POZ: $P = 0.011$; left-side targets at PO4: $P = 0.006$). Likewise, the tight focus of the Nd2 at CZ regardless of the target side was confirmed by an electrode (C3, CZ, C4) × validity (valid, invalid) interaction ($F_{2,34} = 5.988$, $P = 0.006$). The Nd3 had a broad focus spanning much of the frontal scalp and was confirmed by a main effect of validity ($F_{1,17} = 7.602$, $P = 0.014$). In addition to these negative deflections, a positive deflection (marginal main effect of validity; $F_{1,17} = 3.983$, $P = 0.062$) was observed between 500 and 700 ms. We refer to this deflection here as the late positive difference.

We next sought to test whether these attention-related modulations might reflect differential activity in brain re-

gions known to be active during auditory spatial processing. We first fitted sources for the early phase of the N1 generated by left- and right-field validly-cued targets. Since the N1 is believed to be generated in primary or adjacent auditory cortex, its sources can act as a landmark intrinsic to the ERP dataset against which to compare the loci of other fitted dipoles. For this purpose, we found it unnecessary to model the later radial component of the N1 (the N150). For the N1, bilaterally symmetric dipoles were seeded in Heschl's gyrus (Rademach et al., 2001) and constrained such that their medial–lateral (x) extent was fixed and the anterior–posterior (y) and dorsal–ventral (z) positions were mirror symmetric. Such bilaterally-symmetric dipoles in Heschl's gyrus accounted for 99.3 and 99.1% of the distribution of the N1 peak for left and right stimuli, respectively, and were oriented orthogonal to the supratemporal plane of the MNI representative brain, suggesting an anatomically plausible model (Fig. 3). The best-fit locations of these dipoles were at ±42, −21, 12 and ±42, −21, 9 for left and right stimuli, respectively.

Left- and right-target Nd1 modulations were fitted separately, first with a single source dipole in the hemisphere contralateral to the target. Initial seeds were placed in Heschl's gyrus and both their orientation and their location were initially unconstrained in the fitting procedure. Heschl's gyrus was chosen as the seed location for the Nd1 to act as a "null hypothesis." If the Nd1 is indeed generated outside of primary or secondary auditory cortex, the source fitting algorithm would need to move the dipole away from its initial seed. This is a more conservative approach than simply placing the seed at a hypothesized location. For left targets, a single dipole located near the TPJ (standard stereotactic coordinates: 25, −46, 19), and 2.5 cm posterior to the left-target N1 generator, accounted for 94.4% of the left-target Nd1 scalp distribution (Fig. 3).

A single dipole model explained only 86.9% of the scalp distribution of the right-target Nd1, and the location of this dipole in parietal cortex (−33, −71, 31) was dissimilar to
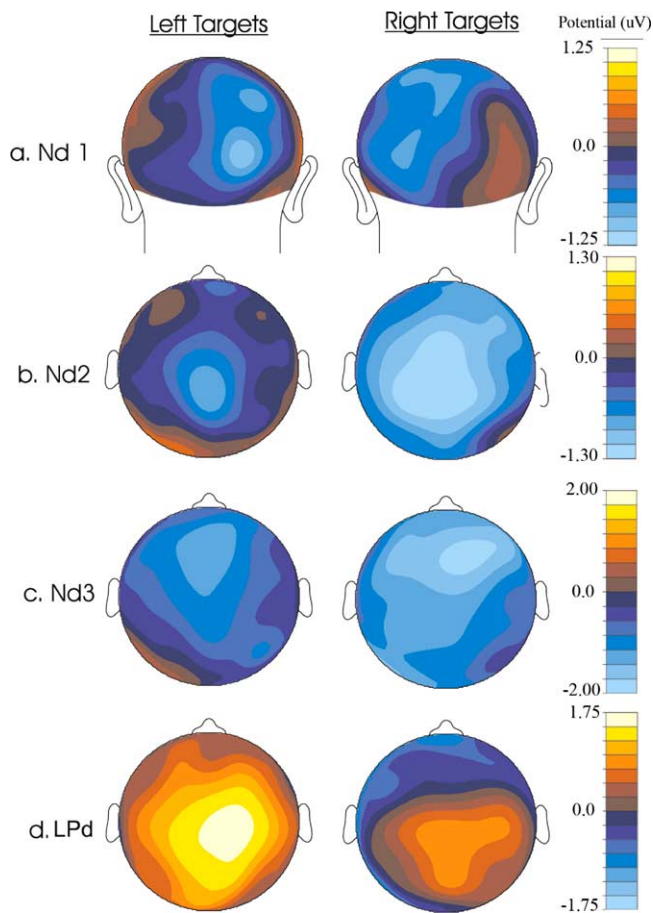
Fig. 2. Comparison of the scalp distributions of the Nd1, Nd2, Nd3, and LPd (valid-cue-trial minus invalid-cue-trial voltage difference): (a) the contralateral distribution of the Nd1; (b) the focus of the Nd2 at CZ; (c) the distributed frontal Nd3; (d) the parieto-central LPd. Note that only the Nd1 distribution is contralateral with respect to the target.

in the TPJ could explain this pattern of electrical activity. We seeded two sources, one in the right TPJ at the coordinates of the left-target Nd1 source (25, −46, 19) and one mirror symmetric to this in the left TPJ (−25, −46, 19). These dipoles were then fixed at these locations but allowed to change in magnitude and orientation. This configuration of dipoles in bilaterally symmetric TPJ accounted for 87.3% of the variance in the scalp topography of the right-target Nd1.

4. Discussion

As expected, the focusing of auditory attention at varying locations in space resulted in both behavioral and electrophysiological consequences. Responses were significantly faster and more accurate (marginally significant) for attended targets, and the ERPs elicited by such 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), as well as with the generally contralateral organization of most sensory systems.

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 et al., 2001; Rauschecker & Tian, 2000; Tata, 2003; Zatorre et al., 2002). Indeed, in the case of the left-target Nd1, the best-fitting dipole was located very close to the TPJ. Thus the present result suggests that, unlike sustained auditory spatial attention, which is thought to operate on early stages of processing including primary and/or secondary auditory cortex (Hillyard et al., 1973; Woldorff et al., 1993), the mechanism of transient auditory spatial attention operates at later stages and in cortical areas that are involved in representing auditory space. We conclude that transient spatial auditory attention does modulate at least one of the several brain regions that comprise an auditory "where" pathway.

the left-target Nd1. One possible reason for this is that the fitting algorithm placed the dipole in this location as a best compromise to fit a signal generated by two or more dipoles. Consequently, we considered whether a more complex configuration of dipoles could better explain the right-target Nd1 distribution. We specifically asked whether bilateral sources
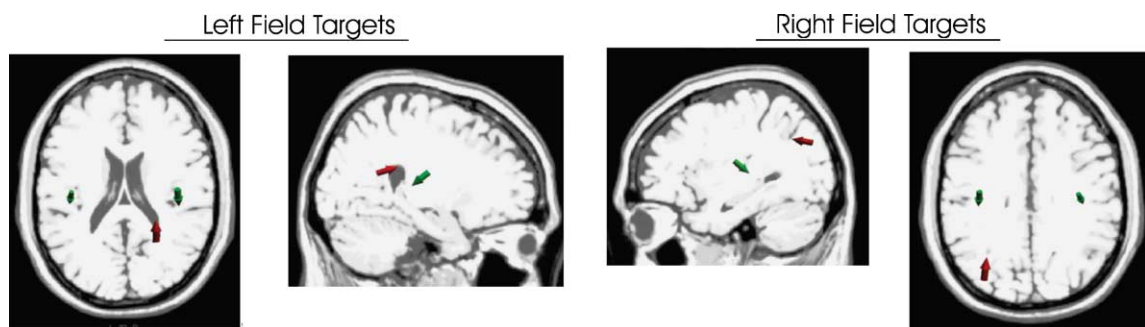

Fig. 3. Source analysis of the Nd1. Unconstrained equivalent source dipoles for the Nd1 distribution (red arrows) are shown superimposed on the MNI representative brain (both axial and sagital slices are through the Nd1 generator). The N1 generators (green arrows) in Heschl's gyrus are included as landmarks.

What is the functional significance of the Nd1? Schröger and Eimer (1997) have argued that the auditory Nd1 principally reflects a "cost" on invalid trials rather than a "benefit" on valid trials. If so, the Nd1 would be a correlate of one of the various cognitive actions that take place on invalid-cue trials. Among the first of these operations is the need to register a discrepancy between the locus of attention and the locus of the relevant stimulus—a situation reminiscent of the "mismatch" paradigm, which generates the well-known mismatch negativity (MMN) (see Näätänen, 1992; Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001; Picton, Alain, Otten, Ritter, & Achim, 2000 for reviews). This ERP component is elicited when an occasional stimulus deviates from a series of standard stimuli, and a recent investigation (Tata, 2003) of the MMN elicited by spatial deviants found fundamental similarities between it and the Nd1. Deviations in spatial location yielded contralateral MMN deflections with generators in or near the TPJ. In addition to similar coordinates, the spatial MMN and the attention-related Nd1 components had similar latencies (~150 ms for the Nd1 and ~160 ms for the MMN). 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). Since the Nd1 can be thought of as a positive ERP deflection elicited (on invalid-cue trials) when the location of a target did not match the location at which it was expected (i.e. the cued location), both the Nd1 and the spatial MMN might reflect the operation of neural circuits activated when the brain registers a discrepancy between stimuli at anticipated and unanticipated locations. An important distinction should be made however: whereas the Nd1 is evoked by moment-to-moment changes in stimulus location, the MMN requires numerous repetitions of the "template" stimulus before it emerges. It may be that listeners engaged in a transient attention task can in fact register the current locus of attention as a "template" on a moment-by-moment basis; or it may simply be that the Nd1 and the MMN have some neural circuitry in common but are correlates of different cognitive operations.

In a somewhat different interpretation, the present study can be seen as consistent with a recently advanced theory (Griffiths & Warren, 2002) regarding the function of the planum temporale, a region on the supratemporal plane posterior to Heschl's gyrus. This theory views the PT as a "computational hub" that segregates auditory information on the basis of complex spectro-temporal patterns. In particular, the theory predicts that the PT would be critically involved in handling the so-called "cocktail party effect"—the attentional selection of one stream of auditory information out of a noisy background on the basis of location and frequency characteristics. The present study has demonstrated that cueing a listener to focus attention on a location in space modulates the brain's response to auditory information presented at that location. In particular, the locus of the Nd1 was found to be close to the TPJ for left-field targets, possibly in the posterior region of the PT. The experimental paradigm employed here is somewhat different from the noisy environment envisioned in the cocktail party scenario. Nevertheless, it seems possible that the Nd1 reflects a modulation of processing within the PT as a result of the selection of auditory information on the basis of spatial location. It should be kept in mind, however, that this proposed function of the PT is not inconsistent with the notion of a posterior "where" pathway within the auditory system.

Whereas a single dipole accounting for the Nd1 elicited by left-field targets was localized to an area near the right TPJ, no simple configuration of dipoles compellingly explained the Nd1 elicited by right-field targets. The clearly lateralized nature of the right-target Nd1 over the left posterior hemisphere suggests that a source in the left TPJ might be a principle component of this modulation. It seems likely, however that additional, possibly bilateral, sources are involved. It is not surprising that attentional modulation of 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 in audition (De Renzi, Gentilini, & Barbieri, 1989; Griffiths et al., 2000; Zatorre et al., 2002) as well as vision (Posner, Walker, Friedrich, & Rafal, 1984), and deals with both left and right hemispace, whereas left parietal cortex deals with only right hemispace. Furthermore, recent studies have found evidence for specialization of the right hemisphere for spatial processing of sounds (Palomaki, Alku, Makinen, May, & Tiitinen, 2000; see also Tervaniemi & Hugdahl, 2003, for a review of lateralization within auditory pathways). Thus, at least at the stage of processing indicated by the Nd1, 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. The Nd1 modulation, particularly in the case of right-field targets, probably reflects a superposition of two or more generators located in posterior parietal cortex.

Regardless of the sensory modality, the focus of selective attention can be oriented voluntarily (a goal-driven response on the part of the perceiver) or reflexively (a stimulus-driven response to sudden events in the sensory environment). The direct-cue paradigm employed in this study leaves an interesting question unanswered: do voluntary and reflexive orienting of attention yield similar modulations of the auditory ERP? Comparisons of these two modes of attention orienting have revealed important differences in regard to behavioral measures (McDonald & Ward, 1999; Spence & Driver, 1994). It therefore seems likely that these two modes of orienting should manifest different modulations of the ERP, provided they could be disentangled. In the direct-cue paradigm employed here, both voluntary and reflexive orienting guided attention to the cued location. In a companion to the present study, a counter-cue was used in which voluntary and reflexive attention were engaged at different locations. The companion study found that the Nd1 and Nd2 modulations were most likely a consequence of reflexive orienting while the later Nd3 and LPd modulations

were consequences of both reflexive and voluntary orienting (Tata, 2003).

The present study was aimed at elucidating the cortical generator(s) of the Nd1 modulation, without specifically investigating the later Nd2 and Nd3 components. The functional significance of the Nd2, Nd3, and LPd modulations is not known. The frontal and central distributions of these later modulations is similar to the later negative deflections commonly observed in sustained-attention paradigms (Hillyard et al., 1973) and may reflect a convergence of the mechanisms of transient and sustained attention. The LPd observed between 500 and 700 ms is, to our knowledge, an as yet unreported attentional modulation, the significance of which is unclear. An important physiological difference between these later modulations and the Nd1 is worth noting: only the Nd1 was distributed contralaterally with respect to the target. The later components were focused at the midline, suggesting bilateral generators, and possibly signifying a distinction between early sensory processes and later cognitive operations. Further investigation of the cortical sources of these later modulations will advance our understanding of the role of attention in modulating the auditory "where" pathway.

5. Conclusion

Selective attention to the spatial location of an upcoming auditory stimulus modulated both the behavioral and physiological responses to that stimulus. The earliest ERP correlate of this transient focusing of attention, the Nd1, most likely reflects modulation of spatially-tuned auditory neurons in the putative posterior "where" auditory pathway in human cortex. This suggests the intuitive notion that spatial attention acts to modulate the behavior of neurons in regions of the brain concerned with the spatial representations of auditory stimuli. Thus attentional mechanisms seem to share (or exploit) a parallel functional segregation with the processing pathways of the auditory system in general.

Acknowledgments

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