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Tonotopic Organization of the Human Auditory Cortex

Abstract. *Neuromagnetic measurements of responses to auditory stimuli consisting of pure tones amplitude-modulated at a low frequency have been used to deduce the location of cortical activity. The evoked field source systematically increased in depth beneath the scalp with increasing frequency of the tone. The tonotopic progression can be described as a logarithmic mapping.*

In humans, there is a topological correspondence between the periphery and the primary sensory cortex in both the somatic and visual sense modalities. Evidence from the cat (*1*), squirrel (*2*), and monkey (*3*) suggests that there may also be a human tonotopic mapping as well, but thus far evidence of such mapping is lacking. We report evidence from neuromagnetic studies indicating the existence of an orderly projection of frequencies onto the human auditory cortex.

Previous measurements of magnetic fields after auditory stimulation have revealed transient fields outside the human scalp (*4–6*). The equivalent sources of these fields may be modeled as current dipoles in the vicinity of the auditory cortex of each hemisphere oriented normal to the lateral sulcus. The direction of current flow producing these fields is opposite to the flow associated with corresponding components of auditory evoked scalp potentials. Consequently, the most likely source of the evoked field is the net flow of intracellular currents within the cortex forming the floor of the lateral sulcus rather than the volume currents that are associated with the evoked potentials.

Techniques used in biomagnetic studies have been described (*7*). Our magnetic field sensor consists of a second-derivative gradiometer with 2.4-cm diameter and 3.2-cm baseline between adjacent coils coupled to a SQUID sensor (S.H.E. Corporation). This assembly provides both the sensitivity required to measure evoked fields and a satisfactory reduction of environmental noise without the aid of magnetic shielding. All superconducting circuits and elements were contained in a superinsulated fiber glass Dewar, which permitted placing the pickup coil of the gradiometer as close as 8 mm to the scalp. The Dewar was oriented so that the magnetic field component normal to the scalp was monitored by the gradiometer. The output voltage of the SQUID electronics, which is simply proportional to the net field sensed by the gradiometer, was applied to a bandpass filter tuned to the stimulus modulation frequency with roll-off of 48-dB per octave on the high- and low-frequency sides.

Auditory stimuli were presented binaurally by means of standard airline plastic earphones, the transducers of which had been tested to avoid undesirable magnetic artifacts. The stimuli consisted of pure tones, the amplitudes of which were sinusoidally modulated. The depth of modulation was somewhat less than 100 percent, and the modulation frequency was much lower than that of the carrier frequency. Hence, the Fourier spectrum of the acoustic signal was composed of a carrier frequency and two sidebands shifted from the carrier by an amount equal to the modulation frequency. The acoustic signal was therefore confined to a narrow bandwidth. A 1024-channel signal averager triggered by the oscillator providing the modulation signal was used to average the filtered SQUID output to reveal the steady-state response at the modulation frequency. Four different carrier frequencies were used for both of our two subjects. For subject S.W. they were 200, 600, 2000, and 5000 Hz; because subject C.P. did not respond strongly to the 5000-Hz signal, the frequencies were 100, 200, 600, and 2000 Hz. Since responses with strong amplitudes were obtained at a modulation frequency of 32 Hz in pilot studies, we used that value (*8*). Initially, one stimulus amplitude was set at about 80-dB sound pressure level so that it could be easily perceived above the

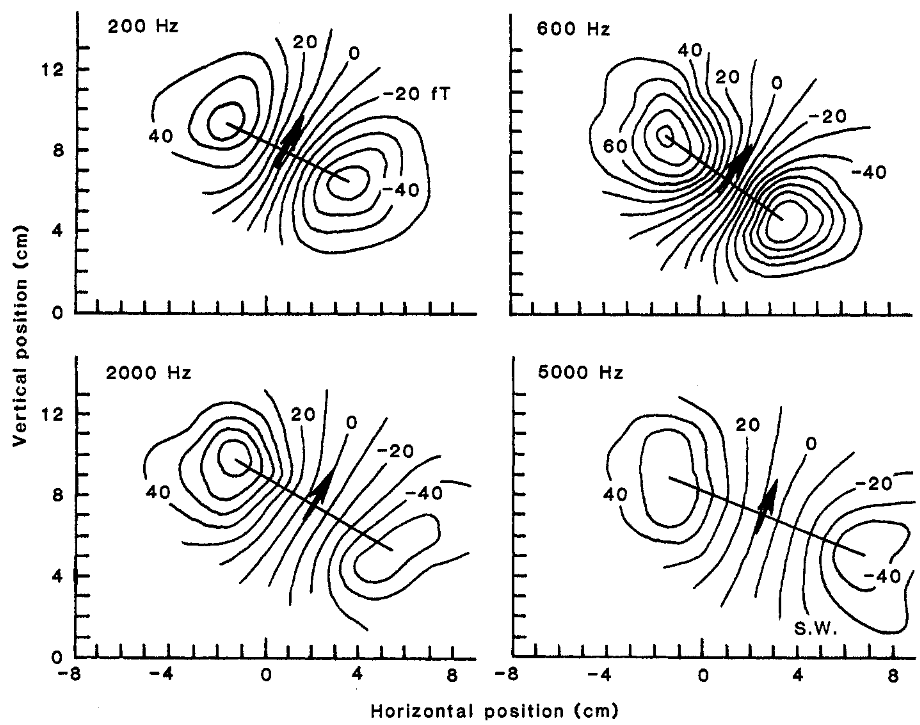

Fig. 1. Isofield contours for the component of the evoked magnetic field normal to the scalp detected over the right hemisphere of subject S.W. The origin is at the ear canal, the corner of the eye lies at position (0, 9), and the vertical axis points to the vertex. Arrows denote the position and the orientation of the equivalent current dipoles for 200-, 600-, 2000-, and 5000-Hz tones. The sense of the arrow is arbitrarily chosen.

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background acoustic noise. The amplitudes of the other stimuli were then adjusted by the subject until they seemed to be equal in loudness to that of the initially selected stimulus. Responses were averaged for about 30 seconds (corresponding to 1000 sweeps) to achieve a satisfactory signal-to-noise ratio. At least two measurements were obtained at each position over the scalp.

Figure 1 illustrates constant field contours for subject S.W. obtained by an interpolation fit of the data by the Laplacian method. The following coordinate system was chosen to define the grid: the origin was set at the ear canal, with the horizontal position measured along the "equator" connecting the origin and the outer canthus of the eye; the vertical distance was measured up the appropriate "meridian" from this line toward the vertex. The amplitude and phase of the sinusoidal responses at 32 Hz were measured at about 40 positions on the grid at 1-cm intervals within a 10 by 10 cm region of the scalp. Responses to the four tones were measured at each position without moving the probe. A reversal of polarity (180° phase difference) distinguished emerging and reentering fields. For each tone, two separated regions of maximum emerging and reentering field were observed. These patterns approximate those of a current dipole lying beneath the scalp and midway between the two maxima (Fig. 1). The position of this midpoint lies approximately over the primary auditory area of the cortex.

Under the assumption that the active cortical region can be represented by a current dipole, it is possible to determine its location inside the brain (*9*). In particular, through the use of a conducting sphere model for the posterior portion of the head, in which the conductivity may vary radially (*10*), measuring the angle identified by the two maxima with respect to the center of the sphere permits the depth of the dipole from the surface toward the center of the sphere to be determined. For this purpose an average radius for the head of each subject was estimated from measures of its curvature. The actual distance between the maxima was measured over the scalp, and the corresponding angles were evaluated. Depths were computed from these values with a correction to take into account the finite baseline of the gradiometer (*11*). Figure 2a shows the depth beneath the scalp of the current dipole representing the evoked source as it varies with frequency for each of the two subjects. The values of these depths

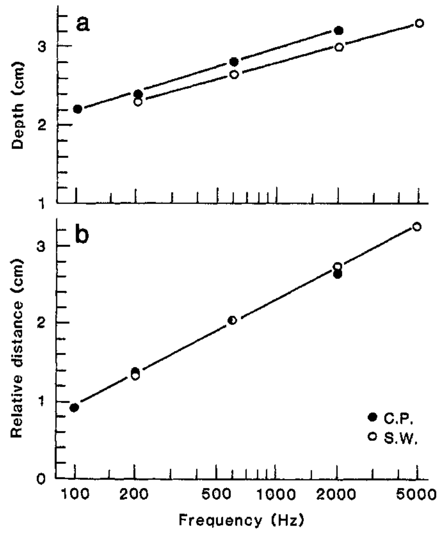

Fig. 2. (a) Depths beneath the scalp of the equivalent current dipoles representing cortical activity for the two subjects plotted as a function of the logarithm of the frequency. (b) Cumulative three-dimensional straight-line distance between adjacent dipoles as a function of the logarithm of the frequency.

are consistent with the sources lying on the auditory cortex at positions in the lateral sulcus successively farther from the scalp with increasing frequency. The progression of depths for both subjects is adequately represented by a logarithmic function of frequency.

The rate of increase in depth with frequency differed slightly between subjects, even though the radius of curvature of their heads was identical (7.5 cm). The lateral translation of the source with frequency also differed between the two subjects, probably reflecting differences in cortical anatomy. To take into account these individual differences we computed the straight-line distance in three dimensions between each source and then determined the cumulative point-to-point distance to estimate relative distances along the cortex (Fig. 2b). The origin of the vertical scale was arbitrarily chosen for the two subjects so that the relative distance extrapolated to zero at a frequency of 20 Hz. The progression in relative distance for the two subjects was the same linear function of the logarithm of frequency.

Evidence from microelectrode studies made directly on the brain of cat (*1*), squirrel (*2*), and monkey (*3*) suggests a similar tonotopic map. In these animals, as well, the projection sequence is essentially logarithmic over the middle decade of the spectrum. The logarithmic tonotopic projection in Fig. 2b may be related to the reason the just noticeable frequency difference within the bandwidth 500 to 5000 Hz is nearly a fixed percentage of the frequency, which implies that the least noticeable decrement of the logarithm of the frequency is a constant, independent of frequency (*12*). In the cochlea the point of maximum sensitivity indicated by electrical measurements shows a similar displacement with the logarithm of the frequency (*13*). This suggests a direct mapping of the cochlea on the cortex. If we assume that the active region of the primary auditory cortex has a uniform width and density of neurons, the logarithmic tonotopic map implies that the same number of neurons in the cortex is dedicated to each octave in frequency span.

The auditory cortex of infrahuman species has been revealed by microelectrode studies to have a complicated organization with several projection areas (*14*). The relatively simple structure revealed in humans by our neuromagnetic studies may be due to the comparatively coarser measure of this technique. More refined studies with a gradiometer of higher resolution may be needed to discriminate contributions from different areas.

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