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EVIDENCE FOR MULTIPLE AREAS IN THE HUMAN AUDITORY
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M PELIZZONE ET AL. 1984 18 N00014-76-C-0568

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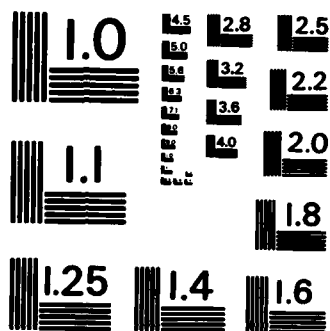
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REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER 18	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) Evidence for Multiple Areas in the Human Auditory Cortex		5. TYPE OF REPORT & PERIOD COVERED Publication
7. AUTHOR(s) Marco Pelizzone, Sameul J. Williamson, and Lloyd Kaufman. Dr. Pelizzone is supported by Swiss National Science Foundation.		6. PERFORMING ORG. REPORT NUMBER
9. PERFORMING ORGANIZATION NAME AND ADDRESS Neuromagnetism Laboratory, Depts. of Physics and Psychology, New York University, 4-6 Washington Pl., New York, NY 10003.		8. CONTRACT OR GRANT NUMBER(s) M00014-76-C-0568
11. CONTROLLING OFFICE NAME AND ADDRESS Office of Naval Research (Code 441) Department of the Navy Arlington, VA 22217		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS NR 201-209
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)		12. REPORT DATE
		13. NUMBER OF PAGES 5
		15. SECURITY CLASS. (of this report)
		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE
16. DISTRIBUTION STATEMENT (of this Report) Distribution unlimited		
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)		
18. SUPPLEMENTARY NOTES To be published in Proceedings of the 5th World Conference on Biomagnetism, Pergamon Press: New York (1984).		
19. KEY WORDS (Continue on reverse side if necessary and identify by block number) Neuromagnetism; evoked responses; magnetoencephalogram; SQUID.		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) Neuromagnetic measurements of the transient responses to tone burst stimuli of different frequencies and of the response evoked by amplitude modulated tones in the steady state paradigm are compared on the same subjects. The activity underlying the dominant 100 ms component of the transient response to a tone burst is insensitive to the frequency of the tone. The activity evoked in the steady state paradigm is tonotopically organized and its source is shifted laterally from that of the tone bursts. These results show that it is possible with the neuromagnetic measurements to differentiate spatially and functionally different regions across the human auditory cortex.		

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EVIDENCE FOR MULTIPLE AREAS IN THE HUMAN AUDITORY CORTEX*

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ABSTRACT

Neuromagnetic measurements of the transient response to tone burst stimuli of different frequencies and of the response evoked by amplitude modulated tones in the steady state paradigm are compared on the same subjects. The activity underlying the dominant 100 ms component of the transient response to a tone burst is insensitive to the frequency of the tone. The activity evoked in the steady state paradigm is tonotopically organized and its source is shifted laterally from that of the tone bursts. These results show that it is possible with the neuromagnetic measurements to differentiate spatially and functionally different regions across the human auditory cortex.

KEY WORDS

Neuromagnetism; evoked responses; magnetoencephalogram; SQUID

INTRODUCTION

The primate auditory cortex is divided into several distinct functional areas with tonotopic projections of the entire basilar membrane in some of them (Brugge, 1982). Recently, neuromagnetic studies have shown that the location of cortical activity evoked by amplitude modulated tones in the steady state paradigm follows a tonotopic organization in which the activated region progresses along the cortex as a function of the stimulus frequency (Romani et al., 1982a, 1982b). These results must be contrasted with other neuromagnetic studies measuring the transient response to tone bursts stimuli which did not reveal the same kind of systematic and precise functional organization when the carrier frequency was changed (Elberling et al., 1982; Arlinger et al., 1982; Tuomisto et al., 1983). This discrepancy between the steady-state and transient data prompted us to directly compare responses to both kind of stimuli in the same subject.

METHODS

Our magnetic field sensor consisted of a second-order gradiometer with 2.4-cm diameter and 3.2-cm baseline between adjacent coils coupled to a SQUID. The output voltage from the SQUID electronics, which is simply proportional to the

net magnetic flux sensed by the gradiometer, was passed through a comb filter to reduce the pickup of noise at the power line frequency and then through a bandpass filter with 48 db/octave rolloff to select the bandwidth of interest.

Auditory stimuli were presented binaurally to the subjects by means of standard airline plastic earphones. Two different classes of stimuli were used. First, the transient responses were evoked by tone bursts of 200 or 400 ms duration, depending upon the subject, presented with a random interstimulus interval (ISI) of 3.5 ± 0.5 sec. Different carrier frequencies between 200 and 5000 Hz were used and also different rise and decay times for the envelope of the tone burst. The amplitudes were adjusted at the different frequencies so that they were subjectively equal in loudness. In general the stimuli remained in the range of 80-90 dB SPL. The measured power spectrum of the tone bursts at the output of the earphone was centered at the nominal frequency with typical width at half height corresponding to the inverse of the duration of the tone burst. The subject was asked to count the number of stimuli to ensure attentiveness. Responses were averaged for at least 100 trials in a filter bandwidth of 0.5 to 45 Hz. In the second set of experiments, steady-state responses were evoked by continuous tones whose amplitudes were sinusoidally modulated at a frequency of 32 Hz. Responses were averaged for at least 2000 modulation cycles and the field patterns were deduced from the amplitude and phase lag of the response at 32 Hz (see Romani et al. 1982b for more details).

We used both paradigms on three subjects and compared the evoked field patterns across their right hemisphere.

RESULTS

To detect in an efficient way small shifts in the location of the activity evoked by the different paradigms, we mapped the responses by steps of 1 cm at locations along a line crossing the two extrema and along two lines perpendicular to this direction at each extremum. This strategy gave at least 20 points for each map, each location being replicated at least twice.

The measured field patterns for subject PL and four different stimuli are presented in Fig.1. The isofield contours were calculated by computer using an interpolation fit of the data by the Laplacian method. The origin of the coordinates system is the ear canal, with the horizontal position measured toward the outer canthus of the eye and the vertical position measured perpendicular to this line. For this subject, we used three different 400 ms tone bursts of 200, 1000 and 2000 Hz with rise/decay time of 48, 12 and 6 ms respectively. The wave forms of the transient responses were very similar for the three different stimuli, with one dominant component occurring after about 100 ms (N1) and another one, with opposite polarity, after about 180 ms (P2). Nevertheless, our data indicate that due to the different rise times, the latencies of all the components of the response to a 200 Hz tone burst were longer by about 20 ms than for the 2000 Hz tone burst. The field patterns corresponding to the dominant component of the transient response occurring about 100 ms after stimulation were almost identical for the three different tone bursts (Fig.1, TB). On the other hand, the field pattern of the activity evoked by a continuous 1000 Hz tone amplitude modulated at 32 Hz had almost the same span between the extrema, but was clearly shifted laterally from that of the tone bursts (Fig.1, SSMT). Due to the weak signals in that particular case, we replicated the measurement at least six times at each location so that the signal to noise ratio was comparable to the transient measurements.

To compare in a systematic procedure the location of the cortical activity evoked

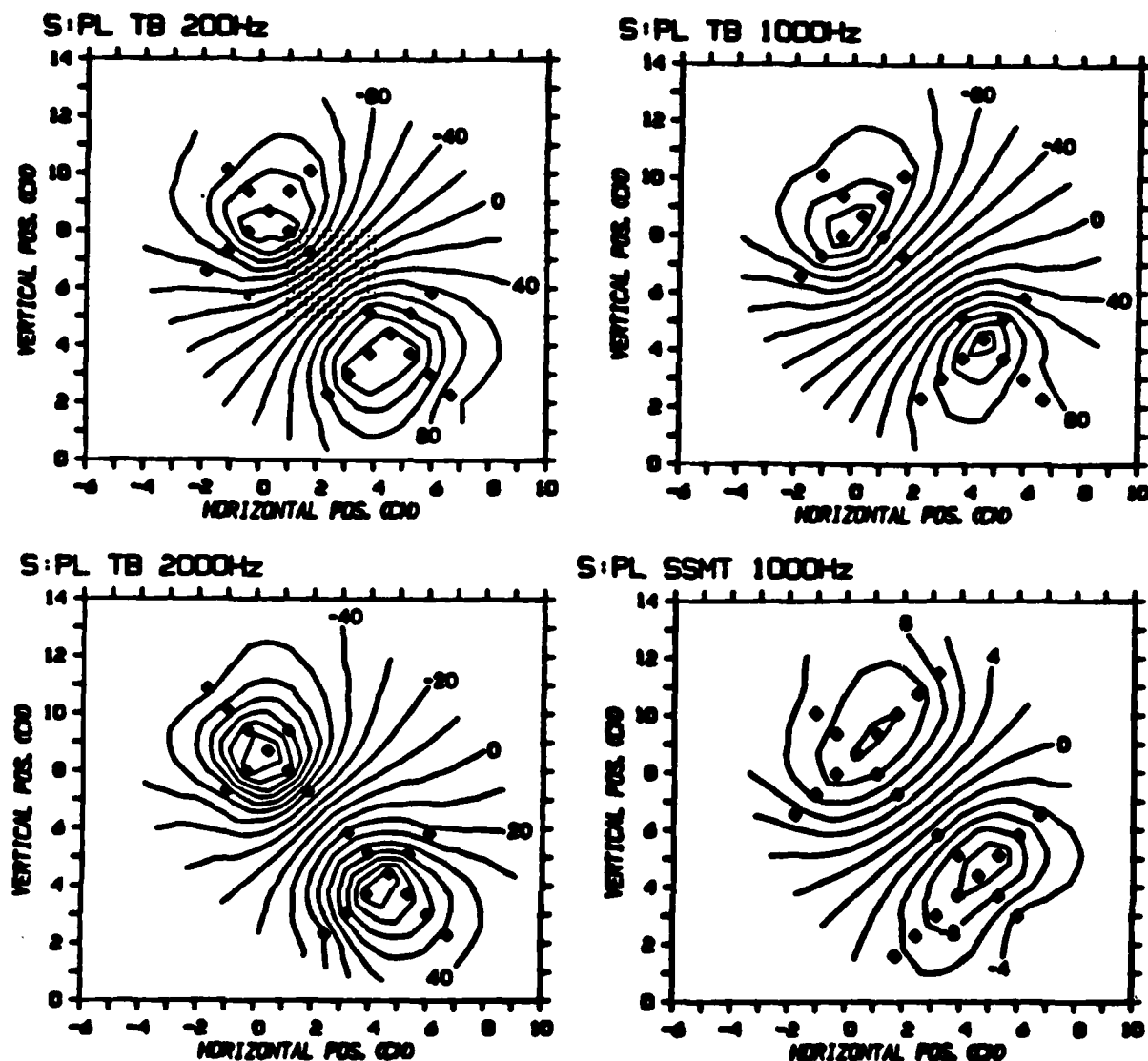


Fig. 1. (TB) Observed field patterns for the 100 ms component of the transient response to a tone burst of 200, 1000 and 2000 Hz respectively; (SSMT) observed field pattern for a steady-state amplitude-modulated tone of 1000 Hz. The origin of the coordinate system is the ear canal, with the horizontal position measured toward the outer canthus of the eye and the vertical position measured perpendicular to this line.

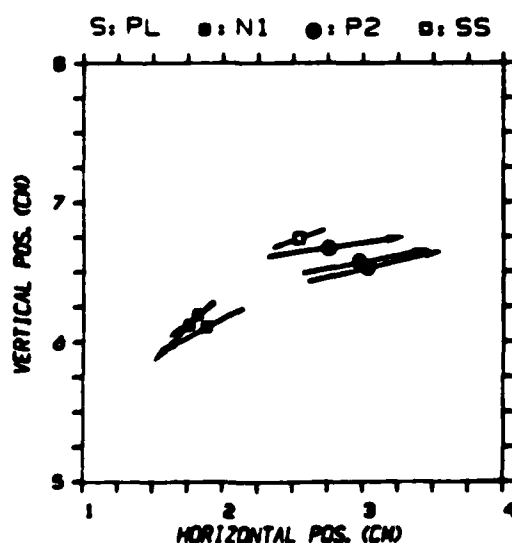


Fig. 2. Calculated best dipoles for the N1 and P2 components of the transient response to a tone burst and for the steady-state response (SS). This map is an enlargement of the central stippled region in one map of Fig. 1.

by these different stimuli a current dipole in a conducting sphere was used as a theoretical model in the following steps. The field due to a single current dipole in a 8 cm radius conducting sphere was calculated, as it is sensed by our second order gradiometer, and the sum of the squared deviations between the calculated and observed fields was computed. The parameters determining the dipole were then adjusted by computer until the sum of the squared deviations was minimal. Finally, the isofield contours of the best fit were plotted and compared with the data to make sure that no erroneous result was introduced by a local minimum in the sum of the squared deviations. For this subject with three different tone bursts, the parameters of the best fit gave the same surface location within ± 1 mm, the same depth within ± 1 mm and the same orientation within ± 8 deg for the source underlying the dominant 100 ms component of the transient response. As for the raw data, the location of the source evoked by a 1000 Hz amplitude modulated tone lies at the same depth but is shifted laterally by about 1 cm. The calculated dipoles are shown in Fig. 2, which is an enlargement of the central region of the maps. It is noteworthy that the same 1000 Hz carrier frequency is present in the amplitude modulated stimulus as in one of the transient stimuli.

Similar measurements on two other subjects confirmed the essential features of the findings. For subject MP, the activity evoked by a continuous 200 Hz amplitude modulated tone is also shifted anteriorly when compared to the activity underlying the 100 ms component of the transient response to a 200 Hz tone burst. For subject SW, the activity evoked by a continuous 1000 Hz amplitude modulated tone lies exactly on his tonotopic map (see Romani et al., 1982), but is shifted posteriorly when compared to the activity underlying the 100 ms component of the transient responses to clicks and to 1000 and 5000 Hz tone bursts.

Another dominant component of the transient response occurred about 180 ms after stimulus presentation for subject PL. The variability of the data at this latency was somewhat greater than for the 100 ms component and the state of alertness of the subject did affect the measurements. This component also showed a larger intersubject variability. Nevertheless for subject PL, the field patterns at a latency of 180 ms showed two well defined extrema slightly shifted from that of the 100 ms component. The parameters of the best single current dipole fits gave the same surface location within ± 2 mm, the same depth within ± 2 mm and the same orientation within ± 5 deg for the three different tone bursts (see Fig. 2). Thus, even if the intrinsic variability of the data was greater at this latency, the fits gave consistently a surface location also shifted anteriorly by about 1 cm when compared to the 100 ms component and no evident tonotopic organization for the 180 ms component of the transient response.

DISCUSSION

In contrast to the results reported by Elberling et al. (1982), but in agreement with the fine mapping on one subject in the work of Tuomisto et al. (1983), the present measurements reveal no significant shifts in the location of the source of the N1 component of the transient response when the carrier frequency of the tone burst is changed, whereas the sources evoked by steady-state amplitude-modulated tones lies in an area of the auditory cortex which is tonotopically organized. Thus the N1 source and the steady-state sources exhibit different functional properties. Even if the same carrier frequency is used in both paradigms, two spatially different areas are excited. The distinct character of these sources is also consistent with the different latencies of the responses: about 50 ms for the steady-state response and about 100 ms for the N1 component of the transient response.

Our measurements on the 180 ms component of the transient response are consistent with the results of Tuomisto et al.(1983) in the sense that they suggest different neural origins for N1 and P2. The form of the N1-P2 complex did show a considerable intersubject variability due to a poorly developed P2 in some of them. Measurements on a larger number of subjects are needed to confirm the findings on P2.

The excellent reproducibility of the field patterns, which has been observed by a careful mapping for different stimuli with sessions extending on a time scale of many weeks, allows to infer minor displacements in the location of multiples sources within the human auditory cortex. This prospect is particularly promising in view of the future application of large arrays of sensors.

CONCLUSION

These results indicate that: (1) it is possible with neuromagnetic measurements to differentiate spatially and functionally different regions across the human auditory cortex and (2) the 100 ms component of the transient response to a tone burst is insensitive to the pitch of the tone or to the exact shape of the envelope of the wave form. This component may well be associated primarily with the onset of a stimulus and be less sensitive on its details. This is consistent with the widely held notion that the pathways of the auditory system are divided among several functions and that some are tonotopically organized, while others are not.

ACKNOWLEDGEMENTS

We thank Dr. Yoshio Okada and Dr. Ken Schafer for their generous help. We also thank Prof. Anthony Movshon for kindly providing much of the computer software used in data analysis.

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*Supported in part by National Institute of Health Grant NS-19463-01 and Office of Naval Research Contract N00014-76-C-0568.

+Supported by the Swiss National Science Foundation.

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