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Research paper

Hemispheric asymmetry in mid and long latency neuromagnetic responses to single clicks

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ABSTRACT

We examine lateralization in the evoked magnetic field response to a click stimulus, observing that lateralization effects previously demonstrated for tones, noise, frequency modulated sweeps and certain syllables are also observed for (acoustically simpler) clicks. These effects include a difference in the peak latency of the M100 component of the evoked field waveform such that the peak consistently appears earlier in the right hemisphere, as well as rightward lateralization of field amplitude during the rise of the M100 component. Our review of previous findings on M100 lateralization, taken together with our data on the click-evoked response, leads to the hypothesis that these lateralization effects are elicited by stimuli containing a sharp sound energy onset or acoustic transition rather than specific types of stimuli. We argue that both the latency and the amplitude lateralization effects have a common origin, namely, hemispheric asymmetry in the amplitude of the magnetic field generated by one or more sources active during the M100 rise. While anatomical asymmetry cannot be excluded as the cause of the amplitude difference, we propose that the difference reflects a rightward asymmetry in the processing of sound energy onsets that potentially underlies the lateralization of several functions.

1. Introduction

Determining the neural basis of hemispheric differences in auditory processing is crucial to the formulation of a biologically-based theory of speech lateralization. However, the discovery of neurobiological asymmetries potentially related to functional lateralization effects and the explication of *causal* relationships linking the asymmetries to such effects is quite difficult. One method of attacking the problem is to use magnetoencephalography (MEG), which allows the magnetic field response evoked by auditory signals to be measured for the individual hemispheres with very high sensitivity. Neurobiological asymmetries become evident with this methodology because they produce hemispheric differences, that is, lateralization, in various attributes of the magnetic field response. The temporal resolution of MEG makes it possible to determine the timing of identified differences with a high degree of precision, thus constraining the potential sources of asymmetric activity in the temporal dimension.

In this study, we seek to characterize lateralization in the magnetic field response evoked by a simple, single click stimulus by identifying statistically significant effects that are consistently present across two separate experiments. We especially wish to determine if two potentially related lateralization effects, previously observed in the M100 component[1] of the response evoked by other auditory stimuli, are present in the response to the click. These effects include hemispheric asymmetry in the latency of the M100 peak and in magnetic field amplitude during the M100 rise. An earlier M100 peak has been observed in the right hemisphere for a variety of stimuli, including tones (Gabriel et al., 2004; Huotilainen et al., 1998; Jin et al., 2007; Kanno et al., 2000; Kirveskari et al., 2006; Pardo et al., 1999; Roberts et al., 2000; Rosburg et al., 2002; Salajegheh et al., 2004), vowels (Kirveskari et al., 2006; Poeppel et al., 1997) and syllables starting with a stop consonant (Gage et al., 1998, 2002; Obleser et al., 2003). In addition, rightward

Abbreviations: AM, amplitude-modulated; CALM, continuously adjusted least squares method; FM, frequency-modulated; HG, Heschl's gyrus; LH, left hemisphere; MEG, magnetoencephalography; MRI, magnetic resonance imaging; RH, right hemisphere; RMS, root-mean-square; SPL, sound pressure level; SQUID, superconducting quantum interference device; TSPCA, time-shift principle component analysis algorithm

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[1] Also known as the N1m, the M100 is the prominent component of the evoked field that peaks approximately 100 ms after stimulus onset.

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lateralization of both M100 peak latency and response amplitude has been found in the magnetic field response to frequency-modulated (FM) sweeps (König et al., 2008) and in the tangential component of the N100 electric potential response for white noise and tone stimuli (Hine and Debener, 2007). Although many, seemingly disparate stimuli appear to produce rightward lateralization in M100 peak latency, an earlier M100 peak has been observed in the left hemisphere for tones with gradual onsets (Pardo et al., 1999). This suggests that M100 lateralization effects may be associated with onset characteristics and, indeed, the various stimuli found to elicit rightward lateralization are commonly characterized by their relatively sharp acoustic onsets. Because the onset of the click stimulus is extremely sharp, we hypothesize that its magnetic field response will exhibit significant rightward lateralization in M100 peak latency and in the amplitude of the field response during the M100 rise.

2. Materials and methods

2.1. Experiment 1

2.1.1. Subjects

Fourteen subjects (mean age 24.3, 8 male) took part in the experiment after providing informed consent. All were right-handed (Oldfield, 1971), reported normal hearing, and had no history of neurological disorders. On the hearing check administered prior to the experiment, all subjects perceived stimulus sound levels as comfortable and of equal loudness in both ears.

2.1.2. Stimuli

Eleven stimuli were generated as wav files, 500 ms in length with a sampling frequency of 16 k Hz (using Matlab 7, The Mathworks, Inc.). The stimuli consisted of single clicks (0.0625 ms square wave, positive polarity) and click pairs (two 0.0625 ms square waves, positive followed by negative polarity). For single clicks, the square wave onset was offset from stimulus time zero by 0, 20, 40, 60, 100, or 140 ms. For click pairs, the interval between square wave onsets was 20, 40, 60, 100, or 140 ms. Sound levels for all stimuli were set to $\sim$70 dB SPL.

2.1.3. Procedure

Stimuli were delivered binaurally through plastic tubing connected to ear pieces inserted in the ear canals of the subjects (EAR Tone 3A System), with presentation controlled via Presentation version 11.3 (Neurobehavioral Systems, Inc.). The eleven stimuli were presented 96 times each in pseudo-random order. The experiment was divided into four identical blocks, providing subjects with an opportunity to rest between blocks. In order to maintain alertness, the subjects were asked to indicate whether they heard a single click or a click pair by pressing one of two buttons on a response pad held in one hand. They were encouraged to be accurate but told that response time was not important to the results. Response-to-next stimulus intervals were set to random values between 2000 and 2125 ms, producing random ISI's of at least 2 s. Subjects were instructed to switch hands between blocks to balance any hand-related effects and to proceed (by a button press) with the next block when they were ready and alert.

2.1.4. Neuromagnetic recording

The neuromagnetic data were acquired in a magnetically shielded room (Yokogawa, Japan) using a 160-channel, whole-head axial gradiometer system (5 cm baseline, SQUID-based sensors, KIT, Kanazawa, Japan). MEG channels included 157 head channels plus 3 reference channels that recorded the environmental magnetic field data for noise reduction purposes. Data were continuously recorded using a sampling rate of 1000 Hz, on-line filtered between 1 and 200 Hz with a notch at 60 Hz.

2.1.5. Data processing

The recorded data were noise-reduced off-line using the CALM algorithm (Adachi et al., 2001). For one subject, approximately half of the recorded data had to be discarded due to noise contamination resulting from nearby construction activity. The examined MEG data for each stimulus condition covered 1000 ms epochs that included 400 ms pre-trigger and 600 ms post-trigger periods. Latency times for the processed data were adjusted for the 20 ms delay between trigger generation and the actual time of stimulus presentation. Epochs with neuromagnetic responses >2500 fT were automatically rejected.

For this study, further analysis of the data included only those epochs representing the response to the single click stimuli (the click pair data forms the basis of a separate study). Each epoch was time shifted by its associated stimulus offset from time zero in order to align stimulus presentation times, then 860 ms of the epoch were retained for further processing ($-$400 ms to 460 ms). For each subject, the adjusted epoch data for each MEG channel were averaged, and the average was baseline-corrected based on the 400 ms period prior to time zero to produce an estimated evoked response. The mean number of epochs included in the average for each of 13 subjects was 519 (range 492–546). For the subject with noise-contaminated data, 255 epochs were included in the average.

2.2. Experiment 2

2.2.1. Subjects

Nineteen subjects (average age 22.2 years, 4 male) took part in the experiment after providing informed consent. All were right-handed (Oldfield, 1971), reported normal hearing, and had no history of neurological disorders. On the hearing check administered prior to the experiment, all subjects perceived stimulus sound levels as comfortable and equal in both ears.

2.2.2. Stimuli

Two stimuli were generated as wav files, 500 ms in length with a sampling frequency of 16 k Hz (using Matlab 7, The Mathworks, Inc.). The stimuli consisted of a single click (0.0625 ms square wave, positive polarity) and a click pair (two 0.0625 ms square waves, positive followed by negative polarity) with a 40 ms interval separating the square wave onsets.

2.2.3. Procedure

The procedures were identical to those followed in Experiment 1 except that the two stimuli were presented 480 times each (in pseudo-random order) with presentation divided into 8 identical blocks.

2.2.4. Neuromagnetic recording

The neuromagnetic signal data were acquired as described for Experiment 1. Data were continuously recorded using a sampling rate of 1000 Hz, on-line filtered between 1 and 100 Hz with a notch at 60 Hz.

2.2.5. Data processing

Recorded data were noise-reduced using the time-shift principle component analysis algorithm (TSPCA) (de Cheveigné and Simon, 2007). The examined MEG data for each stimulus condition covered 860 ms epochs that included 400 ms pre-trigger and 460 ms post-trigger periods. Subsequent processing of the data was the same as described for Experiment 1. Further analysis of the processed data again included only those epochs representing the response to the single click stimuli. The total number of accepted epochs averaged 472 per subject (range 441–480).