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<th>Cortical neuromagnetic fields preceding voluntary jaw movements</th>
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INTRODUCTION

Slow cortical potentials reflecting the central programming of voluntary jaw movements (readiness potentials, RPs) were reported to appear preceding the movements. However, the current source producing the RP has not yet been localized. This study aimed to determine the cortical regions involved in the central programming of bilaterally symmetrical voluntary jaw movements, by locating the current source of the neuromagnetic counterpart of the RP (readiness field, RF). The RFs were found in the fronto-lateral region bilaterally, starting around 860 and 600 ms prior to the onset of masseter and digastric electromyograms (EMGs), respectively, and gradually increasing in magnitude to the peak within 100 ms before the EMG onset. Thus, the RFs appeared long before the reported onset of the excitability increase of pyramidal tract neurons. The current sources producing the RFs were located in the precentral gyrus bilaterally, with no bilateral differences in strength. We conclude that the primary motor cortex is involved bilaterally in central programming as well as in execution of bilaterally symmetrical voluntary jaw movements.

KEY WORDS: MEG, readiness field, voluntary jaw movements, equivalent current dipole, precentral gyrus.

MATERIALS & METHODS

List of Abbreviations

ANOVA, analysis of variance; ECD, equivalent current dipole; EEG, electroencephalogram; EMG, electromyogram; EOG, electro-oculogram; HPI, head position indicator; MEG, magnetoencephalography; MEF, motor-evoked field; MRI, magnetic resonance image; PMF, post-movement field; RF, readiness field; RP, readiness potential; SQUID, superconducting quantum interference device.

Subjects

Subjects were five healthy, right-handed male volunteers (25-31 yrs of age) with no disorders in oral function. Written informed consent to this study was obtained from each subject before the experiment, which was approved by the Ethics Committee of Tokyo Dental College.

Experimental Procedures

A 306-channel SQUID (superconducting quantum interference device) neuromagnetometer (Vectorview, Neuromag Co., Helsinki, Finland) was used.
for recording magnetic fields from 102 positions over the whole scalp. At each position, a pair of gradiometers measured the two orthogonal derivatives, one along the latitudes and the other along the longitudes, of the radial component of the magnetic field.

Scalp EEGs were recorded with silver-silver chloride disc electrodes on Fz, Cz, and Pz (according to the International 10-20 System) monopolarly with reference to the left earlobe. An electro-oculogram (EOG) was recorded with a pair of silver-silver chloride disk electrodes on the left side, to detect the records contaminated with magnetic field artefacts caused by eye movements. Surface electromyograms (EMGs) were recorded from the left masseter and digastric muscles with a pair of silver-silver chloride disc electrodes.

The locations of three anatomical landmarks (the nasion and bilateral pre-auricular points) and two pairs of head position indicator (HPI) coils, attached to the forehead and the mastoid process bilaterally, were determined with a three-dimensional digitizer (Isotrak, Polhemus Inc., Colchester, VT, USA). At the start of each recording session, we determined the exact locations and orientations of the sensors with respect to the head by measuring the magnetic fields produced by currents applied to the HPI coils.

Each subject was seated comfortably in a magnetically shielded room and gazed at a spot of light on a screen 1 m in front of him. The subject was instructed to perform either bilaterally symmetrical jaw-closing or jaw-opening movements from the mandibular rest position at his own pace. The subjects performed jaw movements at an interval ranging from 2 to 8 sec (ca. 5 sec on average). When two successive jaw movements were performed at an interval of less than 4 sec, both trials were excluded from the analysis. One experimental session consisted of trials of either jaw-closing or jaw-opening movements and lasted until 100 artefact-free records were obtained.

For determination of brain anatomy, MRIs of the brain were obtained on each subject with a 1.5-T whole-body scanner (Symphony, Siemens, Erlangen, Germany).

Data Analysis

On-line analysis
All signals were digitized at 601 Hz, and band-pass-filtered (0.1-80 Hz for MEG and EEG, 0.03-15 Hz for EOG, and 100-200 Hz for EMG). These EEGs, EOGs, EMGs, and a subset of MEGs were displayed on a screen so that the task performance by the subjects could be monitored. The intervals of the jaw movements were monitored by the EMGs. We monitored each subject's behavior with a video camera, to confirm that he was alert and paying attention to the spot of light.

In parallel with the digitization mentioned above, EMG signals were also recorded with a band-pass filter of 10-2000 Hz to generate triggering pulses for averaging the MEGs, EEGs, and EMGs with respect to the onset of masseter or digastric EMG. In one session, the MEGs, EEGs, and EMGs of 100 trials free of artefacts were averaged.

The analysis period was set to 3000 ms, from 2500 ms preceding to 500 ms following the onset of masseter or digastric EMG. Trials contaminated with magnetic field artefacts were automatically rejected.

Off-line analysis
Isocontour maps were constructed from the measured data at selected time points by the method of minimum norm estimates (Hämäläinen and Ilmoniemi, 1994). To identify the sources of movement-related magnetic fields, we divided the signals into several periods. During each period, one equivalent current dipole (ECD) was first determined by the least-squares search for a subset of channels over the areas where movement-related magnetic fields were visually detected. Goodness-of-fit (gof) of the model was also calculated to express (in percentage) how much the dipole model accounted for the measured signal variance. Only ECDs attaining more than 80% gof were accepted for analysis, in which the entire time period and all the channels were taken into account for computation of the parameters of a time-varying multidipole model (Hämäläinen et al., 1993). We identified the next ECD by first removing the effects of the previous sources from the magnetic signal pattern (signal space projection method; Uusitalo and Ilmoniemi, 1997) and then searching for additional sources at the response of the residual waveforms.

The three-dimensional location, orientation, and strength of the ECD in a spherical conductor model were determined on the three-dimensional coordinate frame detected by HPI coils. We then superimposed the ECDs on the subject's MRIs to determine the source locations with respect to the anatomical structures.

The times of onset and peaks of RFs were determined with a temporal resolution of 2 ms, since the RF signals were digitized at 601 Hz (1.66-ms interval). The onset of the averaged RF was determined by the method of Nagamine et al. (1996): The mean ± 2 SDs of the activity during 300 ms (from 2500 to 2200 ms preceding the EMG onset) was defined as a level of the resting activity; with the least-squares method, a linear regression line was drawn for the slow MEG field for the period from the time when the signal exceeded the range of the resting activity to the EMG onset; and the intersection of the regression line with the baseline was adopted as the onset of the RF (see Fig. 2).

The difference between the means of the onset and peak times of magnetic fields, as well as the strength of ECD, was statistically tested by one-way ANOVA; the significance level was set to $P = 0.05$.

RESULTS

Cortical Magnetic Fields in Association with Self-paced Voluntary Jaw Movements

We found slow cortical magnetic fields and potentials from the bilateral fronto-lateral scalp region preceding the EMG onset of the muscle involved in jaw-closing and jaw-opening movements (Fig. 1; subject 5). The slow magnetic fields started 500-1000 ms preceding the onset of EMG activities, and gradually increased in magnitude, reaching the peak of 50-100 fT within 150 ms preceding the onset of the EMG (upper and lower pairs of MEG traces in Fig. 1). In association with jaw-opening movements, this slow field was followed by four successive peaks (MEF I, II, III, and PMF) after the onset of EMG activity (Fig. 2), as reported by Kristeva et al. (1991). In the magnetic fields accompanying jaw-closing movements, however, no motor-related magnetic fields could be discerned after the masseter EMG onset, due to contamination of large artefacts. Accordingly, we confined the analysis to the field preceding the onset of EMG, i.e., the RF.

In association with jaw-closing movements, the RF started at $844 \pm 156$ ms (mean ± SD, $n = 5$) and $866 \pm 255$ ms ($n = 5$) on the right and left sides, respectively, and reached
the peak of 50-100 fT at 102 ± 58 ms and 66 ± 33 ms (n = 5), on the right and left sides, respectively, preceding the masseter EMG onset. Likewise, in association with jaw-opening movements, the RF started at 618 ± 392 ms and 591 ± 248 ms (n = 5) preceding the onset of the digastric EMG on the right and left sides, respectively, and reached the peak of 50-100 fT at 2 ± 30 ms prior to the digastric EMG onset on the right side and 7 ± 11 ms following it on the left sides.

There were no significant bilateral differences in either the onset time or peak time of the RF accompanying the jaw-closing and jaw-opening movements (P > 0.05, n = 5). Nor was there significant difference in the RF onset times between the jaw-closing and jaw-opening movements on either side (P > 0.05, n = 5). The peak was reached earlier in the jaw-closing than the jaw-opening movements on either side (P < 0.05, n = 5), however.

The ECDs producing the RF distribution were located in the anterior wall of the central sulcus bilaterally on the sagittal planes of MRI of the subject’s brain (Figs. 3B1, 3B2, red circles) and directed anteriorly (Figs. 3B1, 3B2, red bars). In all subjects, the ECDs were located in the lateral precentral gyrus at rather a deep portion of the central sulcus. The source strength of the ECDs for the RF (Fig. 3B3) showed a gradual increase, with a time course similar to that of the RF (Fig. 1). The source strength of the ECDs attained the maximum value at the peak of the RFs, i.e., 60 ms and 102 ms on average, preceding the onset of masseter EMG on the left and right sides, respectively. The locations of the ECDs in the lateral precentral gyrus on both sides were confirmed on the three-dimensionally reconstructed MRI of the subject’s brain (Figs.

Figure 2. Expanded cortical magnetic field accompanying jaw-opening movements in subject 3. Rightmost vertical line indicates the time of onset of digastric EMG. Abbreviations: RF, readiness field; MEF, motor-evoked field; PMF, post-movement field. Horizontal thick straight line indicates the average level of the resting magnetic field; shaded areas above and below show 2 SD of the resting field, respectively. These values were obtained from the resting field for the period of 300 ms at the beginning of the window (leftmost period indicated by bilateral arrow). Dotted line represents regression line to determine the time of RF onset.
3C1, 3C2, red circles). In three of the five subjects, the ECDs producing the RF associated with jaw-closing movements were located in the precentral gyrus on both sides. In the remaining two subjects (subjects 1 and 4), the ECD was located in the precentral gyrus on one side, but the ECD was not found in the brain on the other side.

The strength of the ECDs for the RF was 25.5 ± 11.1 nAm on the right side and 28.8 ± 14.2 nAm (n = 4) on the left side; there was no bilateral difference (P > 0.05, n = 3).

Jaw-opening movements
The isocontour maps of the RF (Figs. 4A1, 4A2; subject 1) on the left and right sides were drawn at 80 ms prior to the digastric EMG onset, and the ECDs producing the RF distribution were located in the fronto-lateral region and directed anteriorly (green arrows in Figs. 4A1, 4A2). On the sagittal planes of MRI of the subject’s brain, the ECDs were located in the anterior wall of the central sulcus bilaterally (Figs. 4B1, 4B2, red circles) and directed anteriorly (Figs. 4B1, 4B2, red bars). The source strength of the ECDs (Fig. 4B3) showed a gradual increase, with a time course resembling that of the RF (Figs. 1, 2), and reached the maximum at the peak of the RF. In the three-dimensionally reconstructed MRI of the subject’s brain, the ECDs of the RF accompanying jaw-opening movement were confirmed to be located in the lateral precentral gyrus on both sides (red circles in Figs. 4C1, 4C2). The ECDs producing the RF accompanying the jaw-opening movements were located in the lateral precentral gyrus bilaterally at rather a deep portion of the central sulcus in all five subjects.

The strength of the ECDs for the RF was 21.2 ± 2.7 nAm and 21.4 ± 1.9 nAm (n = 5) on the right and left sides, respectively; there was no bilateral difference (P > 0.05, n = 5).

DISCUSSION
The present study not only has confirmed the bilateral presence of the RF preceding voluntary jaw movements (Narita et al., 1998), but also has determined the location of the ECDs producing the RF on the MRI. The ECDs of the RFs accompanying jaw-opening movements were located in the lateral precentral gyrus bilaterally in all five subjects. Those accompanying voluntary jaw-opening movements were also located in the lateral precentral gyrus bilaterally in three of five subjects and unilaterally in the remaining two subjects. Thus, the ECD locations of the RF accompanying the voluntary jaw movements would correspond to the area representing the jaw movement in the precentral gyrus (Penfield and Boldrey, 1937).

Studies of cortical magnetic fields accompanying voluntary unilateral finger movements generally agree on the occurrence of slow magnetic fields preceding the movement with contralateral dominance (Deecke et al., 1982; Cheyne and Weinberg, 1989; Kristeva et al., 1991; Nagamine et al., 1996;...
Babiloni et al., 2001). In contrast, the RF accompanying bilaterally symmetrical jaw movements appeared in the cerebral cortex bilaterally, with no significant bilateral difference in the source strength.

Erdler et al. (2000) classified the slow cortical magnetic fields preceding voluntary finger movements into two components: readiness fields 1 and 2, which appeared 1.9-1.7 s and about 0.5 s prior to the movement onset, respectively. The current sources producing the former were localized in the supplementary motor area, while those producing the latter had their sources in the primary motor cortex. The RFs preceding voluntary jaw-closing and jaw-opening movements started to appear around 860 ms and 600 ms preceding the EMG activities in the masseter and digastric muscles, respectively. Accordingly, the RFs observed in the present study would correspond mainly to readiness field 2.

Transcranial magnetic stimulation of the human brain revealed that the excitability of pyramidal-tract neurons started to elevate 80-120 ms prior to the onset of voluntary finger movements (Starr et al., 1988; Chen et al., 1998; Chen and Hallett, 1999; Leocani et al., 2000), indicating that the RF starts to appear long before activation of pyramidal-tract neurons, which are directly involved in the execution of movements. It is strongly suggested that the early phase of RF accompanying voluntary jaw movements is not associated with increased excitability of pyramidal-tract neurons accompanying jaw movements. We conclude that the primary motor cortex is involved in programming of bilaterally symmetrical voluntary jaw movements as well as in their execution.

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