

Spatially Distributed Cortical Excitation Patterns of Auditory Processing during Contralateral and Ipsilateral Stimulation

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Abstract

■ Utilizing the high spatial and temporal resolution of magnetoencephalography in conjunction with magnetic resonance images, the current study explored the underlying electrical patterns of cortical excitation during both contralateral and ipsilateral auditory stimulation. Instead of studying only the peaks of the N100 component of the evoked magnetic field, a 30-msec window was chosen about the area where the peaks occurred and the intracranial sources generating that component were estimated at successive 5-msec intervals. Results

indicated that the sources for both contralateral and ipsilateral conditions were best represented as a continuous movement of activation in an anterior–inferior direction along the superior surface of the temporal lobe. Although the peak magnetic fields of the N100 to contralateral stimulation were of shorter latency and higher amplitude, the generating sources of both had very similar time-dependent movement patterns, and comparisons of source localizations were dependent on the latency at which they were contrasted. ■

INTRODUCTION

Brain research has traditionally progressed along two major tracks. One approach includes studies of micro-anatomy, biochemistry, and electrophysiology of single neurons or small defined groups of neurons. The other includes studies of large ensembles of neuronal activity including areas such as cognition and behavior, which have been studied using electroencephalography (EEG), computerized tomography (CT), magnetic resonance imaging (MRI), regional cerebral blood flow, and positron emission tomography. There has been much interest recently in finding methodologies and paradigms that will bring some of these diverse efforts closer together, thus enhancing their efficiency.

Magnetoencephalography (MEG) is an innovative procedure that utilizes low-temperature superconductive materials to measure magnetic fields produced by electric currents in the brain (Cohen 1972; Kaufman & Williamson 1980, 1982; Williamson & Kaufman 1981a, 1987). Magnetic fields have unique features that provide complementary information to traditional EEG measures. First, MEG signals travel through the various layers of inhomogeneous brain and skull tissues with relatively little distortion (Cuffin 1982; Barth, Sutherling, Broffman, & Beatty 1986). Second, the MEG sensors (i.e., coils)

primarily detect fields from current sources tangential to the scalp, while radial sources remain essentially invisible. MEG measurements are also reference independent and there is no concern with level of resistance between the scalp and the sensors (Cohen 1972; Williamson & Kaufman 1981; Romani & Narici 1986).

One of the major putative advantages of MEG is its high spatial resolution, which allows localization of the electrical source generating extracranial magnetic fields (Cohen 1972; Williamson & Kaufman 1981b; Romani, Williamson, & Kaufman 1982). Several studies using artificial conductive spheres with implanted dipole sources and craniums from cadavers indicated that a source localization accuracy of within a few millimeters is obtainable, especially in the more superficial sources (Barth et al. 1986). Although, to date, localization has been limited to the single dipole model, computational models that can use multiple dipoles are being developed (Nunez 1986). Human studies of the N100 auditory response have verified the efficiency of MEG to localize the signal source (Romani & Narici 1981; Eberling, Bak, Kofoed, Lebech, & Särmark 1982), and recent studies from our laboratory in which MEG sources were projected onto subjects' MRIs demonstrated that the source was located in the vicinity of the primary auditory cortex (Papanicolaou, Baumann, Rogers, Saydjari, Amparo, & Eisenberg

1989); source localization was reliable across repeated measurement sessions (Baumann, Rogers, & Papanicolaou 1989). In addition to the good spatial resolution provided by MEG, it also can provide time resolutions of better than 1 msec (Hari & Lounasmaa, 1989). It is hoped that the high spatial and time resolutions of MEG can be exploited to bridge some of the gaps between the microlevel and macrolevel tracks of brain research.

The N100 component of auditory evoked potentials has been extensively studied. The abiding interest in the N100 is the result of the fact that it varies with parameters of the physical stimulus as well as cognitive factors, most notably attention (for an extensive review see Näätänen & Picton 1987). In electrophysiological studies using arrays of electrodes distributed over the hemisphere, the source was estimated to be in the general area of the Sylvian fissure (Wood & Wolpaw 1982). Subsequently, in MEG studies the source of the equivalent N100 was precisely located on the supratemporal plane within the Sylvian fissure (Romani & Narici 1986; Eberling et al. 1982; Papanicolaou et al. 1989).

Evoked potential studies comparing the N100 during contralateral and ipsilateral stimulation have been equivocal in that some have reported differences (Majkowski, Bochenek, Bochenek, Knapik-Fijalkowska, & Kopec 1971; Wolpaw & Penry 1977) whereas others reported no asymmetries in either latency or amplitude (Peronnet, Michel, Echallier, & Girod 1974; Pantev, Lütkenhöner, Hoke, & Lehnertz 1986). Evoked magnetic field studies, however, have consistently reported that the N100 has a larger amplitude and shorter latency during contralateral stimulation than during ipsilateral stimulation (Reite, Zimmerman, & Zimmer 1981; Eberling et al. 1982; Pantev et al. 1986; Hari & Mäkelä 1988).

Distinct changes in both the latency and morphology of the N100 of the evoked potential at different scalp sites and the fact that its duration is quite long compared to the oscillations produced during stimulation of a column of cortical pyramidal cells have led researchers to postulate that it is a composite wave resulting from a number of different generators (Wood & Wolpaw 1982; Scherg & Von Cramen 1986). However, an alternative hypothesis to those of a single or multiple yet stationary and simultaneous generators would be that the N100 is a composite wave resulting from the consecutive activation of adjacent cortical columns in the auditory cortex.

RESULTS

Clear evoked magnetic fields characterized by a prominent N100 component to both contralateral and ipsilateral stimulation were obtained for all subjects. Since magnetic fields curl around the electrical current perpendicular to the flow, this, by convention, produces positive values where the field exits the brain with the highest magnetic value representing the maximum extreme and negative values occur as the magnetic field

reenters the head with the highest negative value referred to as the minimum. A comparison of the N100 peak amplitudes and latencies for both the maximum and minimum extrema, using dependent *t* tests, indicated that contralateral peaks had shorter latencies at both extrema. The mean latencies during contralateral and ipsilateral stimulation were 91.66 and 112.50 msec [$t(11) = -4.73, p < .001$] at the maximum peaks and 100.00 and 117.08 msec [$t(11) = -4.66, p < .0007$] at the minimum extrema. Peak amplitudes at the maximum magnetic fields were 338.75 and 220.08 ft [$t(11) = -5.69, p < .0001$] for contralateral and ipsilateral stimulation and -404.42 and -343.42 ft [$t(11) = -1.48, n.s.$], respectively, at the minimum peaks.

Figure 1 shows a sample of magnetic field waveforms for a single subject taken at 10 different points on the lateral side of the head over the right hemisphere. The drawing of a head in the center gives the approximate location of the recording sites of these waveforms. In this case, point 1 would represent the minimum and point 10 the maximum. Note that the magnetic field strength falls off rapidly away from the two extrema in all directions producing a characteristic isofield map as illustrated in Figure 2. In this case the maps appear quite similar for both contralateral and ipsilateral stimulation.

The major emphasis of this project was to study time-dependent changes in the location of the N100 source

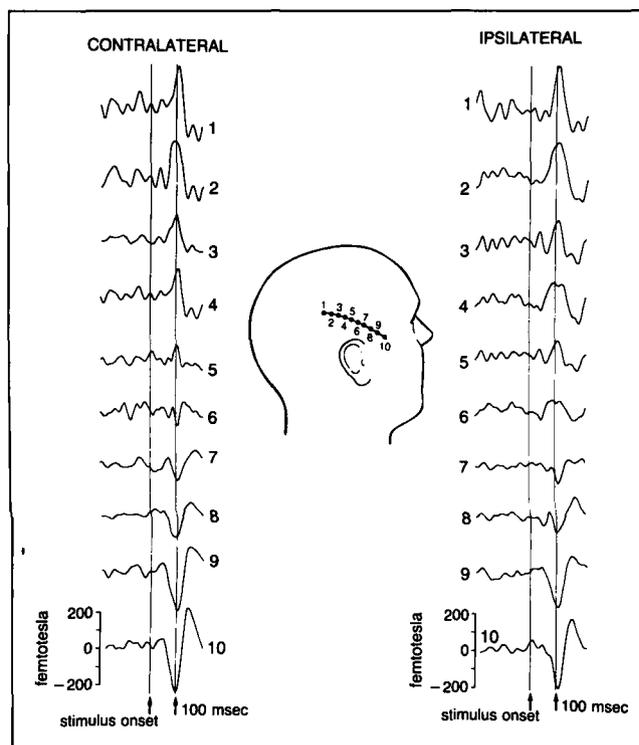


Figure 1. A sample of magnetic field waveforms during contralateral and ipsilateral conditions for a single subject. The schematic of the head in the center gives the approximate area from which waveforms were measured with point 1 representing the minimum and point 10 the maximum extrema.

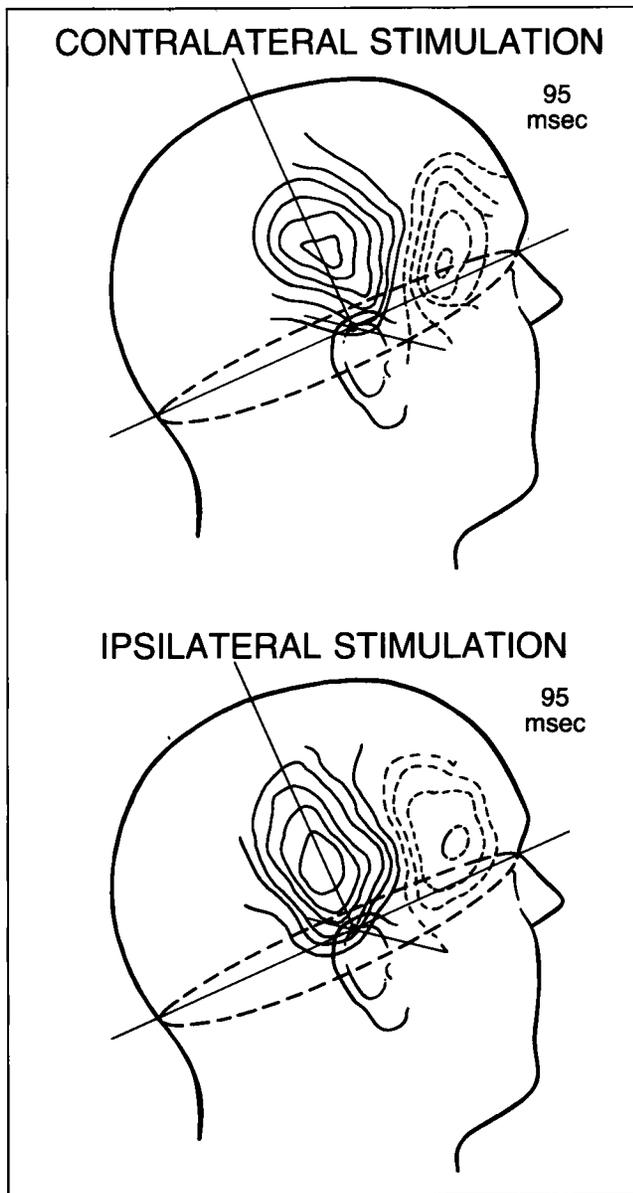


Figure 2. Illustration of the isocontour magnetic field maps for the same subject at 95-msec latency for contralateral and ipsilateral stimulation. Note that values fall off rapidly in all directions from the extrema and that both maps appear similar.

during sequential 5-msec intervals in a 35-msec window around its peaks and to compare these locations during contralateral and ipsilateral stimulation. Figure 3a is a three-dimensional representation of the movement of the N100 source modeled after a single equivalent dipole during contralateral stimulation for the same subject whose evoked magnetic fields and contour maps are represented in Figures 1 and 2. The box drawn on the subject's sagittal MRI image in the bottom of the figure represents the area from which these dipoles occurred. Figure 3b shows the time-related changes in the source during ipsilateral stimulation. It is evident in both conditions that the source moves in an anterior direction

along the superior surface of the temporal lobe near the primary auditory cortex.

Figure 4 summarizes means and standard errors across all 12 subjects for the time-dependent changes in the generator source during successive 5-msec intervals between 80 and 115 msec for the contralateral condition and between 90 and 125 msec for the ipsilateral condition. Each graph represents the three-dimensional coordinate system superimposed on the head. The x axis represents the anterior-posterior direction, which indicated that a significant movement occurred in the anterior direction during successive intervals. A regression analysis of location on time indicated a significant linear anterior movement during both the contralateral [$F(1,71) = 6.54, p < .01$] and ipsilateral conditions [$F(1,60) = 5.78, p < .01$]. There were no differences in the slopes of the regression lines between contralateral and ipsilateral conditions.

The z axis, which represents the superior-inferior direction on the subjects' heads, indicates that, for this group of subjects, movement also occurred in an inferior direction for both contralateral [$F(1,71) = 6.47, p < .01$] and ipsilateral conditions [$F(1,60) = 4.48, p < .03$] presentation of auditory stimuli. There was no significant time-dependent change along the y axis (lateral-medial). The orientation of the dipole rotated in a clockwise direction about the x axis plane approximately 17° in a significant linear fashion [$F(1,17) = 4.14, p < .05$] during contralateral stimulation. For ipsilateral stimulation the rotation was similar but nonsignificant.

Final comparisons were made between the location of the dipoles during the three latencies at which the contralateral and ipsilateral conditions overlapped, which was at 100, 105, and 110 msec poststimulus. Although the N100 components overlap to an even greater extent, dipole localization was limited because of the lower signal-to-noise ratio away from the peak of the waveforms. The only significant differences using a repeated measures multivariate analysis of variance was in the anterior-posterior plane, which indicated that neuronal activation associated with ipsilateral stimulation was slightly posterior [Wilks $\lambda = .5208; F(2,15) = 4.60, p < .03$] to that associated with contralateral stimulation.

DISCUSSION

These results indicate that both contralateral and ipsilateral stimulation produce a relatively large negative magnetic waveform that results from nonstationary activation of electrical sources in the primary auditory cortex and that involves successive movement of the source in the anterior and inferior directions. It appears that the downward movement of the generator sources follows the typical sloping of the temporal lobe, which was confirmed by plotting the waves on MRI scans of the subjects' brains. In the example illustrated in Figure 3, this inferior movement did not occur. However, close inspection of

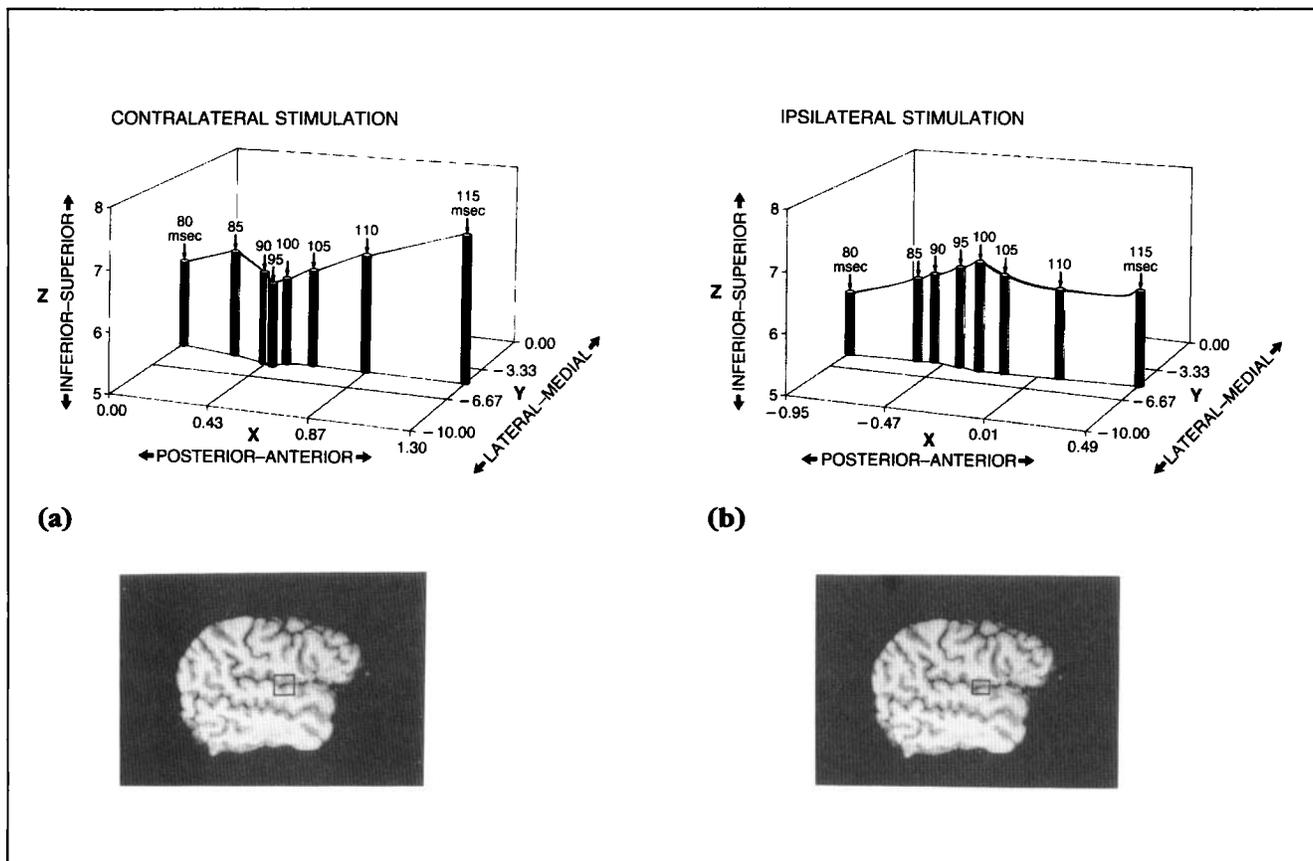


Figure 3. (a) A three-dimensional representation of the movement in centimeters of the dipole at successive 5-msec intervals during contralateral stimulation for the same subject. The area outlined on the sagittal MRI slice indicates the area of the brain that the dipole traversed. (b) A three-dimensional representation of the movement in centimeters of the dipole at successive 5-msec intervals during ipsilateral stimulation. The area outlined on the sagittal MRI slice indicates the area of the brain that the dipole traversed.

the superior surface of the temporal lobe areas outlined on the MRI scans shows that the temporal lobe was flat in that subject.

There is some anatomical/physiological basis for propagation of electrical activity to occur between adjacent cortical columns in the primary auditory cortex. For example, architectonic studies of cortical cells indicate that corticocortical interconnections are present in which pyramidal cells send short axons down through superficial white matter layers and reemerge onto adjacent pyramidal cells at tangential locations (Braitenberg 1985). The primary auditory cortex is characterized by a rich abundance of myelinated short cortical interconnections as compared to association cortex, which typically send these intracortical fibers over relatively longer distances (Brugge & Reale 1985). In fact, one of the more distinguishing gross morphological differences between primary sensory and other cortical areas is the appearance of this dense layer of short myelinated axons. The time constants of the pyramidal cells are approximately 8 msec and the propagation of excitatory activity along corticocortical connections is of the order of 0.5–1.0 msec (Nunez 1986). Thus, the local consecutive source movement

could result from successive activation of sets of cortical columns followed by activation along corticocortical fibers or by direct interaction between cortical pyramidal neurons and adjacent ones. The N100 wave then could be conceived of as the summed sequential activity of these cortical columns.

An alternative hypothesis for the apparent movement of the source has been proposed involving the summed activity of discrete stationary asynchronous dipoles. Scherg and Von Cramen (1985) proposed that the increased peak latency of the N100 auditory evoked potential along the coronal plane could be explained by the presence of two dipoles: one on the superior surface of the temporal lobe (tangential to the surface of the head) and the other on the lateral surface of the temporal lobe (radial to the head). Yet this hypothesis does not adequately explain the present data for the following reasons: The movement of magnetic fields along the anterior surface of the temporal lobe cannot be explained by the interaction of a radial and tangential source because MEG does not reflect the activity of radial sources (Cohen 1972; Kaufman & Williamson 1980, 1982). However, two dipoles, both tangential to the outer surface of the head,

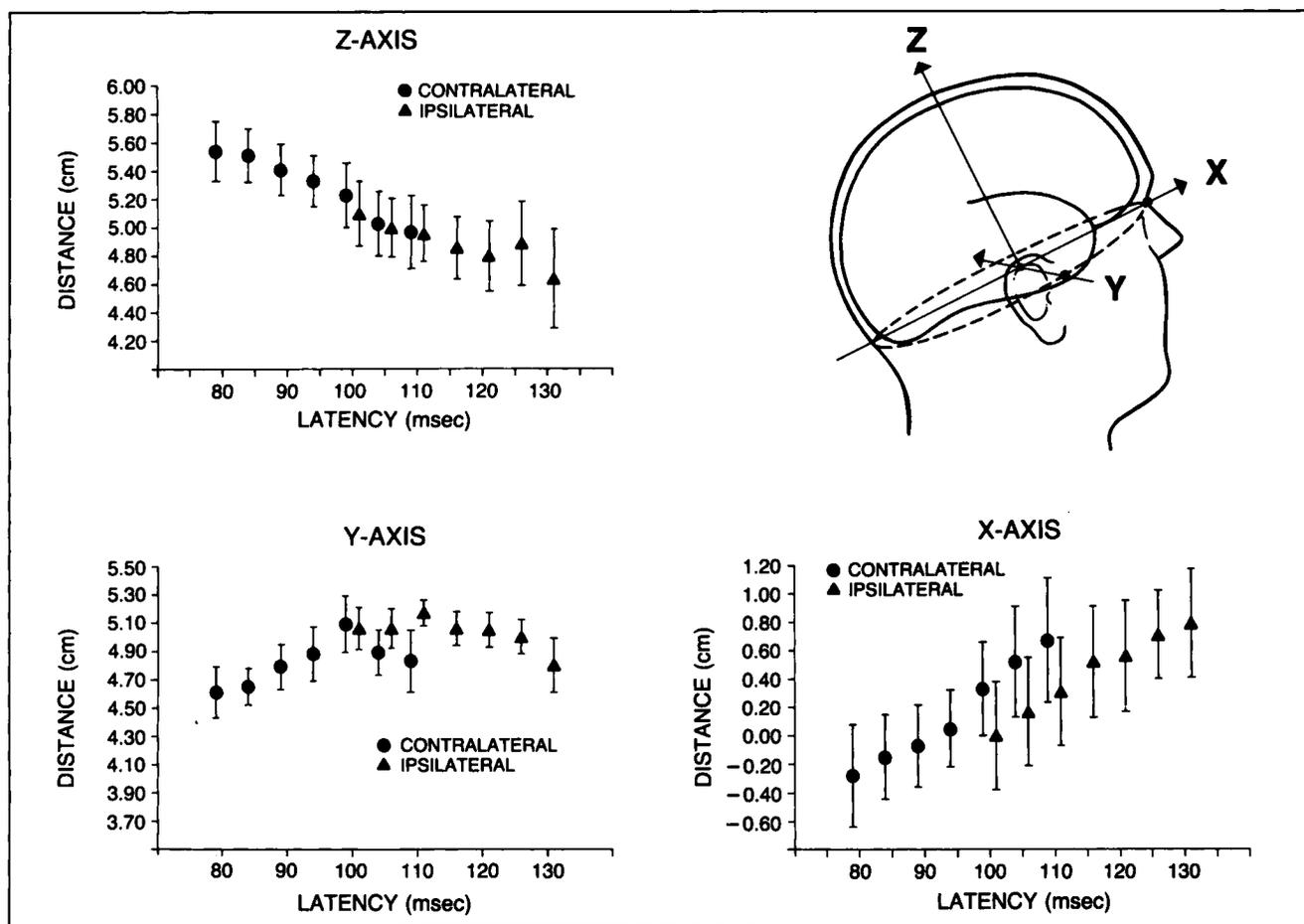


Figure 4. The three separate graphs indicate the group mean and standard error for movement of the generator source during consecutive 5-msec intervals for both contralateral and ipsilateral stimulation conditions for all 12 subjects. Each graph represents movement in a different plane as illustrated on the schematic of a head. A significant linear regression was present during both contralateral and ipsilateral conditions in both the *x* axis (anterior–posterior plane) and the *z* axis (superior–inferior plane).

aligned along the anterior–posterior axis could conceivably produce the appearance of anterior movement; however, this would necessitate that the model be modified to include at least three dipoles to explain both the electrical and magnetic data. The presence of multiple dipoles is often discernible on the isofield contour maps when they show more than two extrema (Nunez 1986). In the present study no such evidence was apparent. Additionally, in several of the subjects whose time-series dipoles were superimposed on their MRI scans, it was evident that they followed the contour of the superior surface of the temporal lobe. For example, in Figure 3a, the dipole during contralateral stimulation follows the supratemporal surface even to the extent that it follows the sulcus next to the transverse gyrus. Finally, there is no compelling anatomical or physiological evidence to justify the multiple stationary dipole model. Consequently, its utility in interpreting the present findings remains questionable.

Results of comparisons between ipsilateral and contra-

lateral conditions agree with earlier findings that contralateral stimulation produces a larger response, which peaks at a shorter latency (Reite et al. 1981; Eberling et al. 1982; Pantev et al. 1986; Hari & Mäkelä 1988). However, there are discrepancies between these and previously reported data in regards to the location of the N100 sources. Previous studies indicated that the generator of the N100 to ipsilateral stimulation is anterior to the N100 source to contralateral stimulation (Eberling et al. 1982; Pellizone, Williamson, & Kaufman 1985). However, in the current study comparisons of the locations of the generators at various latencies show that this difference is due to the time lag between the peaks of the two conditions. When sources accounting for the N100 are compared at the same latencies, sources of ipsilateral stimulation appear to be slightly posterior to those of the contralateral response. Examining Figure 4, it is evident that if a comparison of the *x* axis values was made at the peaks of the minimum (90 and 120 msec for contralateral and ipsilateral, respectively), the source of

the ipsilateral response would appear to be anterior. Thus, the previously reported anterior location of the ipsilateral dipole appears to be a time-dependent difference of two continuously moving sources that peak at different latencies.

In summary, the present results indicate that the N100 auditory evoked magnetic response is a composite waveform reflecting the sequential activation of a series of adjacent cortical columns arranged on the superior surface of the temporal lobe within the primary auditory cortex. Although the waveforms for contralateral and ipsilateral stimulation conditions differ in latency and amplitude, the underlying processes appear to be similar in that they move approximately the same distance over the same amount of time.

Interdisciplinary studies of the anatomy and physiology of the primary auditory cortex coupled with MEG studies of the relationships between changes in waveforms associated with various stimulus and cognitive manipulations could enhance our current understanding of cortical processing. For example, evoked potential studies of auditory processing in monkeys has demonstrated that the middle and long latency components (P12, P22, N60, and N100) have electrical centroids aligned anteriorly along the supratemporal surface (Arrezo, Pickoff, & Vaughan 1975). The present results suggest that instead of discrete steps from one generator to another, a continuous spread of excitation forms spatiotemporal patterns of neuronal activity. It can be assumed that these patterns are an initial phase of higher order processing since it has been well established that simple tone discrimination occurs in the absence of the primary auditory cortex (see Beach 1960). Thus, future studies of the effects of cognitive variables on long latency evoked responses (e.g., N100, P200, and P300) that investigate changes in spatiotemporal patterns of cortical activation should further enhance our understanding of the physiological determinants of these cognitive processes.

METHOD

Twelve normal volunteers ranging in age from 22 to 54 years including six males and six females participated in the study. Each subject was individually tested in a magnetically shielded chamber (Vacuumschmelze GmbH). A 1000-Hz tone of 50-msec duration (10 msec rise/fall and 30 msec plateau) was generated by a Nicolet Compact Four stimulus generation module. The intensity of the tone was 105 dB nHL at the source, which was channeled to the subject's ear via a 3-foot-long plastic tube with a 0.053-inch inner diameter terminating in an insert earphone (Nicolet TIP-300), yielding an estimated intensity level at the ear of 95 dB. Similarly, a white masking noise was generated to the opposite ear, which was 60 dB nHL at the source and approximately 50 dB at the subject's ear. One hundred responses were delivered to each ear

with a stimulus delivery rate that varied randomly between 0.33/sec and 0.5/sec around a mean ISI of 0.4/sec.

A seven-channel Neuromagnetometer (Biomagnetic Technologies Inc. Model 607) utilizing second-order superconductive quantum interference devices (SQUIDs) with a coil diameter of 1.8 cm and a 4 cm baseline was used to measure averaged evoked magnetic fields over the right hemisphere of each subject. Recording sessions consisted of eight placements of the recording device, which were distributed over the right side of the head yielding 56 measurements of average evoked fields. Signals were bandpassed from 0.3 to 50 Hz and digitized at 200 Hz for 1-sec epochs, which included a 0.5-sec baseline period. The order of placements of the sensors was randomized for each subject. Both contralateral and ipsilateral stimulation were delivered to each subject before moving the sensing device. The order of ear stimulation was also randomized. The entire recording procedure for each subject took less than 2 hrs. The exact location of the sensors in relation to the subject's head was measured using three low-frequency magnetic field sensors placed on the subject's head with a transmitter on the cryogenic container that housed the SQUIDs. Error tolerance for location of the sensors was less than 1 mm.

The spatial parameters (Cartesian coordinates), as well as the strength and orientation of the generator source, were estimated from the 56 magnetic field measurements at a given latency. A finite difference version of the Levenberg-Marquardt algorithm was used for this purpose. Calculations were based on the "open field" dipole model (an electrical source with a positive and negative pole) generating a magnetic field within a spherical container. A 10-cm circular area on the side of the subject's head was digitized and a best fitting sphere was calculated using a least-squares equation. The dipole model produces a distinctive isocontour map consisting of two extrema (maximum–minimum) in which the field strength diminishes in all directions as you move away from the extrema. A measure of goodness-of-fit is obtained by correlating the observed measurements with the predicted values from the model. In the current study a minimum acceptance level was set at $r = .88$ and isocontour maps had to show good dipole fields.

Instead of localizing the source only at the peak of the waveform as is typically done, the location of the dipole was calculated at each successive 5-msec interval for all latencies between 80 and 110 msec following presentation of the stimuli to the contralateral (left) ear and between 90 and 120 msec for the ipsilateral (right) ear.

To be able to visualize the anatomic location of the dipoles, each subject also underwent magnetic resonance imaging (MRI). The external landmarks used to determine the location of the sensors were marked on the MRI by affixing vitamin A pills to the subject. The appearance of the pills on the MRI was used to define a

coordinate system corresponding to that employed in the MEG system.

Note

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