Neuroimage of Voluntary Movement: Topography of the Bereitschaftspotential, a 64-Channel DC Current Source Density Study

R. Q. Cui, D. Huter, W. Lang, and L. Deecke

University Clinic of Neurology and Ludwig Boltzmann Institute of Functional Brain Topography, University of Vienna, Vienna, Austria

Received January 20, 1998

The Bereitschaftspotential (BP) was recorded at 56 scalp positions when 17 healthy subjects performed brisk extensions of the right index finger. Aim of the study was to contribute to our understanding of the physiology underlying the BP and, in particular, to specify the situation at BP onset. For this purpose, the spatial pattern of the BP was analyzed in short time intervals (35 and/or 70 ms) starting 2.51 s before movement onset. For each time segment a spherical model of the BP was calculated by using spline interpolation. Then the spatial distribution of the electric potential at the scalp surface was transformed into a spatial distribution of current source densities (CSD map). Onset times of the BP and onset times of initial CSD-activity ranged between 2.23 and 1.81 s before movement onset. We selected a time window between 1.6 and 1.5 s before movement onset in order to analyze the spatial CSD pattern in each subject. In 10 subjects there was a significant current sink in the scalp area located over medial-wall motor areas (pre-SMA, SMA proper and anterior cingulate cortex: electrode positions C1, C2, FCz, Cz) in the absence of a significant current sink over the primary motor cortex (MI: electrode positions C3, CP3, and CP5). In three subjects significant current sinks were present at both sites and in another three subjects a current sink only over the lateral motor cortex was observed. In one subject no significant current sinks were measured. It is concluded that there is a large group of subjects (13/17) in whom BP at onset is associated with a current sink over medial-wall motor areas. At a later time interval (0.6 to 0.5 s before movement onset), significant current sinks were found in 13 subjects in medial and in 10 subjects in lateral recordings. These data were considered to be consistent with the hypothesis that, at least in a majority of subjects, medial-wall motor areas are activated earlier than lateral motor areas when organizing the initiation of a simple self-paced movement. Surface-recordings of the EEG do not allow further specification of cortical areas, which contribute to the current sinks. But in context with the current literature of the electrophysiology of nonhuman primates and of brain imaging in humans it is suggested that SMA and anterior cingulate cortex contribute to the current sink, the fronto-central midline, and that the primary motor cortex (MI) contributes to the current sink in the scalp area, which is located above MI and closely posterior to it.

INTRODUCTION

Since early evidence of supplementary motor area (SMA) participation associated with voluntary movement (Deecke and Kornhuber, 1978; Lassen et al., 1978) different methods of functional brain imaging showed that medial-wall motor areas (pre-SMA, SMA proper, anterior cingulate cortex) as well as the primary motor cortex (MI) are activated when healthy subjects perform repetitive, voluntary finger movements (functional MRI (fMRI): Boecker et al., 1994; Hikosaka et al., 1996; magnetoencephalography (MEG): Cheyne et al., 1991, 1995, intracortical recording: Rektor et al., 1994; electrocorticography (ECoG): Ikeda et al., 1993, 1995, biophysical modeling of surface-recorded EEG: Preamstra et al., 1996; PET: Jahanshahi et al., 1995; Stephan et al., 1995; Picard and Strick, 1996; Boecker et al., 1998). Further evidence comes from electrophysiology in nonhuman primates showing that neuronal activity in pre-SMA, SMA proper, anterior cingulate cortex, MI, and the lateral premotor cortex (PMC) precede the initiation of self-initiated movements in nonhuman primates (Tanji, 1994; Shima et al., 1991; Rizzolatti et al., 1996). The main argument that neuronal activities in the frontocentral mesial cortex (SMA and CMA) are not epiphenomena comes from observation in patients having lesions of that part of the brain. In the acute state, lesions of the frontocentral mesial cortex cause akinesia, defined as a lack of internally mediated voluntary movements of the contralateral part of the body (Förster, 1936; Laplane et al., 1977).

A main controversy is whether the medial-wall motor areas and the lateral motor areas form a functional network which together subserves the organization of a voluntary movement or whether there is functional...
specificity and hierarchy. One hypothesis related to that controversy is that the activity of the medial-wall motor areas precede that of the primary motor cortex (M1). This hypothesis would imply that there is a temporal sequence in the brain processing, which underlies the transduction of an intention to act into overt behavior (Deecke et al., 1976; Deecke, 1987). The dilemma of this hypothesis is that it is only testable with methods which have a temporal resolution that is sufficient enough to separate in the range of a few hundred milliseconds. Methods, which are related to changes of blood flow and metabolism, are not qualified to solve that issue. Electroencephalography (EEG) would in principal be an adequate method. Movement-related brain activity was studied by ECog of SMA, CMA, and M1 (Ikeda et al., 1992, 1993, 1995; Rektor et al., 1994) but no patient is so far reported who had simultaneous recordings of SMA and M1, which would be necessary in order to clarify the timing patterns of activity in these areas.

But is the hypothesis testable by surface recorded EEG and MEG? Unfortunately, MEG together with presently available biophysical models suffers from the cancellation problem of both SMAs being active simultaneously (Lang et al., 1991). Furthermore, MEG in its present configuration is not sensitive to magnetic fields of radial currents. Advanced techniques of data analysis (e.g., “current multipole expansion,” Nolte et al. 1997) may provide ways to apply MEG for investigations into that question. EEG has the advantage to be not only sensitive to tangential currents but also to radial ones, and this advantage of EEG should be helpful to pick up activity of medial-wall motor areas. The brain potential that precedes the initiation of a voluntary movement is called Bereitschaftspotential (BP). It starts at about 1.5 s before movement onset in electrodes located over medial-wall motor areas and is of negative polarity here when using a far-away reference (e.g., mastoids or linked ears). It has been suggested that the BP at its onset results from a radial current sink which is caused in medial-wall motor areas (Deecke et al., 1976; Lang et al., 1990). BP-topography changes about 750 to 500 ms before movement onset, which is characterized by an increasing lateralization of the BP with larger amplitudes above the contralateral primary motor cortex (M1) as compared to amplitudes above the ipsilateral M1 (Deecke et al., 1976; Shibasaki et al., 1993). The term “early BP-component,” BP1, will be used in order to describe brain potential shifts between BP onset and its change of topography as described above.

By using an equivalent current dipole, Praamstra et al. (1996) recently established a model which consisted of three current dipole equivalents and which explained the spatio-temporal pattern of scalp-recorded BP: One dipole was radial and located in the medial-wall motor areas with direction of current flow pointing into the brain, two lateral dipoles were located in the primary motor cortex of either hemisphere with direction of current flow from lateral posterior to anterior and mesial (see also Knösche et al., 1996). This dipole model is consistent with the patterns of current sinks and sources in the scalp which we have recently described (Cui et al., 1996). But the dipole model of Praamstra and coworkers is in conflict with previous ones by Bötzel et al. (1993) and Böcker et al. (1994a,b).

Current Source Density (CSD) analysis is a method that allows evaluation of the topography of current sources and sinks on the scalp. Current source density is proportional to the sum of partial second derivatives of the potential field (Mackay, 1984). CSD values are proportional to the current entering and exiting the scalp. CSD-maps are more sensitive to high spatial frequency local cortical potentials than it is to potentials of low spatial frequency due to volume conduction from distant sources (Gevins et al., 1994). Furthermore, CSD analysis minimizes smearing effects as caused by the tissue transmission distortion (Nunez, 1994; Perrin, 1987). Therefore, CSD analysis arrives at an absolute and quantitative description of the field distribution, showing more precise localization of the electrical activities than the raw potential distribution (Nagamine et al., 1992). It can provide an estimation of local current density flowing perpendicularly through the skull. The CSD method is much more sensitive to local sources (both tangential and radial ones). The most significant contributions to CSD are believed to be from cortical sources (Nunez et al., 1994).

Prior to the initiation of a voluntary movement, there is a current sink in the scalp located over the frontocentral mesial cortex (Cui et al., 1996). A current sink in this area was also found during the execution of motor sequences which varied with task complexity, i.e., the temporal and spatial structure of the task (Lang et al., 1988, 1990). Single cell recordings in nonhuman pri-mates (Okano and Tanji, 1987; Mushiake et al., 1990, 1991; Tanji, 1994) exhibited neurons in the SMA, which were specifically activated by variations of the temporal and spatial structure of the motor sequence task. Neuropsychological examinations in patients with lesions in the frontocentral mesial cortex (Halsband et al., 1993; Lang et al., 1990; Asenbaum et al., 1992) exhibited not only disturbances of movement initiation but also of performing motor sequences. These results led to the hypotheses that the SMA may be involved in specific transformations of information about the intended and ongoing movement (Tanji, 1994) or in a more general process of transducing the intention to act into action and its willful realization which may covary with task complexity (Lang et al., 1990).

Based on the converging evidence we accepted the
concept that the current sink in the frontocentral midline is an index of activity of medial-wall motor areas. In the present study, we measured the BP at 56 scalp positions and used spherical spline interpolation (Lindinger et al., 1999) in order to obtain a dense description of the spatial BP pattern in short successive time intervals (of 35 or 70 ms). The task was simple. Subjects were required to extend their right index finger at their will within a predefined period. Maps of electric surface potentials were transformed into maps of current source densities (CSD maps). A first step of analysis was to define the onset of cortical activity preceding brisk extensions of the right index finger. It turned out that electric signs of cortical activity started earlier than 1.6 s before movement onset in all subjects. The second step of analysis was to statistically test in single subjects the existence of current sinks over the frontocentral midline and/or the contralateral MI at this early epoch of motor preparation. Results of this test are related to the above-mentioned hypothesis: The existence of a significant current sink in the frontocentral midline in the absence of current sinks in the scalp area over MI at the early time epoch would be consistent with the view that there is a temporal sequence between activities in medial-wall motor areas and in MI. The finding of a temporal sequence of cortical activity may support the concept that medi wall motor areas may be activated earlier in the process to transform the intention to act into action. This is the first study which used statistical analysis of CSD values in single subjects.

**MATERIAL AND METHODS**

**Subjects**

Seventeen right-handed healthy subjects (6 females, 11 males), ranging in age from 21 to 40 years (mean 30.7 years), participated in the experiment. Hand dominance was assessed with a questionnaire and all subjects scored 100% dextrality (Lang et al., 1988).

**Task**

The task was to perform repetitive brisk extensions of the right index finger. Hand and finger were fastened on a manipulandum, which enabled subjects to move the index finger at the proximal joint. Subjects were trained according to the following standard instructions: Initiate movements without any external cues at your own will. Avoid regular pacing, rather initiate movements at irregular intervals between 7 s minimum and 15 s maximum. Perform the movement in a monophasic manner, i.e., keep your index finger extended for about 0.5 s before returning to resting position. Subjects were advised to fix their gaze on a point which was located straight ahead in order to prevent eye movements and to keep their body in a relaxed position and to avoid other movements such as swallowing, masticatory, or orofacial movements. A training period was provided before starting the experiment. By means of the manipulandum the movement was loaded with 100 g inertial load. Two hundred fifty trials were recorded. The investigator viewed the EEG on-line during the experiments together with the signals which indicated finger movements. If the interval between two movements was judged by the investigator to be either too short or too long the subjects were informed to adjust their behavior. Like in all studies of the BP which have been conducted so far quantitative measurements of the time intervals between movement onsets were not performed.

**Data Acquisition**

Direct current electroencephalography (DC-EEG) was recorded using a 64-channel computer-assisted DC amplifier (Lindinger et al., 1991). Besides electrooculogram (EOG), electromyographic (EMG), and other monitoring channels, we recorded from 56 electrodes on the scalp. The electrodes were fixed on the scalp according to the 10–20 system including interpolated electrode positions (cf. Cui et al., 1996). A bandpass filter was set from DC to 70 Hz. In order to reduce skin potentials, resistance, and slow potential drifts (caused by sweating and temperature changes of the subject), nonpolarizable Ag/AgCl electrodes were employed which provided electrode sockets and conductance via salt bridges (as described in detail by Bauer et al., 1989). The skin was scratched with a small needle at the recording sites, thereby reducing electrode impedance to less than 1 kΩ. The right mastoid served as a reference and the ground electrode was placed on the right cheek. The EOG was monitored with two pairs of bipolar electrodes in both vertical and horizontal directions. The EMG activity was recorded with two pairs of bipolar electrodes on the forearm. One pair of electrodes was fixed along the skin surface of the extensor muscles and the other pair was fixed along the skin surface of the flexor muscles. The electrodes in each pair were spaced 5 cm apart. All data were amplified and digitized (16-bit A/D converter at a sampling frequency of 250 Hz) on a PC-supported 64-channel DC-EEG amplifier, stored, and displayed on-line by a computer. EMG onset for each movement was subsequently identified, and artifact-free trials were averaged off-line over an epoch lasting from 3 s before to 0.5 s after movement onset.

**Preprocessing of the Data**

The data were preprocessed and averaged off-line with a software package (Lindinger et al., 1991) and stored on hard disk. For removing eye-blink artifacts from EEG, a linear regression method was applied during off-line analysis using the vertical EOG. Eye
blinks were identified by analyzing the covariance between vertical EOG and an eye-blink template (Lindinger et al., 1991). At least 200 to 230 artifact-free DC-EEG trials were averaged time-locked to the onset of the trigger associated with finger movement.

CSD-Analysis of the Early Component of the Bereitschaftspotential (BP 1)

The slow potential shift which precedes the onset of a voluntary movement has originally been termed Bereitschaftspotential (BP; Kornhuber and Deecke, 1964, 1965). Subsequent studies showed that with unilateral finger movements, the spatial pattern of electric brain potential is not stable but that there is a change of the spatial pattern at about 500 ms before movement onset. During its early component, BP is symmetrically distributed around the frontocentral midline, during its later component, BP becomes asymmetric with larger amplitudes over (and slightly posterior to) the contralateral MI-hand area (Deecke et al., 1969, 1976) and there is a sudden increase of the steepness of the slope (Shibasaki et al., 1981). This phenomenon was consistently observed but the terminology related to it was different and confusing. In order to be in a position to analyze the CSD-map related to the early component of the BP, we had first to define the time points when BP starts and when it changes its spatial pattern and steepness. Two investigators (R.C. and D.H.) determined these time points by analyzing the BP-waveforms and spatial changes of BP-amplitude maps and CSD maps. The method of Shibasaki et al. (1981) was used to determine the changes of steepness of the slope. The time period between these two points is related to the early component of the BP which will be termed BP1. The component of the BP which follows the change of pattern is termed BP2.

The next step was to define areas of interest in the scalp. These are the areas where current sinks have been found in previous CSD studies (Lang et al., 1994; Cui et al., 1996). One area of interest is the frontocentral midline which covers electrode positions Fz, Cz, C1, and C2. The second area of interest is over the MI-hand area and slightly posterior and lateral (C3, CP3, CP5); since the direction of the current flow as caused by MI-activity is directed from posterior lateral to anterior mesial positions with a current sink posterior to the MI-hand area and a current source in mesiolateral frontopolar positions (Lang et al., 1991; Cui et al., 1996). The area subtended by electrodes C3, CP3, and CP5 should be suitable to detect the current sink as produced by surface-to-depth current flow in MI-hand area (Gerloff et al., 1997).

Based on the analyses of BP onset the adequate time period to measure the early BP-epoch (BP1) was 1.6 to 1.5 s before movement onset. An equal distance between the mean onset times of BP1 and BP2 would have been at 1.4 s before movement onset. The time window was selected to be more close to the BP onset. The main point of interest was related to the existence or absence of a significant current sink above the medial-wall motor areas (area of interest subtended by electrodes FCz, Cz, C1, and C2) and the MI-hand area (area of interest subtended by electrodes C3, CP3, and CP5) during the early BP-epoch. This was tested in each individual subject by single trial analysis. In other words, mean CSD-values within the selected time window (1.6 to 1.5 s before movement onset) were calculated in each single electrode of the two areas of interest for each single trial of each subject. The baseline period to which CSD-values were referred was 3.0 to 2.5 s before movement onset. For each subject, t tests (paired, two-tailed) were used in order to test whether there is a significant current sink in an electrode which belonged to the two scalp-areas of interest (significance level: P < 0.05).

CSD-Analysis of the Late Component of the Bereitschaftspotential (BP 2)

Time period selected was from 0.6 to 0.5 s before movement onset. Areas of interest were above the frontocentral mesial cortex (subtended by electrode positions FCz, Cz, C1, C2) and above the MI-hand area (C3, CP3, CP5). Mean CSD values were calculated in the recordings of interest (FCz, Cz, C1, C2, C3, CP3, and CP5) for each single trial in each subject for the time period 0.6 to 0.5 s before movement onset. The baseline period to which CSD-values were referred was 3.0 to 2.5 s before movement onset. T tests were used in order to test whether current sinks were significant (P < 0.05).

RESULTS

Bereitschaftspotential

A slow change of surface-recorded electric brain potentials precedes the initiation of a voluntary movement (BP; Fig. 1 shows a typical recording). With reference at the mastoids, BP is surface-negative with the exception of recordings at frontopolar positions where, for simple movements, a slow positive potential shift is recorded. Maxima of surface-negative potentials are found in frontocentral mesial recordings (C1, C2, Cz, FCz) as well as over and slightly behind the MI that is contralateral to the performing hand (C3, CP3). Mean BP onset is at about 2.2 s in recording C1. In the final 500 ms before movement onset the slope becomes steeper, particularly in recordings contralateral to the performing hand. This results in augmentation of the lateralization of the BP toward the left hemisphere. Historically, the first component of the BP (BP1) lasts from its onset until the sudden change in steepness.
FIG. 1. Bereitschaftspotential preceding voluntary right index finger extensions with loading of 100 g recorded with the 64-channel true DC EEG recording device of a typical subject (Wang J A, M, 33 y). Epoch from $-3$ to $+0.5$ s, movement onset at $t = 0$. A slow negative potential shift precedes the movement at most recording sites except for the frontal leads, where it is positive. The Bereitschaftspotential consists of a gentle slope (BP1) at the beginning, followed by a steeper slope (BP2). The transition from BP1 to BP2 with increasing steepness of slope is best seen in channels FC1, FC3, FC2, and FCz.
The later component of the BP (BP2) starts with the change in steepness. Individual latencies of BP1 and BP2 are displayed in Fig. 2. The onset of BP1 ranged from 2.23 to 1.81 s (mean ± SD, 2.05 ± 0.11 s) before movement onset, the onset of BP2 from 0.97 to 0.41 s (0.69 ± 0.20 s) before movement onset.

Current Source Density Mapping

Figure 3 shows the results of a single subject: In the early period of time (1.6 to 1.5 s before movement onset), which is related to BP1, a current sink was found in the frontocentral midline. At a later period of time (0.6 to 0.5 s), which is related to BP2, the area where current flow is directed into the scalp (current sink) is more widespread (Fig. 4): One area of current sink is above the contralateral primary motor cortex, a second area is above the frontocentral mesial cortex and a third one above the ipsilateral primary motor cortex.

Statistical Analysis of Current Sinks for Time Periods Related to BP1 and BP2

Table 1 presents the results of the statistical analysis of current sinks in the areas above the medial-wall motor areas (Cz, FCz, C1, and C2) and the contralateral MI-hand area (C3, CP3, and CP5) for the early BP component BP1 (measured between −1.6 and 1.5 s before movement onset), the late component BP2 (measured between −0.6 and 0.5 s before movement onset) and at movement onset (measured between −0.1 and 0.0 s).

In 10 of 17 subjects a significant current sink was
detected in the early period of time in at least one of the recordings above the medial-wall motor areas (FCz, Cz, C1, and C2). Three of them (#8, #12, #14) had a significant current sink above the contralateral motor cortex in the early period as well. In three other subjects (#2, #5, #13), there was a significant early current sink above the lateral motor cortex but no significant current sink in the frontocentral midline. In one subject (#6) no significant current sinks were measured.

In the later pre-movement period and at movement onset 13 of 17 subjects had significant current sinks in the frontocentral midline, 10 of 17 subjects had significant current sinks in the area above the contralateral MI.

Table 2 gives the results of a group analysis. During the BP1-period, there was on average a significant current sink in Cz but no significant CSD-values in any recording above the contralateral MI. In the later pre-movement period (BP2-period) and at movement onset significant CSD-values were found in FCz, Cz, and C2. Above the contralateral MI group analysis showed a significant current sink in C3 at movement onset.
The recording site was selected at which the largest and significant CSD values could be measured at the chosen time window. Proportional to the radial current density at a particular recording site. Negative values indicate current flow into the scalp. For each subject, there are significant CSD-values only at the midline; means are about 0.

DISCUSSION

The main finding of the present study is that there is a group of subjects (10 of 17) who present an isolated radial current sink over the medial-wall motor areas in the early stage of the premovement period (cf. Fig. 3). In those subjects, significant changes of CSD-values over the left (contralateral) MI were only found in a later period of time. Data of these subjects are consistent with the a priori hypothesis that there is an early activity in the frontocentral mesial cortex which may precede that in the lateral motor cortex. This hypothesis does not hold for all subjects: There is a group of subjects in whom CSD starts over the contralateral motor cortex (3 of 17). In other subjects either no significant radial current sink was found in mesial and lateral positions (1 of 17) or CSD-values were significant in both mesial and lateral positions during the early stage of the premovement period (3 of 17).

Table 1

Statistical Analysis of Current Source Density (CSD) for Single Subjects during the Early Stage of the Bereitschaftspotential (BP1; –1.6 and –1.5 s), during the Late Stage of the BP (BP2; –0.6 and –0.5 s Prior to Onset of Voluntary Right Index Finger Movement), and at Movement Onset (–0.1 and 0.0)

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Recording points</th>
<th>BP1</th>
<th>BP2</th>
<th>Start of movement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>P value</td>
<td>CSD mean</td>
<td>P value</td>
</tr>
<tr>
<td>No. 1 (Cz)</td>
<td>0.034</td>
<td>(–1.52)</td>
<td>0.033</td>
<td>(–1.81)</td>
</tr>
<tr>
<td>No. 2 (Cz)</td>
<td>0.000</td>
<td>(–1.11)</td>
<td>0.001</td>
<td>(–1.45)</td>
</tr>
<tr>
<td>No. 3 (Cz)</td>
<td>0.000</td>
<td>(–1.75)</td>
<td>0.001</td>
<td>(–3.93)</td>
</tr>
<tr>
<td>No. 4 (Cz)</td>
<td>0.000</td>
<td>(–2.06)</td>
<td>0.013</td>
<td>(–4.06)</td>
</tr>
<tr>
<td>No. 5 (Cz)</td>
<td>0.000</td>
<td>(–1.08)</td>
<td>0.000</td>
<td>(–2.11)</td>
</tr>
<tr>
<td>No. 6 (Cz)</td>
<td>0.000</td>
<td>(–1.20)</td>
<td>0.000</td>
<td>(–2.95)</td>
</tr>
<tr>
<td>No. 7 (Cz)</td>
<td>0.000</td>
<td>(–2.19)</td>
<td>0.000</td>
<td>(–5.72)</td>
</tr>
<tr>
<td>No. 8 (Cz)</td>
<td>0.000</td>
<td>(–0.73)</td>
<td>0.000</td>
<td>(–2.15)</td>
</tr>
<tr>
<td>No. 9 (Cz)</td>
<td>0.000</td>
<td>(–1.75)</td>
<td>0.001</td>
<td>(–3.93)</td>
</tr>
<tr>
<td>No. 10 (Cz)</td>
<td>0.000</td>
<td>(–2.06)</td>
<td>0.013</td>
<td>(–4.06)</td>
</tr>
<tr>
<td>No. 11 (Cz)</td>
<td>0.000</td>
<td>(–1.08)</td>
<td>0.000</td>
<td>(–2.11)</td>
</tr>
<tr>
<td>No. 12 (Cz)</td>
<td>0.000</td>
<td>(–1.20)</td>
<td>0.000</td>
<td>(–2.95)</td>
</tr>
<tr>
<td>No. 13 (Cz)</td>
<td>0.000</td>
<td>(–2.19)</td>
<td>0.000</td>
<td>(–5.72)</td>
</tr>
<tr>
<td>No. 14 (Cz)</td>
<td>0.000</td>
<td>(–0.73)</td>
<td>0.000</td>
<td>(–2.15)</td>
</tr>
<tr>
<td>No. 15 (Cz)</td>
<td>0.000</td>
<td>(–1.75)</td>
<td>0.001</td>
<td>(–3.93)</td>
</tr>
<tr>
<td>No. 16 (Cz)</td>
<td>0.000</td>
<td>(–2.06)</td>
<td>0.013</td>
<td>(–4.06)</td>
</tr>
<tr>
<td>No. 17 (Cz)</td>
<td>0.000</td>
<td>(–1.08)</td>
<td>0.000</td>
<td>(–2.11)</td>
</tr>
</tbody>
</table>

Note. (A) CSD analysis in electrodes of the frontocentral midline (C1, C2, FCz, Cz) and (B) CSD analysis in electrodes located above and closely posterior to the contralateral MI (C3, CP3, CP5). “Mean” values are calculated by the Laplacian transformations and are linear and proportional to the radial current density at a particular recording site. Negative values indicate current flow into the scalp. For each subject, the recording site was selected at which the largest and significant CSD values could be measured at the chosen time window.
by joint studies using EEG and PET or fMRI. For example, a recent study (fMRI) by Dehaene et al. (1997) shows the between-subject variability for the locations of the language areas. But there is also reason to assume that the behavioral context of movement initiation was different among subjects; Libet et al. (1982) classified self-initiated movements upon subjects’ introspective reports. The Bereitschaftspotential started earlier in movements associated with subjects’ “preparation-to-act-soon” but later in those movements where there was a sudden urge for movement initiation. BPs with early onset were characterized by an early and large negative potential shift in recordings over the frontocentral midline. Keller and Heckhausen (1990) distinguished between two types of self-initiated movements, those which were retrospectively reported not to be associated with conscious awareness and those of which subjects were aware of having performed. The Bereitschaftspotential in movements associated with conscious awareness was larger in recordings over the frontocentral midline than in recordings over the lateral motor cortex. The opposite was true for movements, those which were retrospectively reported to have been initiated without subsequent introspective feeling of conscious awareness. From this one can conclude that the behavioral context of movement initiation, in particular the degree by which conscious attention and intensiveness is present may change within and between subjects. There is evidencing that these changes have significant effects on the temporospatial pattern of the Bereitschaftspotential. It is not practical to assess the subjects’ introspective feelings after each single movements in any experimental work in order to control for that variability. But measurements of the time intervals between single movements could be helpful to detect behavioral changes. Changes from irregular time intervals into a regular rhythm of movement initiation may indicate a change into a more automatic way of movement initiation. Between-subject differences may be caused by differences of timing strategies. This source of variability between and within subjects has never been studied so far. A retrospective analysis of our data was not possible since fixed time periods around each movement had been stored but not the continuous EEG together with movements.

Considering the fact that there is no consistent dipole model of the Bereitschaftspotential and the principal difficulties to establish such a model, CSD analysis seems to be the only method of analyzing surface-recorded electric brain activity preceding the onset of a voluntary movement. Within this model, positive results, i.e., the detection of a significant current sink, are more easy to interpret than negative ones, i.e., the absence of a significant current source, which may result from bad signal-to-noise ratio. In order to minimize the likelihood of a false-negative result a large number of movements was performed by each subject.

Which cortical areas may contribute to the current sink in the frontocentral midline, which appeared as early as 1.5 s prior to the initiation of a simple movement. Okano and Tanji (1987) found a large number of neurons in the SMA (proper) which were active 1.5 to 2 s prior to the initiation of a self-paced movement. Shima et al. (1991) reported that activity in many anterior cingulate cells began more than 500 ms and as much as 2000 ms before the initiation of a self-paced movement. Recent brain imaging studies in humans by PET have shown that it may be SMA proper which is activated in the generation of simple repetitive movements, whereas the pre-SMA is activated with more complex motor sequence tasks (Colebatch et al., 1991; Deiber et al., 1991; Boecker et al., 1998; for review: Picard and Strick, 1996; Tanji 1996). For that reason, it is suggested that activity in SMA (proper) and anterior cingulate cortex is the cause of the current sink in recordings of the frontocentral midline, which

### Table 2

<table>
<thead>
<tr>
<th>Recording points</th>
<th>BP1 P value</th>
<th>CSD mean</th>
<th>BP1 P value</th>
<th>CSD mean</th>
<th>BP2 P value</th>
<th>CSD mean</th>
<th>Start of movement P value</th>
<th>CSD mean</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. Frontocentral Midline</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fcz</td>
<td>0.434</td>
<td>(−0.06)</td>
<td>0.039</td>
<td>(−0.66)</td>
<td>0.019</td>
<td>(−1.10)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cz</td>
<td>0.007</td>
<td>(−0.52)</td>
<td>0.002</td>
<td>(−1.31)</td>
<td>0.002</td>
<td>(−1.70)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C1</td>
<td>0.943</td>
<td>(0.01)</td>
<td>0.286</td>
<td>(−0.65)</td>
<td>0.079</td>
<td>(−1.40)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C2</td>
<td>0.092</td>
<td>(−0.27)</td>
<td>0.021</td>
<td>(−0.87)</td>
<td>0.019</td>
<td>(−1.34)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>B. Contralateral MI</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C3</td>
<td>0.394</td>
<td>(−0.22)</td>
<td>0.135</td>
<td>(−0.74)</td>
<td>0.019</td>
<td>(−1.23)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cp3</td>
<td>0.570</td>
<td>(0.05)</td>
<td>0.485</td>
<td>(−0.09)</td>
<td>0.286</td>
<td>(−0.14)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cp5</td>
<td>0.924</td>
<td>(−0.08)</td>
<td>0.905</td>
<td>(−0.26)</td>
<td>0.938</td>
<td>(−0.41)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. The question of interest was whether the mean CSD values of individual subjects significantly differ from the baseline level (paired t test). This analysis was separately performed for each recording site and time period (BP1, BP2, movement onset).
starts as early as 1.5 s before movement onset. In the group analysis the early current sink was significant in Cz but not in the more anterior position FCz, a finding which may indicate the center of activity in the caudal (SMA proper) but not the rostral (pre-SMA) part of the SMA.

In conclusion, the majority of subjects showed the sequence of activity postulated by our hypothesis (cf. Deecke and Lang, 1996) that in the premovement motivational “cascade” when it comes to intention or the channeling of motivation into execution of movement, medial-wall motor areas are activated earlier than the primary motor cortex MI.

ACKNOWLEDGMENTS

Authors thank Dr. G. Lindinger for technical directions and Ms. Maggie Lee Huckabee for proof reading the manuscipt. The first author expresses his sincere gratitude for being supported by the Austrian Academic Exchange Service (OAG) and The Program of International Relations of the University of Vienna and the HFSP (Human Frontier Sciences Program).

REFERENCES


