



Research report

Internally driven vs. externally cued movement selection: a study on the timing of brain activity

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Abstract

Brain imaging studies in man and single cell recordings in monkey have suggested that medial supplementary motor areas (SMA) and lateral pre-motor areas (PMA) are functionally dissociated concerning their involvement in internally driven and externally cued movements. This dichotomy, however, seems to be relative rather than absolute. Here, we searched for further evidence of relative differences and aimed to determine by what aspect of brain activity (duration, strength, or both) these might be accounted for. Event-related potentials (ERPs) were recorded while healthy, right-handed subjects selected one of three possible right hand digit movements based either on 'internal' choice or 'external' cues. The results obtained from ERP mapping suggest that movement selection evokes the same electrical brain activity patterns in terms of surface potential configurations in the same order and at the same strength independent of the selection mode. These identical configurations, however, differed in their duration. Combined with the results of a distributed source localization procedure, our data are suggestive of longer lasting activity in SMA during the 'internal' and longer lasting activity in PMA during the 'external' condition. Our results confirm previous findings in showing that SMA and PMA are distinctively involved in the two tasks and that this functional dichotomy is relative rather than absolute but indicate that such a dissociation can result from differences in duration rather than pure strength of activation. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

To investigate the cerebral substrates of different kinds of movements, motor acts have been classified along various axes, one of which contrasts internally driven and externally cued movements. Several behavioral paradigms have been used to elucidate the differences between these types of motor actions. Remembered vs. visually guided movement sequences have been compared in single-cell studies in monkeys [e.g., Ref. [26]]. In humans, freely

selected vs. sensory-cued and self-paced vs. sensory-triggered movements have been contrasted using PET [6,7,16,20] and EEG [12,16,27]. These studies provided converging evidence that internally driven and externally cued movements are, respectively, mediated by the central components of the medial and lateral pre-motor system, thus by the supplementary motor area (SMA) and the lateral pre-motor area (PMA). The SMA shows increased blood flow during 'internal' as compared to 'external' motor tasks [6,7,20]. Moreover, the amplitude of pre-movement event-related potentials (ERPs) over midline frontal structures as well as the amount of active SMA neurons are increased during internally driven with respect to externally triggered motor acts [12,26,27]. The PMA, on the other hand, appears to be more engaged in externally

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cued movements as suggested by the higher number of active neurons [26] and the sub-threshold increase of blood flow in this area [20] with respect to internally driven actions. However, some of these studies have shown that the functional dissociation of SMA and PMA is far from absolute, because SMA activity has also been reported with externally cued and PMA activity with internally driven movements [7,16,20,26].

The extent to which this functional differentiation involves differences in duration or strength of activation cannot easily be determined with imaging techniques such as PET and fMRI. In fact, relative activity differences may result from differences in activation duration or activation strength alone, or a combination of both. Instead, the question is best addressed by EEG recordings, which have an excellent temporal resolution. Some EEG studies provided evidence for an absolute rather than a relative dichotomy insofar as they demonstrated that medial frontal pre-movement potentials presumably generated by SMA sources [4] are present only during internally driven motor acts [12,27]. However, others reported motor readiness potentials over midline frontal areas to be stronger for internal than external motor tasks [16]. This would indicate that variations in activation strength contribute to the relative differences at issue. No EEG study attempted to search for differences in duration of activation.

The present ERP study was designed to address the following three points. First, we aimed to confirm the presence of relative differences in brain activity concerning internally driven and externally cued motor acts. Second, we wanted to determine which aspect of brain activity (duration, strength or both) is most responsible for these differences. Finally, we searched for evidence of discrepancies in the activation sequence. The behavioral paradigm employed allowed to contrast the electrical brain activity associated with either internally driven or externally cued movement selection. A methodological problem with 'internal' and 'external' movement selection is that the former process can be initiated any time by the subject, while the latter has to take place by definition in response to an external signal [6,7]. As in a previous study on internal motor selection [7], we thus presented in both conditions ('internal' and 'external') a visual stimulus prompting movement selection and pinpointing the selection process in time. In the former condition, subjects were required to select motor acts based on (internal) free-choice and in the latter based on the information contained in the visual cue. EEG data time-locked to these stimuli were analyzed. To stress the movement selection process, we asked subjects to choose the motor act in response to these signals without executing it. Only thereafter and in response to a delayed 'go' signal, the actual movement had to be performed. The separation of the selection and execution process in time allowed to isolate those brain activity patterns, which were specific to the selection phase, i.e., associated with motor selection independent of motor exe-

cution. Furthermore, to encourage rapid movement selection time-locked to the first signal, subjects were asked to imagine the movement as soon as possible after stimulus appearance.

2. Materials and methods

2.1. Subjects and apparatus

Twelve healthy, right-handed subjects (six women, six men, ages: 21–27 years) participated in the study. EEG was recorded using a 64-channel system (M&I, Prague; software: Neuroscience Technology Research, Prague, Czech Republic). The behavioral paradigm was implemented on a Power Macintosh 7100/66 (software: MacProbe®, Aristrometrics, Woodland Hills, CA, USA). The computer screen and response keys were used for stimulus presentation and response data collection, respectively (temporal resolution < 1 ms). All subjects gave their written informed consent.

2.2. Experimental setup and behavioral paradigm

Subjects were seated comfortably in a chair in front of the computer screen. Their right upper extremity rested on a table with the thumb, index and middle fingers placed on three distinct response keys. The position of the head was stabilized by a head- and chin-rest. Subjects were tested in two experimental blocks of 60 trials each. In each trial, two visual stimuli of 0.5° visual angle were flashed consecutively on the screen for 60 ms below a central fixation cross. The second stimulus followed the first one by a random delay varying between 2 and 3 s. Trials were separated by an interval varying between 4.5 and 5.5 s. Subjects were required to fixate the central cross throughout the experiment, to select one of the three fingers and to imagine the act of pressing the corresponding key after the first stimulus ('instruction' stimulus). The actual movement had to be performed only after the second ('go') stimulus. Subjects were encouraged to elicit kinesthetic motor images. Speed was emphasized for both overt and covert responses. In one block ('external' task), 'instruction' stimuli consisted of either an unfilled circle, an unfilled square or an unfilled triangle shown in randomized order and digit movements had to be selected on the basis of a pre-learned arbitrary visuo-motor association (○: index, □: middle finger, △: thumb). In the other block ('internal' task), 'instruction' stimuli consisted of unfilled circles only and subjects could freely choose between one of the three fingers (○: index, middle finger or thumb). In this block, subjects were explicitly instructed to select the finger only in response to the 'instruction' stimulus and to randomize their choices from trial to trial. The delayed 'go'-stimulus, which prompted the subjects to perform the

pre-selected motor act, was always the same and consisted in both blocks of a filled circle (●). The two blocks were counterbalanced across subjects. Prior to the experiment, subjects performed a training session including motor selection and response generation.

2.3. ERP-recordings and averaging

EEG was sampled at 1000 Hz from 48 electrodes and bandpass-filtered 1–50 Hz. Data were recorded with Cz as the reference and later rescaled against the average reference. Electrode impedance was kept below 5 k Ω . After off-line rejection of eye movement and eye blink artifacts monitored with bipolar EOG leads, two sorts of ERPs were computed for each subject and condition separately (individual ERPs). The first was aligned to the onset of the ‘instruction’-stimulus (from 0 to 500 ms after stimulus onset; *selection phase*) and the second to the onset of the delayed response (from 200 ms before to 200 ms after the response onset; *response phase*). We analyzed EEG activity in a time-window of 500 ms after the ‘instruction’-stimulus, since all task-related processes including the selection of the motor act have to take place in this time window, as suggested by behavioral and transcranial magnetic stimulation (TMS) data. Mean reaction time (RT) is about 500 ms when healthy subjects select and execute digit movements based on visual ‘instruction’ stimuli [7] and single TMS pulses applied over the sensorimotor cortex interfere with performance of this task in a time interval of 220–300 ms after visual stimulus onset [36]. For the response phase, we focused on a smaller time window, given the evidence for much faster digit responses to unstructured ‘go’-stimuli [23].

To correct for individual variations in electrode positions, we interpolated the 48 single traces of each individual ERP from the individual electrode arrays measured with a 3D digitizer (ISOTRACK[®], Polhemus, Colchester, VT, USA) to a standard array of 48 electrodes using nearest neighbor interpolation. The resulting, spatially normalized individual ERPs were used to calculate averages across subjects (grand-mean ERPs).

2.4. Data analysis

‘Internal’ and ‘external’ conditions were contrasted with respect to the characteristics of the surface potentials and the distribution of the underlying brain sources. Analysis of ERPs and sources was performed both on grand-means and on individual data.

2.4.1. ERP data

The procedure used to analyze the grand-mean ERPs is based on surface potential configurations (topographic ERP maps). In other words, grand-mean ERP data are repre-

sented as time series of successive ERP maps rather than as multiple single waveforms over time. All four grand-means (selection and response phase of the ‘internal’ and ‘external’ condition) were first subjected together to a temporal segmentation procedure. The procedure is based on the observation that surface maps remain typically stable for a certain time period. And, it has been suggested that each of these time periods represents a functional microstate during information processing [e.g., Refs. [1,17,18,21,22,24,30,37]]. These periods of stable map configuration have been referred to as segments. Segmentation procedures have thus been designed to reduce the series of ERP maps to series of time segments with stable/invariant surface map configurations whose data can be characterized by one single ERP (template) map. Here, we used a procedure based on *k*-means spatial cluster-analysis for temporal segmentation in which the optimal number of clusters (ERP template maps explaining the data set) is defined by a cross-validation criterion [29]. Entering all four grand-mean ERPs in the cluster analysis thus allows to define those template maps, which explain the whole data set and to compare them between the selection and the response phase as well as between the two modes of motor action.

In a second step of the analysis, we searched for the template maps in individual ERPs using an ERP fitting procedure based on spatial correlation coefficients [2,17,30,37]. This provides information on each map’s representation in each individual ERP and condition (map occurrence in time, duration of the presence of a map, maximum map strength). These data were subjected to paired *t*-tests to check for possible between-condition differences. For multiple comparisons, we applied the Bonferroni correction.

2.4.2. Source localization

The distribution of the sources in the brain, which gave rise to ERP maps of interest was estimated using a source localization procedure. We used a global linear inverse solution that estimates the current density distribution in the whole brain (LORETA) [28]. This method is a modified weighted minimal norm solution that searches for the smoothest distribution by minimizing the norm of the Laplacian of the current vectors. A three-shell spherical model was used. LORETA solutions were calculated within a regular grid of 1152 nodes, lying within the upper hemisphere. A detailed discussion of this method and its limitations is provided elsewhere [10,11,25]. To take into account interindividual variability, LORETA solutions were calculated for the individual surface maps corresponding to the grand-mean template maps of interest. From the individual map series corresponding to a given template map (as determined by ERP map fitting), we selected those maps with maximum map strength for source localization. Individual LORETA results were subjected to region of interest (ROI) analysis. Mean activity within

ROIs was analyzed using paired *t*-tests. For multiple comparisons, the Bonferroni correction was applied.

3. Results

3.1. Behavioral data

Responses to the ‘go’-signal were highly accurate. Errors occurred in 3.3% of the trials in the ‘external’ condition (wrong responses and omissions) and in 2.5% of the trials in the ‘internal’ condition (omissions only). Mean RT was 293.4 ms [‘internal’ condition: 291.4 ± 43.0 (thumb), 284.5 ± 43.2 (index), 300.7 ± 63.3 (middle)]/‘external’ condition: 295.1 ± 56.7 (thumb), 290.1 ± 62.2 (index), 298.2 ± 80.3 (middle)]. RTs did not significantly differ neither between conditions nor between fingers as revealed by a Condition (‘internal’ vs. ‘external’) × Finger (thumb vs. index vs. middle finger) repeated-measure ANOVA yielding no significant main effects (Condition: $F_{1,11} = 0.07$, n.s.; Finger: $F_{2,22} = 1.7$, n.s.) and no significant interaction ($F_{2,22} = 0.3$, n.s.). Fingers were selected equally often (range: thumb in 31.8% of the ‘internal’ trials, middle finger in 33.1% of the ‘external’ trials) and no significant differences existed — neither between nor within conditions — regarding the frequency with which

each of the three fingers was selected (χ^2 -values ranging from 0.03 to 0.04, $df = 1$, n.s.).

This indicates that the experimental paradigm was effective in inducing the required behavior. Subjects selected the movements correctly (low error rates) and were in both conditions equally prepared for the delayed responses (no RT differences between conditions), i.e., have to have made their choices in both conditions before the delayed ‘go’-cue. Because there was no between-condition differences in the frequency with which individual fingers were selected, differences in the type of the selected movement cannot be held responsible for ERP differences.

3.2. ERP-DATA

Fig. 1 depicts global field power (GFP) of the successive maps of the grand-mean ERPs over time as well as the results of the segmentation procedure. GFP is the spatial standard deviation of a map’s potential distribution and represents a measure of the map’s strength [21]. The segmentation procedure revealed between six and nine segments of stable ERP map configurations per condition (‘internal’ or ‘external’ task) and phase (‘selection’ or ‘response’ phase). In the period in which internal or external response choices had to be performed (selection phase), the most prominent segments in terms of GFP were

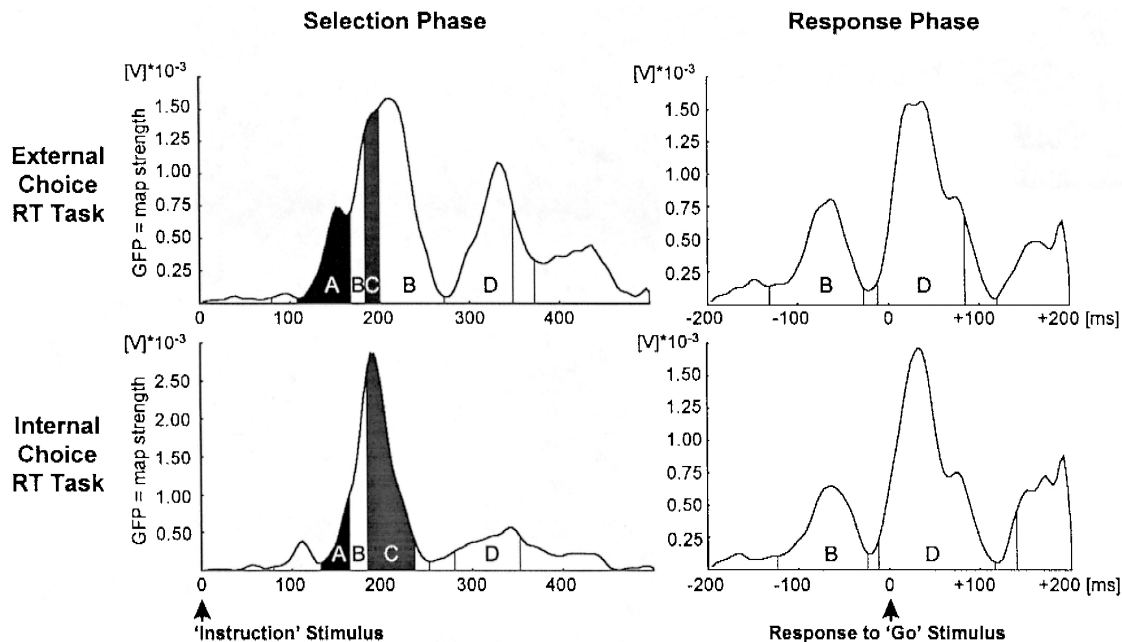


Fig. 1. Grand-mean ERP (time)-segments with stable surface ERP map topographies. Map strength (= GFP) of each successive ERP map is plotted over time for the selection (left graphs) and the response phase (right graphs) as well as the ‘external’ (upper graphs) and the ‘internal’ condition (lower graphs) separately. The most prominent segments in terms of GFP of both the selection and the response phase are characterized by four map topographies (A–D) as indicated by the temporal segmentation procedure. Segments of interest most probably associated with movement selection (present only in the selection phase) are highlighted in different gray tones. Since surface map configurations are invariant within segments, segment data can be characterized by one single ‘template’ map (shown in Fig. 3).

characterized by four map topographies (maps A–D). However, only two (maps A and C) were specific for the selection phase (see Fig. 1). Accordingly, only these maps are likely to reflect electrical correlates of motor selection. The other two maps of the selection phase (maps B and D) reappeared in the delayed response phase prompting the pre-selected motor act. They most likely represent the motor imagery component in the selection and the motor execution component in the response phase. This is in line with numerous studies, which have provided evidence that motor imagery and execution share common cortical substrates [e.g., Refs. [19,32,35]]. Here, we concentrate on the selection-specific maps A and C.

ERP fitting of maps A and C to individual data of the selection phase showed that each map was found in 10 or more subjects in both the ‘external’ (A in 12 subjects, C in 10 subjects) and the ‘internal’ condition (A and C in 12 subjects). χ^2 -tests revealed that the presence of a map in 10 or 12 out of 12 subjects is significantly different from chance ($n = 10$: $\chi^2 = 5.33$, $df = 1$, $p = 0.0209$; $n = 12$: $\chi^2 = 12$, $df = 1$, $p = 0.0005$). The ERP fitting provided further information on the interindividual variability of the maps’ temporal sequence (time of maximum map strength after stimulus onset), of each map’s strength (maximum GFP value), and of each map’s duration. The map’s strength is related to the strength of the underlying sources [21]. Paired t -tests revealed no differences between conditions regarding the maps’ sequence. That is, neither map A nor C differed significantly between conditions with respect to the time of maximum strength after stimulus onset (Fig. 2a). Significant differences, however, were found in the maps’ durations (Fig. 2b). While map A was of longer duration in the ‘external’ than in the ‘internal’ task ($t = -5.5$, $df = 11$, $p = 0.0006$), map C was longer when ‘internal’ choices had to be performed ($t = 3.6$, $df = 11$, $p = 0.013$). Finally, maximum strength of none of the two

maps was significantly different between conditions (Fig. 2c).

3.3. Source localization

Fig. 3 (left parts) shows the topographic potential configurations of the surface grand-mean template maps A and C, the corresponding surface maps of a single representative subject and the current density distribution estimated from these maps. Map A is associated with lateral frontal and parieto-occipital activity, which is present in the grand-mean as well as in the single subject. The inverse solution of map C shows in both cases medial frontal activity and more variable and weaker parieto-occipital activity. Thus, with respect to frontal activity patterns, i.e., the patterns of our a priori interest, map A had stronger lateral and map C stronger medial frontal sources. To test whether this difference in frontal activity distribution can be statistically confirmed, inverse solutions were calculated for the individual surface maps corresponding to template maps A and C as determined by the ERP fitting procedure. From the series of individual maps corresponding to template maps A and C, we selected those with maximum map strength for source localization. These are the maps whose time points were used for analysis of the maps’ sequence (see above). This yielded for each subject a set of two 3D inverse solutions per condition, one for each match of the template maps A and C in the ‘internal’ and one for each match in the ‘external’ conditions. These data were subjected to ROI analysis (Fig. 3, right part). ROIs were defined over the medial and lateral frontal regions corresponding to the areas activated in the grand-means as described above. Given the limited spatial resolution of the inverse solution and the potential interindividual variability in brain morphology, the size of the ROIs was set sufficiently large (see Fig. 3). Paired t -tests revealed that neither the individual maps A nor the individual maps C differed in mean ROI activity between conditions, neither with respect to their lateral nor medial ROIs. This supports the surface results suggesting that maps A and C are present in identical configuration in both the ‘internal’ and ‘external’ condition. Data were thus collapsed over conditions. Further analysis showed that activity is stronger within the lateral frontal ROI than within the medial ROI for map A ($t = 4.3$, $df = 11$, $p = 0.003$), and that the opposite pattern was present for map C ($t = -4.0$, $df = 11$, $p = 0.006$; see Fig. 3, right upper graph).

The grand-mean as well as the selected single subject data shown in Fig. 3 suggest that simultaneous parieto-occipital activity is present for map A and C. Paired t -tests between a bilateral occipital ROI extending over the deepest four slices and the two frontal ROIs revealed that the occipital source was stronger for both maps (occipital vs. fronto-medial: map A, $t = 6.8$, $df = 11$, $p < 0.001$ /map C, $t = 5.2$, $df = 11$, $p < 0.001$; occipital vs. fronto-lateral:

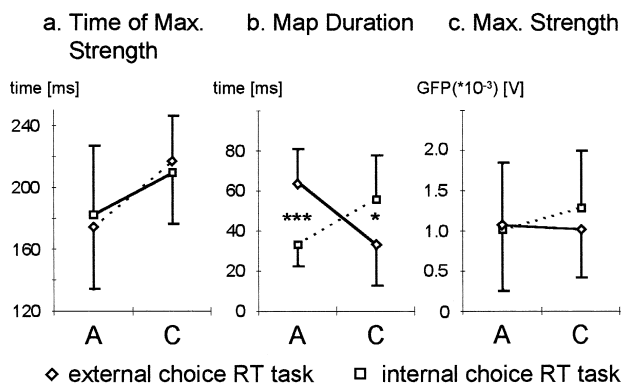


Fig. 2. (a–c) Timing and strength of stable surface ERP maps of interest, as determined by ERP map fitting to individual data. Time of maximum strength after stimulus onset (a), total duration (b) and maximum strength (c) are shown for the two maps of interest (A, C) and the two conditions separately.

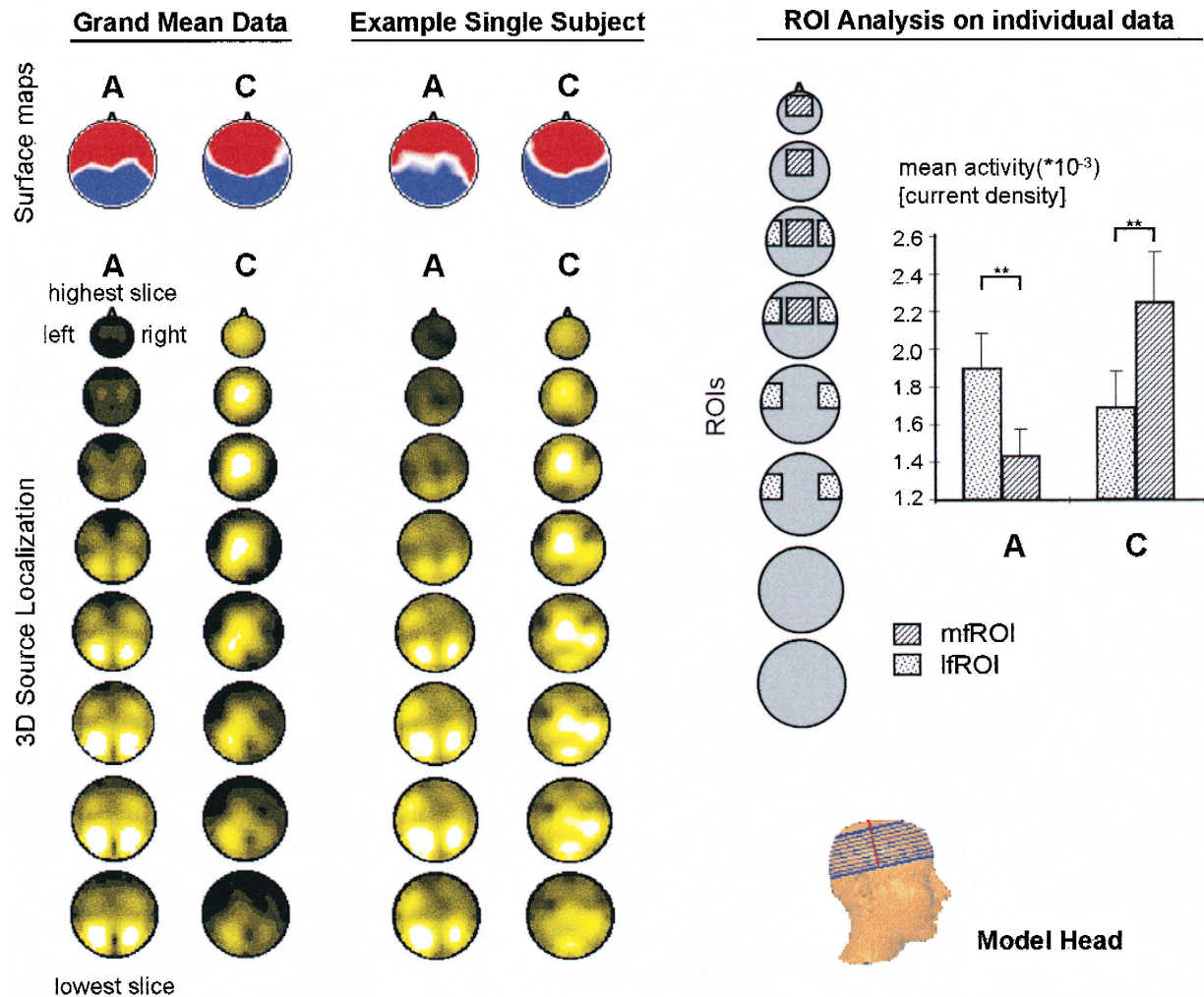


Fig. 3. Estimated brain activity associated with surface 'template' maps of interest of the grand-mean data, an example of a single representative subject and ROI analysis. Left part: surface 'template' maps A and C of the grand-mean data and the corresponding maps of a single subject (determined via ERP fitting) are shown in the upper part. The current density distribution estimated from these maps is displayed below. A global linear inverse solution (LORETA) was used. The images depict the activity on several slices of the spherical model (see also Model Head). Right part: ROIs placed over the medial (mfROI) and lateral frontal cortex (lfROI) and results of the ROI analysis. The bar plot shows mfROI- and lfROI-activity for each of the two maps of interest (mean activity over subjects + S.E.).

map A, $t = 5.7$, $df = 11$, $p < 0.001$ / map C, $t = 7.5$, $df = 11$, $p < 0.001$).

4. Discussion

The present results indicate that electrical brain activity, as revealed by surface ERP map configurations, differs only in one aspect between internally driven and externally cued movement selection, i.e., the duration of activity. Neither the spatial distribution, nor the order or the strength of activation were significantly different between conditions. A distributed source localization procedure suggests that ERP map configurations with longer duration during the 'external' task are associated with activation of lateral frontal sources, while those with longer duration during the 'internal' task correspond to medial frontal activity. These

activity patterns were interpreted to reflect activation of the lateral and medial pre-motor system, respectively. The spatial resolution of the source localization technique does not allow to specify which of the various medial and lateral pre-motor system sub-components are involved. In particular, we cannot discriminate pre-SMA, SMA proper and cingulate motor areas mediating different aspects of motor function [31] nor can we distinguish the anterior–dorsal from the posterior–ventral parts of the PMA, both of which are implicated in externally guided visuomotor acts [6,8,39].

In the present study, movements had to be selected covertly in response to a visual (instruction) signal either based on a free choice or on arbitrary visuomotor associations. A delayed 'go' stimulus prompting the selected response allowed to control for task performance. Between-condition comparisons were performed in the period

following the instruction signal and results were interpreted to reflect differences in movement selection modes. Although the behavioral data indicate that movements were selected correctly and before the 'go' stimulus, it cannot completely be excluded that movement selection occurred at different time points in the two conditions and not as required time-locked to the instruction signal. In fact, during free selection, subjects could have chosen the movement before the relevant visual signal, while in the 'external' condition movement selection has to take place in response to the instruction cue. If so, however, one would expect the evoked ERPs to differ substantially between conditions, or at least to be shifted in time with the ERPs of the 'internal' condition appearing much earlier. The present results do not support this inference.

The results are in keeping with previous studies showing that the PMA is involved to a greater extent in 'external' and the SMA in 'internal' motor actions [6,7,20,26]. Moreover, they support the notion that these actions engage the same parts of the motor system, thus that their functional dissociation is relative rather than absolute [16,20,26], and extend previous findings in suggesting that the systems mediating the two modes of movement selection differ only in their duration but not strength of activation. Taking into account the fact that motor selection was lumped together with the imagination of the motor act in the present paradigm, the results indicate that the dissociation of the two pre-motor systems reported for overt motor performance [6,7,20,26] applies also to motor imagery. This is consistent with PET findings showing that blood flow is increased in the SMA during internal rehearsal of complex finger movement sequences [34] and in the PMA when healthy subjects imagine themselves grasping an object [5]. However, in a recent PET study involving the generation of motor images in both an 'internal' or an 'external' selection mode, Deiber et al. [9] failed to find differences in pre-motor activity either in its medial or lateral part. It is speculated that the discrepancy with our results is due to the fact that Deiber et al. [9] tested their subjects during visual imagination of finger movements, while kinesthetic motor images had to be generated in the present study. This would imply that visual and kinesthetic images of motor actions activate pre-motor systems differently. This hypothesis, however, has to be substantiated.

Our results contrast those of previous EEG studies. These provided evidence that pre-movement potentials of medial frontal structures are stronger or exclusively present during 'internal' as compared to 'external' motor tasks [12,16,27]. No differences regarding duration have been reported. However, the paradigms used in our and the prior EEG studies differ in several points. Concerning the 'internal' motor condition, subjects of the previous EEG study were free to choose the onset of a given movement, had therefore to decide internally when to move (self-pacing), while no decision was required about what to move.

In the present EEG studies, in contrast, subjects were required to freely choose one motor act within a set of different possible movements. They thus decided internally what to move (free selection), while when this act had to be performed was specified by a sensory signal. Self-paced motor tasks as investigated in previous EEG studies are associated with low frequency potentials observed prior to movement onset (early and late readiness potentials). The earlier activity is thought to represent a correlate of motor preparation, the later of the endogenous urge/decision to act [i.e., Refs. [16,27]]. Motor selection is not involved in such self-paced motor tasks, since the motor act itself is pre-defined. Designs as applied in the present study, on the other hand, involve motor selection rather than preparation and are expected to be associated with ERP components of higher frequency than the low frequency pre-movement activity of the prior EEG studies. Given that the behavioral responses to visual stimuli prompting to select and execute a movement occur at about 500 ms [7] and are slowed by single TMS pulses applied over the sensorimotor cortex at 220–300 ms after visual stimulus onset [36], all processes between visual perception and motor response generation including motor selection have to take place within this relatively short time interval. Motor preparation, in addition, is likely to be 'short-circuited' when motor processes are prompted by visual stimuli, at least when the rate of the sensory signals is irregular as in the present study. In this case, slow frequency pre-movement activity is absent, since subjects cannot anticipate and prepare for forthcoming events [16,27]. One might thus argue that different sub-forms of internal motor control (i.e., internal movement selection and 'internal' preparation/decision to act) have been investigated in the present and previous studies. This is of interest with respect to the debate what role the SMA plays in 'internal' motor acts. Despite the abundant evidence for the implication of the SMA in these kinds of movements [6,7,12,20,26,27], it is unclear whether different SMA sub-components are involved in different sub-forms of internal motor control. The present study does not answer this question directly but the inconsistency with the previous EEG results might suggest that SMA mechanisms for internal motor selection are different from those mediating 'internal' motor preparation.

The electrical brain patterns interpreted to be associated with activity in the lateral pre-motor system occurred at about 180 ms and those with activity in the medial pre-motor system at about 210 ms after stimulus onset (time points of maximum strength). The former result is in good agreement with the TMS study of Schluter et al. [36], who found that PMA stimulation interrupted task performance in an externally cued motor selection paradigm at 140–180 ms after the visual cue. In addition to the frontal sources, we found parieto-occipital activity at the same time points. This is not surprising given that a number of recent studies have shown that TMS can affect information processing in posterior visual areas up to 180–200 ms after visual

stimulus presentation [3,15] and that EEG activity over central motor and posterior visual areas can temporally overlap during visuomotor performance [37,38,41,42]. What functional significance could this parieto-occipital activity have? One might argue that it reflects activity related to the imagery component of the present task, since occipital activity is a common finding during imagery of visual stimulus attributes [e.g., Refs. [13,14,40]]. However, we asked our subjects to perform kinesthetic images of the motor act in response to the visual signal rather than to visually imagine the presented stimuli later in time. Deiber et al. [6] suggested that the parietal cortex, which they found to become activated during both externally cued and internally driven motor selection, contributes to the process by which movements are chosen. In this sense, the parieto-occipital activity might relate to the integration of visual into motor information important for motor selection, given the temporal overlap with frontal activity and given that many sites in parietal cortex are essential for visuomotor transformation [33].

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