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Relationship of transient and steady-state auditory evoked fields

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Summary Transient and steady-state auditory evoked fields (AEFs) to brief tone pips were recorded over the left hemisphere at 7 different stimulus rates (0.125–39 Hz) using a 37-channel biomagnetometer. Previous observations of transient auditory gamma band response (GBR) activity were replicated. Similar rate characteristics and equivalent dipole locations supported the suggestion that the steady-state response (SSR) at about 40 Hz represents the summation of successive overlapping (10 Hz) middle latency responses (MLRs). On the other hand, differences in equivalent dipole locations and habituation effects suggest that the magnetically recorded GBR is a separate phenomenon which occurs primarily at low stimulus rates and is unrelated to either the magnetically recorded MRL or SSR.

Key words: Auditory evoked fields; Steady-state response; Gamma band; Magnetoencephalography; 40 Hz auditory evoked potential

Magnetoencephalography (MEG) has become an established method for the noninvasive study of the macroscopic activity of the human cortex (for a recent review see, e.g., Hari 1990). The main sources of cortical auditory evoked magnetic fields are intracellular currents flowing tangentially to the skull, originating in similarly oriented pyramidal cells in the walls of the sylvian fissure. Magnetic studies of the human auditory cortex have demonstrated functional relationships similar to those observed earlier in invasive animal and human studies and have also provided new information about the functional organization of the human auditory cortex (Romani et al. 1982; Pantev et al. 1989), and about the physiology of auditory feature extraction (Hari 1990; Csépe et al. 1992).

Responses evoked by stimuli which follow each other at sufficiently long interstimulus intervals (ISIs) for the auditory system to return (mostly or completely) to its initial state before the next stimulus occurs (Buchwald and Huang 1975) are called transient evoked responses. If the ISI is shortened to such an extent that the transient response to one stimulus has not died away before the next stimulus is delivered, the com-

pound response that appears is generally referred to as a steady-state response (SSR) (Regan 1982) or steady-state field (SSF) in magnetic recording. For a linear system, transient and steady-state descriptions of the system's behaviour are equivalent, and a simple superposition of transient responses with the appropriate time lags perfectly predicts the amplitude and form of the steady-state response. In this case, both phenomena may be regarded as alternative versions of the same response. However, the auditory system shows several types of non-linear behaviour, and therefore transient and steady-state field recordings may provide complementary information about auditory function.

The transient auditory evoked field (AEF) consists of several components which are labelled according to their latency: *the brain-stem AEF* (latency 1–10 msec (Erné et al. 1987)), *the middle latency AEF* (latency 10–50 msec (Pelizzzone et al. 1987)), *the gamma band AEF* (20–100 msec (Pantev et al. 1991b)), *the slow AEF* (latency 40–250 msec (Reite et al. 1978)), and *the sustained field* (Hari et al. 1980; Pantev et al. 1992). Which components are recorded depends mainly on the stimulus paradigm applied. Auditory steady-state responses can be driven by different types of periodically presented short acoustic stimuli, with a maximum response energy for the electric SSR at stimulus repetition rates in the range 35–40 Hz (Galambos et al. 1981). Magnetic steady-state fields (SSFs) have been

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detected using amplitude modulated tones (Romani et al. 1982) and trains of clicks (Mäkelä and Hari 1987) as stimuli.

Overlapping components whose energies belong to different spectral regions can be separated in the frequency domain. In this way the gamma band response (GBR) or gamma band field (GBF) can be extracted from a wide band transient response, leaving the slow-wave AEF, including its most reliable feature, the magnetic correlate of the N100 (M100). Now the question arises: can the SSF be explained as the sum of overlapping transient responses, and if so, does it result from superimposed MLF components or from superimposed GBF? The electrically recorded N100, the magnetic M100, and the electric GBR are all known to grow in amplitude as the interstimulus interval increases above 1 sec (Hari et al. 1982; Näätänen and Picton 1987; Makeig 1990), but the rate dependence of the auditory GBF has not yet been reported, and it is not known whether the rate/amplitude characteristics of the magnetic GBR and M100 are similar or different.

To answer these questions, and to understand better the relation between generators of the different auditory evoked responses, we performed a magnetic study of AEFs evoked by a wide range of stimulus rates, producing responses ranging from well-defined transient responses to steady-state responses. As a reference point for common comparison of the locations of the equivalent sources of these different AEFs, we used the estimated location of the M100 component of the slow AEF (sAEF), which has been shown to indicate the location of the primary auditory cortex and primary association areas (Yamamoto et al. 1988; Papanicolaou et al. 1990; Pantev et al. 1991a).

Methods

(a) Subjects

Four female subjects with no history of otological or neurological disorders and normal audiological status, aged between 23 and 42, participated in this study. All the subjects were right-handed. Consent was obtained from the subjects after the nature of the study was fully explained to them.

(b) Stimulation

Stimuli were delivered to the right ear, and AEFs were recorded from the left hemisphere, since previous studies have shown that stronger AEFs are recorded over the hemisphere contralateral to the side of handedness (Elberling et al. 1981; Hoke 1988) and contralateral to the side of stimulation (Elberling et al. 1981; Reite et al. 1981; Pantev et al. 1986). AEFs were recorded at 7 different interstimulus intervals: 8, 4, 2,

1, 0.1, 0.026 and 0.028 sec (corresponding to rates of stimulation of 1/8, 1/4, 1/2, 1, 10, 36 and 39 Hz respectively).

Stimuli were gaussian tone pulses with a half-value time of 6 msec, a carrier frequency of 1000 Hz, and an intensity of 60 dB nHL (normative hearing level). They were presented in 2 blocks of 256 stimuli each at ISIs of 8, 4, 2 and 1 sec; in 2 blocks of 1200 stimuli each at 0.1 sec ISIs (10 Hz); and in 2 blocks of 1500 stimuli each at rates of 36 and 39 Hz. Stimuli were presented to the subject's ear through a nonmagnetic and echo-free stimulus delivery system with an almost linear frequency characteristic (deviations less than ± 4 dB in the range between 200 and 4000 Hz). During stimulus presentation the subjects were asked to keep their eyes open and to stay awake.

(c) Neuromagnetic recordings

Recording was carried out in a magnetically shielded room (Vacuumschmelze) using a 37-channel biomagnetometer (MagnesTM, Biomagnetic Technologies). The detection coils of the biomagnetometer are arranged in a circular concave array 144 mm in diameter, with a spherical radius of 122 mm. The axes of the detection coils are normal to the surface of the sensor array. The distance between the centres of two adjacent coils is 22 mm; each coil itself measures 20 mm in diameter. The sensors are configured as first-order axial gradiometers with a baseline of 50 mm. Each coil is connected to a superconducting quantum interference device (SQUID) that produces a voltage proportional to the field radial to the coil. The spectral density of the intrinsic noise of each channel was between 7 and 9 fT/ $\sqrt{\text{Hz}}$ (for more details see Pantev et al. 1991a). A sensor position indicator system determined the spatial locations of the sensors relative to the head and also indicated if head movements had occurred during the recording. The sensor array was centred over a point in the left supratemporal cortex, lying 1.5 cm superior to the point T3 of the 10–20 system for electrode placement. Using a bandwidth of 0.1–100 Hz, the following blocks of stimulus-related epochs were recorded: (a) 2 blocks of 256 epochs of 1 sec for the 8, 4, 2 and 1 sec ISIs; (b) 2 blocks of 1200 epochs of 0.2 sec for the ISI 0.1 sec; and (c) 5 min of continuous data for the SSFs.

(d) Data analysis

Wide band responses to each block were first averaged, after artifact rejection which discarded about 5–10% of artifact-contaminated epochs due to eye blinks or muscle activity. Since the wave forms of the averaged responses recorded in the two blocks (test-retest) were highly reproducible, a grand average of the two was used for further evaluation. The wide-band responses were digitally filtered with passbands 0.1–20 Hz and 24–48 Hz, using a first order Bessel filter (6

dB/oct). To avoid phase shifts, the data were filtered twice (forward and backward); thus the effective slope of the filter characteristic was 12 dB/oct. Root-mean-square (RMS) field values over the 37 recording channels were calculated separately for every sampling point.

Source analysis using a single moving dipole model was applied to each of the obtained field distributions. A spherical model was fitted to the digitized head shape of each subject, and the location (x , y , z positions), orientation and amplitude of a best-fitting equivalent current dipole (Geselowitz 1970; Sarvas 1987) were estimated for each point in time. The origin of the head-based coordinate system (determined by the sensor position indicator) was the midpoint between the preauricular points. The x -axis joined the origin to the nasion; the y -axis passed between the preauricular points with positive values towards the left preauricular point. The z -axis was perpendicular to the x - y plane. Correlations between the theoretical field generated by the model and the observed field were used to estimate the goodness of fit of the model parameters. Only estimates with a goodness of fit above 0.90 were analysed further.

In order to estimate the recovery function of the GBF and the M100 of the sAEF, we determined the dependence of the field amplitude upon stimulus rate, which we call the "rate-amplitude characteristic." To

determine this characteristic, we used the mean RMS field value across all recording channels rather than amplitude at any one channel (e.g., at the field maximum or minimum), since this value better represents the whole field distribution. For further evaluation of the data, we compared: (1) the mean RMS value at the peak of the M100, (2) the mean RMS value of the 3 largest peaks in the transient GBF (near to 50 msec after stimulus onset), (3) the mean RMS value at the peak of the major MLF component Pa, and (4) the mean RMS value of two successive outgoing and ingoing peaks of the SSF. Statistical analysis of the calculated RMS values and ECD parameters for the different transient and steady-state components was carried out using the paired t test.

Results

Inspection of single subject averages (of which two are presented in Fig. 1) demonstrates the recently discovered transient auditory evoked gamma band response (Makeig and Galambos 1989; Pantev et al. 1991b). The figure illustrates the wide-band and the bandpass filtered (1–20 Hz and 28–48 Hz) activity obtained at the posterior field maximum from two subjects for interstimulus intervals of 8, 4, 2 and 1 sec. It is clear that the oscillatory GBF corresponds well to

Fig. 1. A and B: wide-band and bandpass-filtered (1–20 Hz and 28–48 Hz) activity obtained at the posterior field maximum using interstimulus intervals of 8, 4, 2 and 1 sec for two subjects (P.E. and M.A.).

Fig. 2. Evoked responses from one subject (P.E.) at the 7 stimulus rates investigated. The left side of the figure shows 1–20 Hz bandpass data at the 4 slowest rates (top), and wide-band data (middle and bottom) for 3 faster rates. The right side of the figure (top and middle) shows the same responses filtered in a 24–48 Hz band. The middle panel presents the MLF wide-band results on the left, and the same response after filtering between 24–48 Hz on the right. In each panel, stimulus onset is at time 0. In the lower parts of the figure, solid lines show the posterior, and dashed lines the anterior, extrema of the evoked fields.

the difference between the wide-band (unfiltered) data and the 1–20 Hz filtered data, and that it is not created by a ringing of the filter used to separate the GBF and AEF components.¹ The figure also illustrates that the amplitudes of both the slow AEF and the GBF increase with increasing ISI, and also that the subject with the smaller M100 does not have a correspondingly smaller GBF.

In Fig. 2, a set of experimental data containing the slow AEF (1–20 Hz), the transient GBF (24–48 Hz),

the MLF and the SSF (0.1–100 Hz), obtained at the 7 different stimulus rates is shown. The appearance of the stimulus is marked by a filled triangle on the abscissa. The upper part of the figure presents the slow AEF and the GBF at ISIs of 8, 4, 2, and 1 sec as they were recorded at the posterior field maximum. The amplitudes of the M100 and of the GBF appear to decrease as ISI decreases, the M100 decreasing faster than the GBF. Note that, at the rate 10 Hz (ISI 0.1 sec), the amplitude of the Pa component of the MLF (middle, left) is clearly larger in the wide-band response than in the 24–48 Hz filtered version (middle, right), but it is very similar to the amplitude of the SSF at 36 and 39 Hz (bottom, left). The solid lines show the posterior, and the dashed lines the anterior, extrema of the evoked field, with a clear polarity reversal evident at all peaks, compatible with dipolar (or near dipolar) field distributions of the different components of the transient as well as the steady-state fields.

Mean RMS amplitudes across subjects are presented as a function of stimulus rate in Fig. 3 for the slow AEF and GBF. The RMS values for the MLF and the SSF (with their standard deviations) are also shown

¹ The possibility of such a ringing effect was experimentally evaluated by passing through the filter a synthetic function similar in shape to the sAEF, but with no spectral energy over 24 Hz. The ringing of the filter for this function was found to be 26 dB smaller in amplitude than the GBF. Further, evidence that the GBF has a physiological basis was obtained in control experiments in which GBF amplitude was found to decrease with decreasing stimulus intensity, becoming detectable at stimulus intensities near the hearing threshold. Finally, a spectral analysis of the wide-band response data showed that the evoked wide-band field response contains spectral energy in two distinct frequency ranges, one peak around 10 Hz representing the slow AEF, and another one between 30 and 40 Hz reflecting the GBF (Pantev et al. 1991b).

Fig. 3. Rate-amplitude characteristics for the M100 component of the slow AEF and the GBF based on grand mean RMS amplitude values (left: absolute grand mean amplitudes; right: grand mean amplitudes normalized by dividing by amplitude at 1/8 sec). SSF and MLF RMS amplitudes are also shown for comparison. Vertical bars in the left panel indicate standard deviations.

for comparison. Because of the very different amplitudes of the M100 and the GBF, comparison of their rate of change with stimulation frequency is better seen after they have been normalized by dividing by their respective amplitudes at the 1/8 sec rate. This normalization is presented on the right side of Fig. 3 and shows clearly that the rate-amplitude characteristics for the two phenomena have different slopes. However, at the lowest rate (1/8 sec) both characteristics appear to be accelerating, rather than saturating.

Using the source localization procedure described above, equivalent source locations for the M100, GBF, MLF and SSF were determined for each stimulus rate. The equivalent dipole location of the M100 for each subject at each rate was used as an internal marker of the location of the subject's primary auditory cortex (cf., Pantev et al. 1991b). Mean differences between the estimated source locations of the M100 and the GBF were calculated for each subject and then averaged across subjects, thereby becoming more or less independent of the individual subject neuroanatomy. These means and their standard deviations are shown in Fig. 4.

The mean differences for the different rates were consistent in antero-posterior and medio-lateral directions, but inconsistent in the infero-superior direction. Specifically, the equivalent current sources of the GBF were about 5 mm more anterior and about 5 mm more medial than the respective sources of the M100 ($P < 0.01$).

The consistency of the localization across subjects (Fig. 4) allowed calculation of the grand means of the estimated source locations for each stimulus rate, as

Fig. 4. Mean differences for 4 subjects between the source locations of the GBF and M100 of the slow AEF at 4 interstimulus intervals. Vertical bars show standard deviations across subjects.

shown in Fig. 5. Three separate groups of source locations can be seen. The first (empty symbols) includes the source locations of the M100 at the lower 4 rates; this group is most lateral and posterior. The second group (filled symbols) represents the mean source locations of the GBF at the same rates, also suggesting a source in the supratemporal cortex somewhat medial and anterior to M100. Intriguing results were obtained for the source locations of the 10 Hz MLF-peak Pa and the 36 and 39 Hz SSF, which were found to be nearly superimposed, significantly more medial and more anterior than either the transient GBF or the slow AEF ($P < 0.01$).

Fig. 5. Mean estimated source locations of the slow AEFs, GBF, MLF and SSFs. Antero-posterior, medio-lateral and infero-superior axes of the 3-dimensional plot refer to the head-based coordinate system described under Methods.

Discussion

Results obtained for the source locations of the slow AEF, the GBF, the MLF and the SSF are generally in line with results of previous separate studies of these phenomena (Mäkelä and Hari 1987; Pelizzone et al. 1987; Hari et al. 1989; Pantev et al. 1991b) and allow comparisons of the several magnetic auditory response components.

MLF and M100

In the first MEG study of middle latency evoked fields, Pelizzone et al. (1987) reported a cortical source for the major MLF component Pa significantly more anterior than the source of the M100. Our study confirms this result. Further we found the Pa equivalent current source to be also more medial than the source of the M100. A cortical origin for the electrical MRL, and presumably the MLF, has also been supported by direct cortical measurements of auditory evoked potentials (Celesia 1976), by chronic subdural electrode recordings (Lee 1984), and by the analysis of electrical evoked response sources (Scherg and Von Cramon 1986).

M100 and SSF

A source in the supratemporal cortex of the SSF was found by Romani et al. (1982). Also, the results of an earlier SSF neuromagnetic study of Mäkelä and Hari (1987) are consistent with a cortical source anterior to the source of the M100, in agreement with our results. Their data analysis strongly suggested at least one cortical SSR generator location and rendered the hypothesis of a single midbrain generator improbable. In another magnetic study (Hari et al. 1989), the equivalent SSF source location was found to be medial to that of the M100, again in agreement with our results. From the calculated depths of the sources, Hari et al. (1989) suggested that the SSF may be generated close to the primary auditory cortex, in the area *supratemporalis granulosa* deep within the sylvian fissure (Braak 1980). While they reported slightly more posterior locations of the SSF sources as compared to those of the M100, our study indicates a significantly more anterior source location for the SSF. While both results point to different source configurations for the slow AEF and for the SSF, exact source differences remain to be clarified. The difference in binaural interactions for the SSF and M100, reported by Tiihonen et al. (1989), confirms the conclusion that the neural populations underlying the two responses are not the same.

M100 and GBF

The relative locations of the GBF with respect to M100, which were found at all relevant rates in this study (1/sec to 1/8 sec), are similar to those previously

obtained by Pantev et al. (1991b). In that study, and in line with the present results, the GBF was found to originate in the supratemporal cortex, medial and anterior to the source of the M100. Superimposition of the calculated source locations onto an MRI image supported the correctness of the localization results (Pantev et al. 1991b). If the M100 and GBF, two components of the complex human auditory cortical response, represent responses to information in the same auditory pathway, then their rate-amplitude characteristics might also be similar. The pronounced difference in the slopes of their rate-amplitude characteristics, however, indicates different recovery patterns and hence also different generator mechanisms for the M100 and GBF.

The common change, for both the M100 and GBF, to a steeper rate of increase (Fig. 3) between rates 1/4 sec and 1/8 sec is puzzling. Earlier investigations, using brief tones and 400 msec noise bursts (Hari et al. 1982, 1987), supported the idea that for the magnetic M100, saturation of the rate-amplitude characteristic occurs for ISIs near 10–12 sec. In our experiments, a different trend is seen, and for our subjects the expected saturation of the magnetic rate-amplitude characteristic must begin at still longer ISIs (for which we have no data). Näätänen and Picton (1987), in their review of the N100 response, concluded that a separate sub-component of the electrical response, with a markedly central scalp distribution, appears at ISIs longer than about 6 sec. A similar change in topographic distribution was observed in electrical responses by Hari et al. (1982), and by Makeig (1990) for N100 and also P50. In the present data, however, although amplitudes of both the M100 and GBF grow in a manner incompatible with saturation between 4 and 8 sec ISIs, there is no sign of change in equivalent source location of either the M100 or GBF at our slowest rate (1/8 sec).

Our finding of separate habituation patterns for the auditory M100 and GBF is paralleled by results of an investigation of slow and gamma band evoked responses in the somatosensory system (Kaukoranta and Reinikainen 1985). These authors investigated ISI dependencies of electrical potentials and magnetic fields elicited by median nerve stimulation (ISIs of 1.2, 2.4, 4.8, and 9.6 sec). They modelled the complex spatiotemporal field pattern as a superposition of two groups of deflections which could be separated by filtering into the two frequency bands 0.0512 and 12–40 Hz. While the estimated current sources of both phenomena were located in the rolandic fissure, the rate-amplitude characteristics of the slow and fast frequency components were in agreement with the hypothesis that these mainly reflect activity of separate neuronal populations. As with our auditory results, the recovery characteristic of the somatosensory GBF was

shallower than that of the slower cortical response. It would be of interest to compare these two gamma band evoked responses directly, and also to determine whether they have any common function.

GBF and SSF

The observed pattern of equivalent source locations for the different components allows us to reject the hypothesis that the auditory steady-state response results from addition of successive overlapping transient gamma band evoked responses (Pantev et al. 1991b). The 24–48 Hz band energy in the 10 Hz responses (Fig. 2) is much smaller than in either the SSF or MLF, and the SSF and MLF equivalent source locations are much closer to one another than to the source locations for the GBF (Fig. 5). Our results suggest, therefore, that the GBF and SSF arise at partially or wholly separate source locations in or near the primary auditory cortex.

GBF and MLF

These data suggest that the MLF and GBF have different origins and may arise from different processes in the auditory pathway. The MLF sources are deeper and more anterior to those of the GBF. At rates which seem to be optimal for evoking the MLF (10 Hz) the GBF is strongly suppressed, and filtering the MLF in the frequency band appropriate for the GBR produces only a very small response in this frequency band. To better understand the relation of the GBF and MLF, it would be desirable to study these differences at rates between 1 and 10 Hz.

MLF and SSF

The obtained results support the idea of Galambos et al. (1981) that the electrical SSR, and presumably the magnetic SSF, may result from superposition of the relatively early components of the middle latency response. The present experiments provide the following evidence for this hypothesis: (a) the RMS values of the MLF recorded over the primary auditory cortex are of the same order of magnitude as the RMS values of the SSF (Fig. 2), and (b) the equivalent sources of the MLF and the SSF are grouped closely together, and are distinctly different from those of the transient GBF and the sAEF (Fig. 5).

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