Processing of vowels in supratemporal auditory cortex

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Abstract

The auditory evoked neuromagnetic fields elicited by synthesized vowels of two different fundamental frequencies F0 were recorded in six subjects over the left and right temporal cortices using a 37-channel biomagnetometer. Single equivalent current dipole modeling of the fields elicited by all vowel types localized activity to a well-circumscribed area in supratemporal auditory cortex in both hemispheres. There were hemisphere asymmetries in the amplitude and latency of the M100 response. We also observed changes in M100 latency related to vowel type, but not to F0. There was no clear effect of vowel type or F0 on dipole localization for the M100, but a possible vowel type by latency interaction. These M100 data provide further evidence that vowels are processed independently of their pitch.

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In recent years several groups have investigated the neuromagnetic field evoked by vowel perception using magnetoencephalography (MEG) [3,5,7,8]. One objective has been to differentiate between speech and non-speech sounds. In particular, the source localization and temporal form of the evoked response may yield electrophysiological indices that characterize speech stimuli as phonemes independent of the typical acoustic variation that is ignored when speech is decoded, such as pitch or background noise [1,11].

The acoustic features that give vowels their unique perceptual identity (vowel quality) are the bands of energy peaks at particular frequencies, the formants. The distribution of formants in a vowel is largely a function of articulatory gestures (for example a lowered tongue height yields a higher frequency first formant). Because vowels are spoken at different characteristic pitches, ranging from very low bass to high-pitched children’s voices, the speech perception system must be able to decode and label vowels across a range of fundamental frequencies (including atypical occurrences, e.g. in whispering). At some level of speech perception, vowels and all other speech sounds must therefore be represented as pitch-independent phonemes. This identification is made on the basis of the formant values, which are relatively stable across speakers and articulatory contexts.

MEG data have been used to demonstrate phonetic invariance (the independence of evoked activity from phonetically irrelevant acoustic variation) of responses recorded from auditory cortex [1,11]. Furthermore, a recent experiment using pure tones suggests that, in addition to the probable spatial tonotopic organization of auditory cortex [4,10,14], there may also exist a temporal encoding mechanism for pitch [13].

To evaluate responses to vowels as a function of pitch (F0), phonetic category (formants), and hemisphere, we presented three synthetic vowels (/a/, /i/, and /u/) at two fundamental frequencies (100 and 200 Hz) to subjects while recording the evoked neuromagnetic field from the left or right temporal cortices. The latency, amplitude, and localization of the auditory evoked M100 neuromagnetic field were investigated as a function of pitch and of vowel type.
Three female and three male volunteers (two right handers and one left hander per group; mean age, 29.6 years) participated in the experiment. Subjects gave informed consent under a protocol approved by the UCSF and MIT committees on human studies. None of the subjects had any audiological abnormalities.

Vowels (300 ms) were created using a Klatt formant synthesizer (SenSyn®, Sensimetrics Inc., Cambridge, MA, USA). The source parameters were as follows: amplitude of voicing ramped up to 60 dB in 0–5 ms and remained constant until a rapid decline at 250 ms; amplitude of aspiration ramped up from 0 to 5 dB in the first 30 ms, remained constant till 290 ms, and sharply declined to 0 dB; the fundamental frequency varied from 120 to 90 Hz for the male vowels and from 220 to 190 Hz for the female vowels. Table 1 lists the formant values and formant bandwidths used for the six vowels. Stimuli were presented using PsyScope software [2]. Each vowel was presented 100 times in pseudorandom sequence to allow for signal averaging. The intertrial interval varied between 750 and 1250 ms.

The recordings were made in a magnetically shielded room using a 37-channel biomagnetometer (Magnes, Biomagnetic Technologies, Inc., San Diego, CA, USA). The sensor-array was placed over the left or right temporal lobe and adjusted to best capture the M100 field extrema for a 500 Hz pure tone. Six hundred millisecond epochs (100 ms pre-stimulus to 500 ms post-stimulus onset) were acquired around each stimulus. Neuromagnetic data were recorded from the contralateral hemisphere with a 1.0 Hz high-pass cutoff and a sampling rate of 2083.3 Hz. Following the simultaneous acquisition of the time-varying evoked neuromagnetic field in 37 channels for each epoch, data were sorted and averaged. The averaged waveforms were digitally filtered with a passband of 1.0 to 20 Hz; all further analyses were performed on the filtered data.

Localization analysis was restricted to the M100 evoked response component. The root mean square (RMS) of the field strength across the 37 channels was calculated for each sampled point in time. The M100 RMS peak and latency data were analyzed with standard analysis of variance methods using the UNIXSTAT software. To estimate the source parameters of the M100, a single equivalent current dipole model was used. Representative single dipoles were chosen as follows: the latency of the M100 peak was determined and all dipoles in a 10 ms window around the peak were computed (i.e. peak latency ± 5 ms). Of the dipoles in that interval, the one with the smallest model correlation confidence volume was chosen. For each subject, high resolution volumetric magnetic resonance images (SPGR sequences, 128 × 128 × 124 matrix; resolution, 1 × 1 × 1.5 mm; TR, 36 ms, TE, 8 ms, flip, 70°) were acquired using a 1.5 T SIGNA magnetic resonance scanner (GE Medical Systems, Milwaukee, WI, USA). The left and right preauricular points and nasion were marked during the MEG recordings to allow coregistration of the MEG and magnetic resonance image (MRI) data sets. By superimposing these fiducial landmarks on the MRI of each subject, the position of the computed point sources can be visualized in anatomic context.

For three subjects (F1, M1, and M2), the M100 peak amplitudes measured from the left hemisphere were larger for each stimulus, in one subject (M3, left hander) the left response was larger for five of the six stimuli, and for one subject (F3, left hander) the response amplitudes from the right were always larger. Subject F2 showed no differential response effect of hemisphere. The main effect of hemisphere was not significant, \( F(1,5) = 0.72, P = 0.43 \). There was no significant effect of fundamental frequency on amplitude of the M100 peak, \( F(2,10) = 1.76, P = 0.24 \).

With the exception of the /u/ response, the left hemisphere response latencies exceeded the right hemisphere responses for all vowels, although the effect did not reach statistical significance, \( F(1,5) = 4.00, P = 0.10 \). Statistically, the effect of phoneme type (/a/ versus /i/ versus /u/) on latency was highly significant, \( F(2,10) = 26.98, P = 0.001 \). However, there were no effects of the fundamental frequency F0 on latency, \( F(1,5) = 0.87, P = 0.39 \). For example, both types of /a/ had earlier M100 latencies than the other vowels in both hemispheres.

Fig. 1 plots, in a head-centered coordinate frame, the x (anterior-posterior), y (medio-lateral), and z (superior-inferior) coordinates of the single dipoles in the left and right hemisphere for one subject (M1). For all subjects, the localizations for vowels spatially overlapped with the localizations for independently presented tones and syllables [12]. In all three dimensions, the single dipoles cluster in the same area of auditory cortex. Fig. 2 shows one subject’s (M1) coronal MRI with the dipoles for the (male and female) /a/ vowels coregistered (magnetic source images). Note that the vowel-elicited activity localizes to the supratemporal plane in both hemispheres.

The M100 dipole localizations were analyzed in the medio-lateral axial plane of each hemisphere (see Fig. 1) because (1) it was the localization plane with the most variance and (2) it is the plane of putative tonotopy [4,10,14]. Although there were no main effects of vowel type or fundamental frequency F0 in either hemisphere (vowel type, left hemisphere, \( F(2,10) = 0.51, P = 0.61 \);
vowel type, right hemisphere, $F(2,10) = 1.33, P = 0.31$; fundamental frequency, left hemisphere, $F(1,5) = 0.015, P = 0.91$; fundamental frequency, right hemisphere, $F(1,5) = 0.26, P = 0.64$, there was a notable vowel type x fundamental interaction in the left temporal recordings ($F(2,10) = 3.52, P = 0.074$) attributable to the male /u/ stimuli.

The data for one subject displayed in Fig. 1 illustrate that all the dipoles localized to a well circumscribed area. There is no hint of a vowel space, or any underlying ‘phonotopy’. It is important to bear in mind, also, that the dipoles for pure tone stimuli localized to the same coordinates [12], so the localizations are not distinguishing between speech and non-speech auditory stimulation.

With regard to the lateralization of responses for vowels, the findings to date suggest a moderate bias of processing towards the left temporal lobe [9,15,16]. Most analyses of the latencies and amplitudes of the major evoked response components have failed to detect any significant cortical asymmetries before the sustained field response (beginning approximately 200 ms after stimulus onset), at least with respect to vowels [5].

In MEG studies, Kuriki and Murase [8] localized M100 dipoles generated by vowels consistently more anterior to the M100 dipoles generated by tones in the left hemisphere. Eulitz et al. [5] recently reported a systematic difference between tone and vowel stimuli, but not as early as the M100. They recorded the evoked neuromagnetic field generated by pure tones and vowels from both hemispheres and showed that there was a clear (localizable) effect of the sustained field (SF) that distinguished tone and speech stimuli. Although these investigators found no hemispheric asymmetries between tones and vowels at the M100, they observed a larger amplitude in the SF to vowels as compared to the SF to tones. The SF difference was particularly strong in the left hemisphere. Moreover, the SF had a distribution that allowed them to localize its source to sites slightly anterior to the M100 source. They attributed the larger left temporal SF response to speech-specific processing.

We observed in all subjects a hemispheric M100 latency difference that approached significance. Diesch et al. [3] also observed such a latency asymmetry for both their short and long vowels. If this effect is systematic, it is interesting in that it appears in the opposite direction to that which might be expected. A currently popular idea is that the left hemisphere is both specialized for speech and language and for fast temporal processing [6,17]. If that position is correct, it is relatively counterintuitive that the left auditory cortex uniformly generates longer latencies than the right for the major auditory evoked response component (M100) elicited by speech sounds.

The latency difference for vowel type that we find is quite similar to the data reported by Diesch et al. [3]. In particular, both studies found that /a/ produced significantly shorter M100 latencies than /u/ and /i/. We attribute this latency advantage of /a/ to the proximity of its first two formants to 1 kHz (see Table 1), which is close to the frequency that yields the fastest M100 latency for pure tones. However, the lack of coherent spatial grouping of vowels, and the vowel type x fundamental interaction for localization in the medio-lateral plane question the existence of a spatial map for vowel phonemes. Although the interaction of vowel type and M100 latency was replicated, we find that varying F0 is not associated with...
latency shifts despite the correlation between pure tone frequency and M100 latency [13].

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