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Functional Segregation of Parts of the "Sensorimotor Complex" of the Human Cerebral Cortex by Magnetoencephalography

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A method was developed for the noninvasive mapping of the primary motor cortex in humans. Magnetic responses evoked by repeated voluntary movements of the right index finger were studied in 18 healthy right-handed subjects. Finger movement periods were assessed using accelerometer signals. Continuous evoked brain magnetic activity recorded in the subjects throughout the experimental sessions was assembled into a single sequence which was then fragmented into independent components by independent components analysis and ranked in terms of the quantity of mutual information with the modified accelerometer signal. Averaging of the independent components demonstrating strongest links with finger movements was performed relative to the moment at which the movement started. Modeling of the distribution of the cerebral sources of the two independent components with the largest amounts of mutual information showed that their sources were located in the contralateral motor areas of the cortex, corresponding to anatomical markers of the hand representation area in the primary motor and primary somatosensory cortex. This method provided the fundamental ability to localize the M1 zone at the group level in healthy subjects.

Keywords: actogram, magnetoencephalography, primary motor cortex, independent components analysis.

The precise localization of irreplaceable areas of the cerebral cortex, where damage causes the patient irreversible loss of one cognitive function or another, is extremely important in planning neurosurgical interventions [De Tiege et al., 2009]. One of the most important factors in clinical practice is to locate the hand representation area in the primary motor cortex (M1, Brodmann field 4). However, the standard anatomical orientation marker for identification of the motor representation area of the hand in neurosurgery patients – the omega-shaped area of the precentral gyrus [Yousry et al., 1997] – may be absent, and the motor function itself may be represented anomalously, not in Brodmann field 4 but in other cytoarchitectonic fields of the neocortex [Haseeb et al., 2007]. Identification of the M1 zone in terms of its functional characteristics as the patient performs movements therefore becomes extremely relevant in the pre-operative mapping of the hand representation in the primary motor cortex.

Studies using functional magnetic resonance imaging (fMRI) to map the motor zones of the cortex have demonstrated complex and multicomponent changes in local blood flow in the cerebral cortex associated with the organization of movements [Kobayashi et al., 2003; Meier et al., 2008]. In addition, cases of anomalous activation in a variety of functional brain disorders and associated difficulties in the interpretation of fMRI data have also been described [Krings et al., 2001].

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Studies of brain activity during voluntary motor activity using magnetoencephalography (MEG) have linked the operation of the primary motor, premotor, and accessory motor cortex with the so-called motor readiness field, which is apparent 400–800 msec before movement starts [Hoshiyama et al., 1997; Shibasaki and Hallett, 2006]. The activity of the M1 zone was most marked in the "readiness field" peak immediately before movement started [Hoshiyama et al., 1997]. Judging from published data [Oishi et al., 2003], this is the moment at which the source of the magnetic field found in M1 can be reconstructed using the simplest single-dipole model. After the moment at which the movement starts, the single-dipole model becomes inadequate because of simultaneous activation not only the primary motor areas, but also of the primary somatosensory cortical zones (S1). Activation of S1, which receives feedback signals from muscle proprioceptors, forms, along with the hand representation area in the M1 zone, a marked component of the evoked magnetic field with a latency of about 100 msec after the moment at which the movement starts [Hoshiyama et al., 1997]. Current MEG guidelines for mapping the motor cortex in the pre-operative diagnosis therefore recommend localizing this cortical zone during the time directly (30–40 msec) preceding the start of the movement [Burgess et al., 2011].

Experimental studies on primates have shown that a complex of interacting cortical zones responsible for planning and pretuning of the motor act is activated before the start of the movement: the primary motor, primary somatosensory, parietal, accessory motor, premotor, part of the secondary sensory area, etc. [Riehle, 2005]. This can be explained by the fact that use of the method based on single-dipole modeling of the source of evoked cortical activity linked with the start of movement does not always provide accurate localization of the M1 zone even in healthy humans [Chayanov et al., 2012, Gerloff et al., 1998]. Attempts to identify the motor representation area of the hand in terms of the cortex-muscle coherence peak have also not been successful. Cortex-muscle coherence evaluates the constancy of the phase shift between MEG oscillations and myogram oscillations, and the somatosensory cortex often demonstrates a higher level of cortex-muscle coherence than the primary motor cortex [Witham et al., 2010].

As different zones of the so-called sensorimotor complex already at the movement preparation stage are in an intense interaction with each other, the localization of the M1 zone by MEG using a single-dipole model of the source of cortical activity at any given point in time does not yield reliable results. Thus, anatomical and temporal markers cannot be used for mapping the M1 zone in patients with brain damage. We suggest that reliable identification of the location of the M1 zone might be obtained in terms of its functional properties. Data from microelectrode studies in primates have led to the suggestion that various cortical areas interacting during preparation for and execution of movements, have individual time profiles for activation and can be distinguished on this basis [Riehle, 2005]. We report here an attempt to carry out functional mapping of the M1 zone using a combination of methods based on independent components analysis (ICA), ranking on the basis of the amount of mutual information with a modified accelerometer signal and a distributed model of the cerebral sources of the magnetic field of the component with the time dynamics of activation corresponding to the properties of the M1 zone.

The first stage employed the ICA method [Bell and Sejnowski, 1995] to separate spontaneous magnetic brain activity into independent (in terms of time dynamics) components. At the second stage, the component whose activity had the strongest link to movement was selected using a method based on ranking of these independent components in terms of the amount of mutual information with a modified accelerometer signal [Ossadtchi et al., 2000]. Components with statistically high levels of mutual information were then averaged relative to the moment at which the movement started. On the basis of studies in primates, we expected that the cortical sources of the component whose activation increased sharply immediately before the start of the movement would correspond in terms of location with the location of the M1 zone, which in healthy subjects is located in the anterior wall of the omega-shaped part of the central sulcus. This hypothesis was tested using distributed modeling of the cerebral sources of components of the spontaneous magnetic field by the minimum-norm method.

Methods

Subjects. A total of 18 healthy subjects (ten men, eight women) aged 18–32 (mean 23.5) years took part in the study; two were left-handed and the rest were right-handed. All subjects gave informed consent to take part in the study.

Procedure. A complete description of preparation of subjects for the study and the experimental procedure has been presented elsewhere [Chayanov et al., 2012].

Before the experiment, a FASTRAK (Polhemus, USA) three-dimensional digitizer was used to determine the coordinates of anatomical reference points, as well as inductance indicator coils. The magnetoencephalogram was recorded using a 306-channel programmable VectorView system (Elekta Neuromag Oy, Finland). Finger acceleration on movement was measured using an ADXL330 iMEMS accelerometer (Analog Devices Inc., USA) attached to the nail of the index finger.

Subjects were asked to place the palm in front of them on a special table, to relax, and use the right index finger to make sudden upward movements at a frequency of once every 2–4 sec, returning the finger to the starting position.

Magnetoencephalograph (MEG), electromyogram (EMG), and accelerometer traces were recorded with a sampling frequency of 1000 Hz and a bandpass of 0.1–330 Hz. Head position relative to the sensor system during the experiment was traced in real time using individual inductance coils. Experimental sessions lasted about 8 min. After sessions, MEG-MRI co-recording was performed (superimpo-

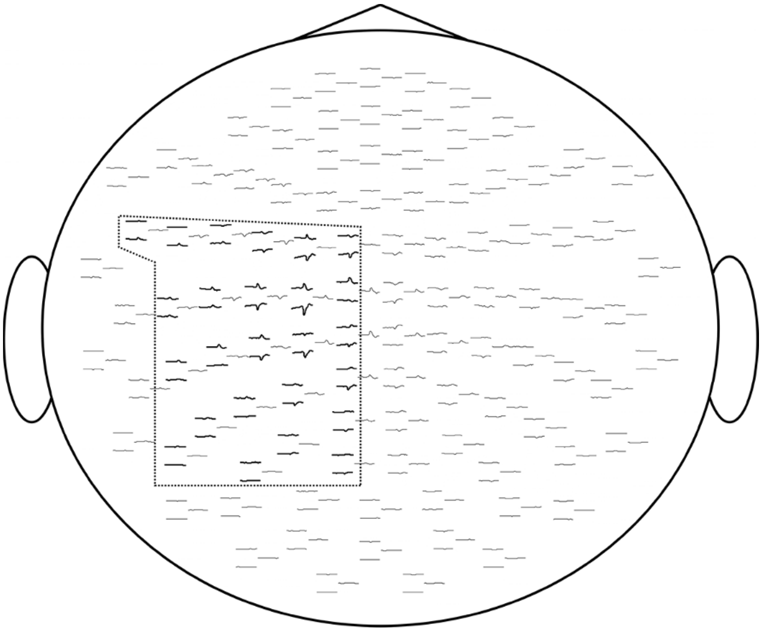

Fig. 1. Distribution by MEG sensors of evoked magnetic activity averaged for the group of subjects performing voluntary movements. Evoked response waveforms at gradiometers located over the central sulcus of the left hemisphere and used for analysis are outlined and highlighted. For each waveform: the horizontal axis shows time relative to the start of the movement, msec; the vertical axis shows signal amplitude, fT.

sition of the MEG coordinate systems onto individual brain MRI images).

Processing of MRI data. Individual frames of structural MRI scans were processed in FreeSurfer [Dale et al., 1999] to reconstruct the surface of the cerebral cortex, with individual positioning of the sulci and gyri. The result of this was that the topographically correct surface of the cortex was represented as a mesh described by the coordinates of nodes and a system of three-point simplexes formed by these nodes. A typical surface contained about 8200 simplexes in each hemisphere. For visualization, perception of the resulting surface was facilitated by "unrolling" ("inflation") for more convenient assessment [Fischl et al., 1999]. Individual brain surface reconstructions were then averaged using FreeSurfer. The resulting model, generalized for all subjects, was used for analysis of MEG data.

Processing of MEG data. Removal of trace artifacts and correction of head position were performed using a temporospatial signal separation method (MaxFilter program, Elekta Neuromag Oy, Finland). Evoked fields were averaged relative to the presumed movement start point, determined in terms of the beginning of elevation on the accelerometer signal. The analysis epoch was from –500 to 500 msec relative to the arbitrary moment of movement initiation and the number of epochs for each subject ranged from 120 to 250.

Extraction of components. This stage in processing was performed for data obtained from 50 gradientometers located in the sensorimotor complex of the left hemisphere (Fig. 1). Data from all subjects were combined into a single sequence (consisting of 3217 finger movement trials) for each of the gradientometers. With the aim of decreasing artifacts at the junctions between different subjects, the mean signal for the whole time interval for each gradientometer and each subject was calculated before the combination process, and this was then subtracted from the signal in tis gradientometer in each time segment. Independent signal components were extracted from the dataset (50 sequences of $8.5 \cdot 10^6$ time intervals) using independent components analysis (ICA) using the "logistic infomax" algorithm (run in EEGLab) [Delorme and Makeig, 2004].

ICA divided the dataset into 50 independent components which were sequentially projected onto gradientometers (in the sensor space). With the aim of assessing the extent to which each component was linked with the actual movement, the mutual information spectrum as proposed because Ossadtchi was used [Ossadtchi et al., 2000]. In accordance with this approach, for each component $z_i(t)$, the mutual information with a synthetic signal corresponding to the period of the initiated movement $q(t)$ was calculated. The $q(t)$ signal was calculated as the convolution of the binary indicator signal for the moment of movement initiation (Fig. 2):

$$q(t) = \sum_{n=1}^{N} (\delta(t - t_n) \times K(t)),$$

for $K(t) = t$, $t \in [-100, 100]$, otherwise $K(t) = 0$, where N is the number of task repeats, and t_n is the time point at which the task started.

All MEG components were ranked in terms of the amount of mutual information with the modified accelerometer signal. It was suggested that components with large amounts of mutual information (measured as described) would provide a better reflection of cortical processes occurring directly before and/or coinciding with movement onset, and thus being associated with the mechanisms of movement preparation and organization. Ranking results selected two components demonstrating the largest amounts of mutual information with the modified accelerometer signal.

Each extracted component consisted of 50 sequences (the number of gradientometers) from the 8.5 million time segments. Averaging of sequences relative to the movement start time yielded an averaged shape for the component projected onto the gradientometers – an analog of an evoked magnetic response in sensor space. The next step consisted of reconstructing the locations and strengths of current sources in the cortex and generating the averaged responses of the corresponding movement-associated components. Reconstruction was performed in the program MNE [Ossadtchi et al., 2000] by nonparametric modeling with regularization using the minimum square energy method (minimum norm estimates). A network of about 5000 dipoles was superimposed on the surface of the cortex of each hemisphere, in the form of a recursively divided octahedron. The possible directions of all dipoles were determined as normal to the surface of the cortex ± 20°. Absolute current strengths in dipoles were determined.

The influences of background noise on the results were assessed using a matrix of covariation between noise obtained using 2-min traces in the empty magnetoencephalography room and data for the sensors obtained during the experiment.

The statistical reliability of activation of each of the cortical sources (dipoles) was analyzed by dynamic statistical parametric mapping (dSPM) [Dale et al., 2000] using the Bonferroni correction. The statistical significance of changes in current strength in each cortical source at each time point on movement execution relative to its current strength during the period long (400–500 msec) before movement initiation was assessed using the F test. This yielded a statistical parametric map of the cerebral cortex, each node of which contained the result of an F test. F test values were converted into p values using 3 as the number of degrees of freedom of the F distribution in the numerator and 300 as the denominator (3 × 100 time points).

Results

The right index finger movement-evoked magnetic field averaged for the whole group of subjects was strongest in sensors over the central sulcus of the hemisphere cortex contralateral to the movement and its structure of components was analogous to the "motor readiness field," as described in the literature (Fig. 3, *A*). The locations of the cerebral sources of the motor fields using a distributed model showed that the overall set of sources lay in the general area of the omega-shaped part of the central sulcus, including parts of the precentral gyrus and also the postcentral gyrus. (Fig. 3, *B*). Thus, the cerebral sources of the motor field include several areas of the sensorimotor complex lying both anterior (motor cortex) and posterior (somatosensory cortex) to the central sulcus.

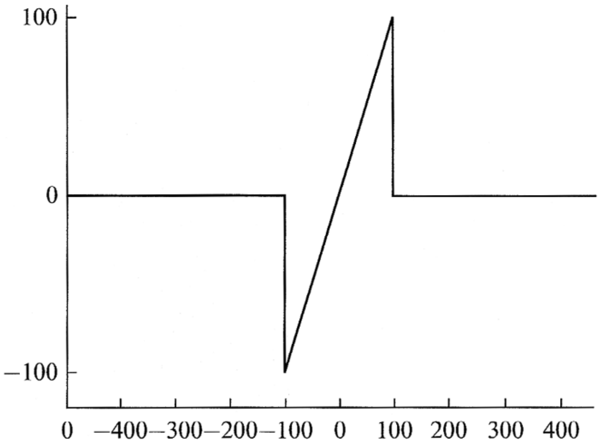

Fig. 2. Shape of signal relative to which the amount of mutual information for the components of the evoked magnetic signal extracted by ICA was calculated. The abscissa shows time relative to the onset of movement, msec; the ordinate shows signal amplitude. U.

We then attempted to extract from the evoked magnetic activity associated with movement initiation those components which reflect the operation of functionally different areas of the sensorimotor complex. The ICA method was used to separate the data into 50 independent components. After ranking the components in terms of the amount of mutual information during the preparation and movement onset period (Fig. 4), the two components with the largest values of this parameter were selected.

The time dynamics of the activation of both of these components demonstrated a slow increase in activation long (400 msec) before the movement, though the components differed in terms of their behavior during the period of time immediately before the movement. In the first-ranking component, a slow increase in activity was replaced by a sharper increase 50–70 msec before movement initiation, reaching a peak at the time of initiation (Fig. 4, *A*). The time dynamics of the second-ranking component were linear, without any change in the rate of rise of activation before the start of the movement (Fig. 4, *B*). After the moment of movement initiation, both components showed marked increases in activity, reaching a maximum at about 100 msec.

Mapping of the sources of the two components of movement-evoked brain activity using a distributed model showed that in both cases the generation zone was located in the cortex contralateral to the movement (the left hemi-

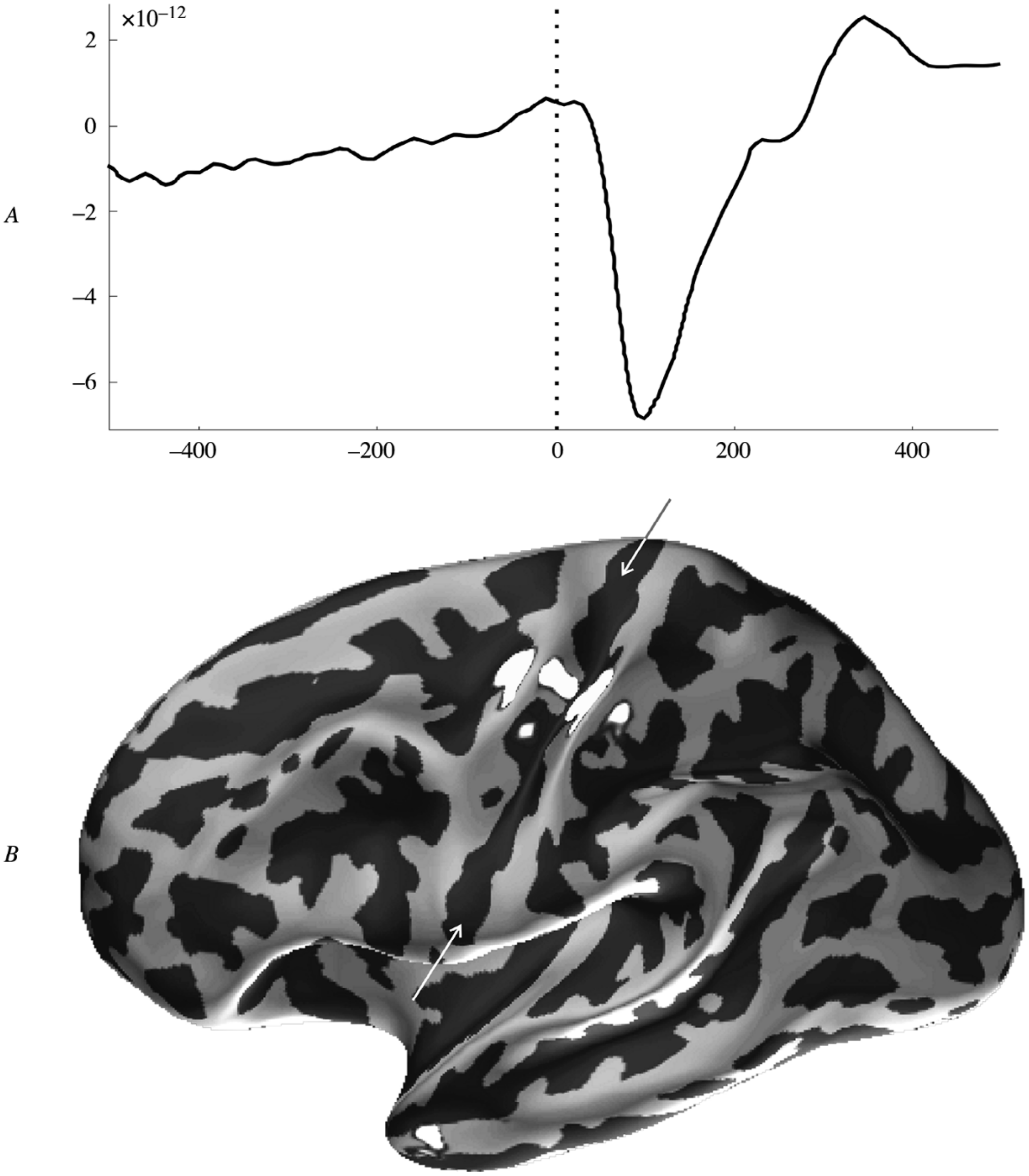

Fig. 3. Reconstructed sources of the “Motor field” (averaged for the group of subjects, left hemisphere). *A*) Averaged MEG signal on sensor 0432, which recorded the maximum response. A lower frequency filter with a frequency cut-off of 30 Hz was used. The abscissa shows time relative to the moment of movement initiation, msec; the ordinate shows the gradient of magnetic field tension, fT/cm. The dotted line shows the moment of movement initiation. *B*) Localization using a distributed model of evoked activation sources at the moment of movement initiation using a group mean model of the brain (left hemisphere). Light gray areas correspond to gyri, dark gray to sulci. White areas show areas of the cortex containing sources with maximum levels of activation at the moment of movement initiation. Arrows show the central sulcus.

sphere), in the area of the central sulcus. However, the two zones did not overlap, with a high threshold of statistical significance. The cortical sources of the first component were located mainly in the anterior wall of the central sulcus in the upper part of its omega-shaped flexure (Fig. 5, *A*, *C*). The sources of the second component were located in the postcentral sulcus and the depth of the central sulcus, in the lower part of its omega-shaped flexure (Fig. 5, *B*, *D*).

Discussion

The time structure of the evoked magnetic field averaged relative to the start of the movement corresponded to existing concepts of voluntary movement-associated evoked brain activity. The movement-evoked magnetic response of the brain included the so-called motor readiness field, which arises long (about 400 msec) before the movement and reaches a peak directly at the moment of its initiation (motor

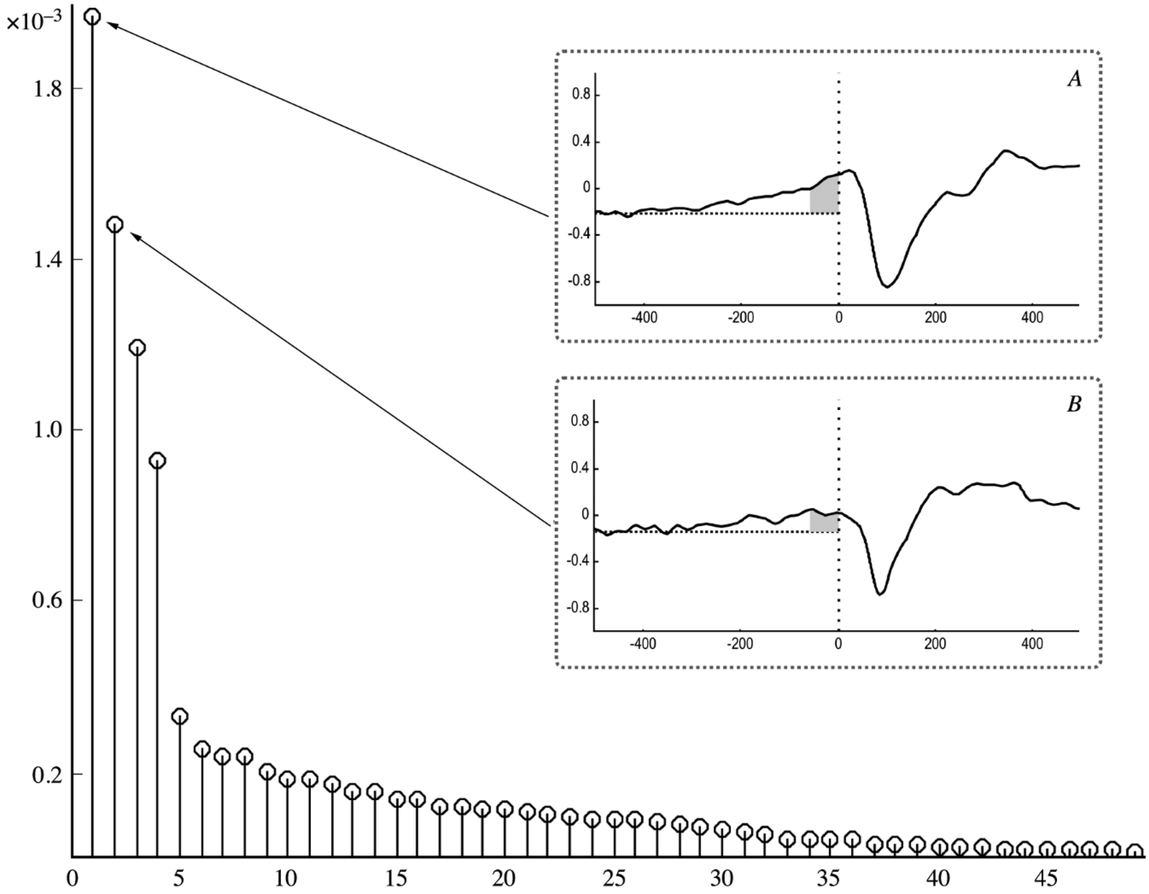

Fig. 4. Relative contributions of independent components of evoked magnetic activity accompanying movement onset. All the components extracted (abscissa) were ranked in terms of the amount of mutual information with the modified accelerometer signal normalized for the total amount of information (ordinate). *A*, *B*) Time dynamics of activation of the sources of the two components with the greatest proportions of mutual information (averaged relative to the moment of movement initiation). The abscissa shows time relative to the moment of movement initiation, msec; the ordinate shows the amplitude of the component, U. A low-frequency filter was used with a cut-off at 30 Hz. Vertical dotted lines on plots *A* and *B* show the moment of movement initiation; the horizontal dotted line shows the background signal level. Dark gray areas show the interval before the start of the movement, during which acceleration of the growth of activation in the first component (*A*) was noted.

field; Fig. 3, *A*). The maximum levels of the motor readiness field and particularly the motor field in sensors positioned over the sensorimotor complex of the cerebral hemisphere contralateral to the hand performing the movement were entirely consistent with published data [Hoshiyama et al., 1997; Shibasaki and Hallett, 2006]. However, the confidence of some authors that the sources of the motor field consist exclusively of pyramidal neurons in field M1, located in the anterior wall of the central sulcus [Cheyne et al., 2006] is not supported by our results. Modeling of the activity of the motor field using a distributed model (Fig. 3, *B*) revealed simultaneous activation in cortical zones corresponding to the typical positions of the motor and somatosensory representations of the hand in front of and behind the central sulcus respectively. Thus, the results obtained using this localizing method supported our previous conclusion from analysis of the results of single-dipole modeling that brain activity generating a motor readiness field represents summation of the activity of a multiplicity of functionally differing and closely located zones in the premotor, primary motor, primary somatosensory cortex, the parietal and several other areas of the brain. These zones are known to make up the sensorimotor complex and in voluntary movements are in continuous interaction during both preparation for a voluntary movement and its execution [Riehle, 2005]. In essence, this is a balance between in activation between different parts of the sensorimotor complex, which at the peak of the motor readiness field is generally (but not always) displaced towards the primary motor area of the cerebral cortex. This means that reliable mapping of only the primary motor area in a specific human being by locating the sources of evoked motor field activity is not present-

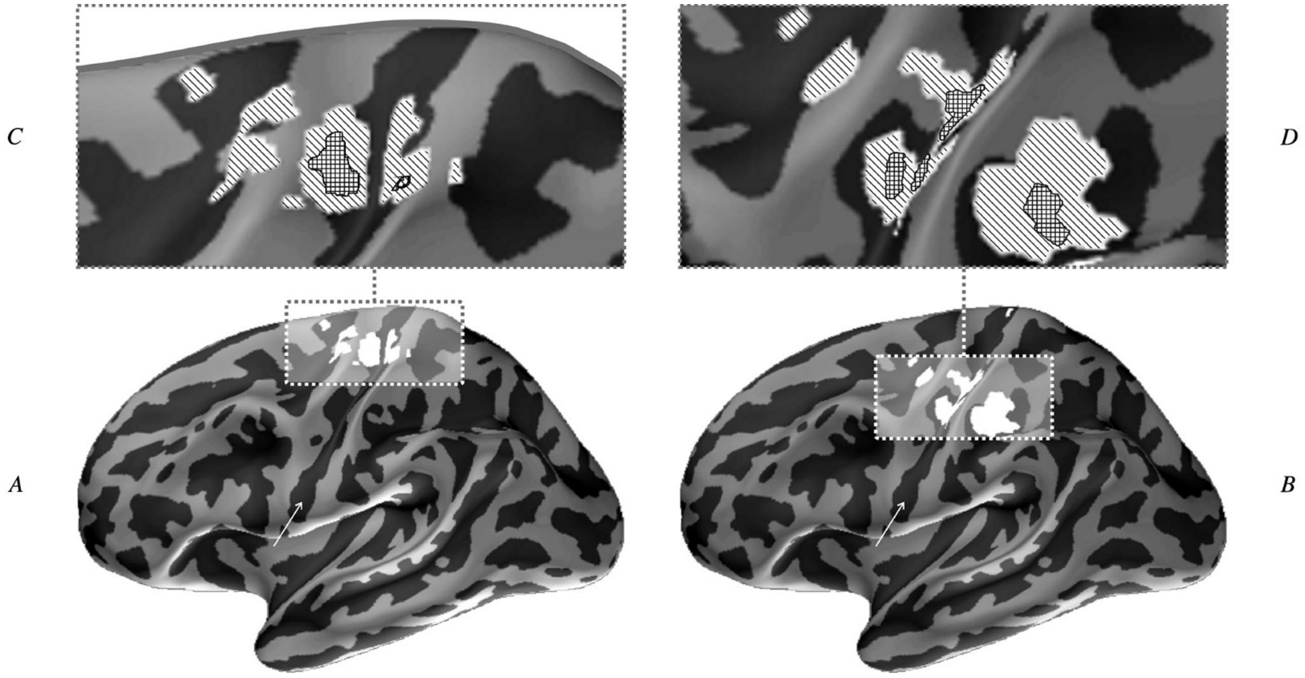

Fig. 5. Localization in the cortex of the left hemisphere of the brain of the sources of the two independent components (*A*, component 1; *B*, component 2) demonstrating the greatest amount of mutual information with the onset of right index finger movement. The unfolded cortical surface of the left hemisphere obtained by averaging individual data from a realistic model of the subjects' heads is shown. Light gray areas correspond to gyri and dark gray to sulci. The arrow shows the central sulcus. The locations of the sources of both components were determined by dynamic statistical parametric mapping using the Bonferroni correction. White areas show areas of the cortex with the sources making the greatest contributions to the amplitudes of the components. Above (*C*, *D*) – magnified images of areas of the unfolded cortical surface corresponding to the areas enclosed in pale rectangles. The shaded areas in *C* correspond to activation at significance levels of $p < 9.6 \cdot 10^{-22}$ (diagonal shading) and $p < 1.8 \cdot 10^{-24}$ (crosshatched). Significance levels in *D* are $p < 2.0 \cdot 10^{-16}$ (diagonal shading) and $p < 2.4 \cdot 10^{-20}$ (crosshatched).

ly possible. Furthermore, in some subjects the motor field may be very weak in evoked magnetic activity, making is unusable for reliable localization.

The present studies attempted to answer the question without locating the motor field, using different areas of the cortex with activity differing in terms of its time dynamics. This study provides the first use of the ICA method for separating the zones of the sensorimotor complex on the basis of their functional specificity in voluntary movements. This method, in combination with the selection of components in terms of the amount of mutual information with the modified accelerometer signal, allowed two independent components to be extracted from the initial signal, these being the components whose activity was most tightly linked with finger movement. On the basis of reported results [Ohara et al., 2000], we expected the activity of the primary motor area to form a component whose average shape during the period preceding the movement would show a smooth increase and a sharp rise (peak) immediately before the beginning of the movement. This component would be located on the anterior wall of the central sulcus or frontal to it. We felt that the second component, associated with the operation of the primary somatosensory area, should have a less marked and linear increase and should be located in the posterior wall of the central sulcus or behind it.

Our results showed that only one of the two components demonstrated a sharp increase in activation immediately before movement initiation (Fig. 4, *A*). In accordance with the initial hypothesis, the increase in the activity of zone M1 neurons before the start of the movement, linked in phase with the moment at which the movement started, reflects the direct link between this cortical zone and movement initiation [Riehle, 2005]. In fact, results obtained by modeling the cortical sources of this component showed that the zone at which it is generated approximately corresponds to the motor representation zone of the index finger in Brodman field 4 (Fig. 5, *A*, *C*). Published data generally support the suggestion that activation in the superior margin of the omega-shaped part of the central sulcus selectively reflects activity of neurons in the primary motor cortex during execution of voluntary index finger movements. The location of the motor representation of the index finger in this area is indicated by data from studies using MEG [Onishi et al., 2011] and fMRI [Dechent and Frahm, 2003]. Data from neuronal studies in primates point to the complexity in the functional organization of the M1 zone (including multiple horizontal connections, convergence of axons from multiple groups of neurons onto a single pool of motoneurons, etc., such that there cannot be clear somatotopy of the fingers in the primary motor cortex [Schieber, 2001]. Mapping results using MEG with electrodes positioned directly on the brain surface [Miller et al., 2009] may emphasize only the main zone of the motor representation of the index finger.

Results obtained from modeling the cortical sources of the second component, tightly linked with movement (Fig. 4, *B*), allowed mapping of its general zone in the depth of the omega-shaped area of the central sulcus, in its lower part (Fig. 5, *B*, *D*), which corresponds to the location of Brodman field 3a (the floor of the central gyrus) and the location of field 2 (the anterior wall of the postcentral gyrus). Data from microelectrode studies in primates [Krubitzer et al., 2004] and neuroimaging studies in humans [Geyer et al., 2000] show that the functions of neurons in field 3a of the primary somatosensory cortex (S1) and its projections onto field 2 are to receive and process afferent signals from proprioceptors in the muscle fibers involved in the movement [Krubitzer et al., 2004]. Field 3a plays a prime role in organizing and executing movements, along with the primary motor area. Apart from the powerful stream of reverse afferentation arriving in this field on movement, the existence of cortocospinal projection neurons in the primary somatosensory cortex has been demonstrated in primates [Widener and Cheney, 1997], as have direct motor pathways arising from the primary somatosensory cortex in mice [Matyas et al., 2010].

We note that according to our data, the positions of the main sources of activation of relative to the omega-like part of the central sulcus were not symmetrical: the sources of the "motor" part of the activation were located higher than the sources of the "proprioceptive." This asymmetry can be explained by the fact that the motor representation of the extensor muscle of the index finger (the extensor indicis proprius), according to published data, is located above not only the motor representations of the other fingers, but also the somatosensory representation itself [Hadoush et al., 2011; Nii et al., 1996; Onishi et al., 2011].

It should be emphasized that the present study stressed the discrimination of activity in the primary motor (M1) and the primary somatosensory (S1) areas of the cortex in the left hemisphere, contralateral to the movement of the right index finger. Restricting our area of interest to the left hemisphere, contralateral to the movement, and allowing participation in the study by subjects with preference for the right and the left hands, means that we are dealing mainly with contralaterality of the cortical representation of the hand in the primary motor cortex, which applies to both right-handers and left-handers [Solodkin, 2001]. Simple movements (including the single elevation of the right index finger selected here) are associated with activation of the sensorimotor complex of the contralateral left hemisphere in both left-handers and right-handers [Solodkin et al., 2001]. We note that judging from published data [Pollok et al., 2006], differences between right- and left-handers in activity in the motor zone of the cortex, linked with a simple voluntary movement, may be present in the premotor zones of the cortex of the ipsilateral hemisphere. However, the question of differences between left- and right-handers in the organization of interhemisphere interactions between cortical areas mediating a simple voluntary movement is beyond the remit of the present study and needs its own separate study.

Conclusions

Thus, the method based on extracting the activity of the primary motor cortex by independent components analysis and subsequent selection of components in terms of the amount of mutual information with the modified accelerometer signal demonstrates that zone M1 can in principle be located at the group level in healthy subjects. The undoubted advantage of this method is the absence of any time relationship with the motor field directly before the onset of movement and its ability to locate the zone generating the component being analyzed at the moment at which it reaches its maximum. The aim of further studies will be to address the use of this method for reliable mapping of the primary motor and somatosensory areas in individual subjects. In our view, the reliable functional discrimination of these areas is directly dependent on the magnitude of the dispersion of the magnetic field of the primary motor area. Use of this method in studies with individual subjects does not therefore have obvious limitations, but presupposes a large (500–1000) number of trials of the voluntary movement.

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