

Mental representations of movements. Brain potentials associated with imagination of hand movements

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Abstract

The present study was designed in order to contribute towards the understanding of the physiology of motor imagery. DC potentials were recorded when subjects either imagined or executed a sequence of unilateral or bilateral hand movements. The sequence consisted of hand movements in 4 directions, forwards, backwards, to the right and to the left, and varied from trial to trial. The sequence had been cued by visual targets on a computer screen and had to be memorized before the trial was initiated. Changes of DC potentials between task execution and imagination were localized in central recordings (C3, Cz, C4) with larger amplitudes when executing the task than when imagining to do so. Stimulation of peripheral receptors associated with task execution or a different level of activation of the cortico-motoneural system could account for this finding. The main result of the present study was that with unilateral performance, the side of the performing hand (right, left) had localized effects in recordings over the sensorimotor hand area (C3, C4) which were qualitatively the same with imagination and execution and quantitatively similar (i.e., without significant difference). Performance of the right hand augmented negative DC potentials in C3, performance of the left hand augmented amplitudes in C4. This result is consistent with the assumption that the primary motor cortex is active with motor imagery. Finally, the question has been addressed whether motor imagery may involve the left hemisphere to a larger extent than the execution of the movement. It is shown that a particular contribution of the left hemisphere associated with motor imagery may only show up under strictly controlled conditions.

Keywords: Imagery; Motor system; Brain potentials

1. Introduction

Motor imagery can be defined as an imagined rehearsal of a motor act without any overt movement. Internally, we realize the ability to simulate a movement within its temporal and spatial sequencing and, by doing so, we produce images of sensation which would arise during execution. A current point of interest is functional similarity between imagined and executed movements.

A close functional relationship has been suggested on the basis of several observations (for review see Decety and Ingvar, 1990). Imagined and executed movements have similar durations (Decety and Michel, 1989; Decety et al., 1989) and similar consequences on vegetative pa-

rameters such as heart rate and respiratory rate (Decety et al., 1991). When subjects imagine to perform a movement by themselves, specific muscles corresponding to the simulated motor act are activated (Jacobson 1932; Wehner et al., 1984). Motor imagery has comparable benefits on the acquisition of a motor skill as task execution without receiving feedback of the result (Mendoza and Wichman, 1978).

The present study was designed to contribute towards the understanding of the physiology of imagined movements. So far the physiology of motor imagery has been investigated by 3 studies of the regional cerebral blood flow (rCBF) by SPECT (single photon emission computerized tomography; Ingvar and Philipson, 1977; Roland et al., 1980; Decety et al., 1988). It was consistently reported that motor imagery does not activate the primary sensorimotor cortex whereas task execution does. Roland et al. (1980) used a manual motor sequence task and found that

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motor imagery only activates the supplementary motor area (SMA). In a recent study regional cerebral blood flow associated with the imagination of a manual motor sequence task was measured by PET (positron emission tomography) which is assumed to be more sensitive than SPECT. Preliminary results of that study substantiate the previous observations that the sensorimotor cortex is not active when imagining to perform the movement (Stephan et al., 1993).

Current discussions of the physiology and anatomical organization of motor imagery have not taken into account some observations on the human EEG which date back more than 30 years. It has frequently been noted in clinical observations that mere thinking about the movement blocks the mu rhythm (Chatrian et al., 1959; Gastaut et al., 1965). Blocking was even present when persons with amputations of limbs imagined to perform movements of the phantom limb (Klass and Bickford, 1957; Gastaut et al., 1965). The central mu rhythm, which has already been described by Jasper and Andrews (1938, "precentral alpha rhythm") and in detail by Gastaut et al. (1965), is blocked prior and during hand movements in a small and distinct scalp area located above the hand area of the sensorimotor cortex (Pfurtscheller and Aranibar, 1978; Pfurtscheller and Berghold, 1990). The mu rhythm is obviously related to a strictly localized beta activity over the human motor cortex, which has been found in the human electrocorticogram (Niedermeyer, 1987). Thus the first goal of the present study was to elucidate electrophysiological differences between motor imagery and actual movement.

Another point of interest is whether the left hemisphere has a dominant contribution to the imagination of a movement. Evidence for a particular involvement of the left hemisphere with visuo-spatial imagery has been reported by Farah (1984). Furthermore, lesions of the left hemisphere cause "apraxia." If we accept a current model of "apraxia" as a disturbance of the ability to produce and maintain mental images of motor acts (Goldenberg, 1992), a particular contribution of the left hemisphere to motor imagery may be reasonable.

Brain potentials were recorded while healthy subjects either imagined a manual motor sequence or executed the task. The duration of performance was about 8 sec. More specifically, the present study measured the slow potential shifts (SPS) or DC potentials which occur in tasks of that duration. These potentials reflect changes of the excitatory synaptic activity of the cortex (Caspers et al., 1980; Speckmann and Elger, 1987; Rockstroh et al., 1989). DC potentials have been recorded during visual imagery (Uhl et al., 1990) and in motor tasks (for review see Lang et al., 1991b).

Two experiments (I and II) were carried out in the present study in order to answer 3 questions: (1) Does the pattern of cortical activity differ between imagination and execution of limb movements? (2) Is there a particular involvement of the left hemisphere in motor imagery? (3)

Is the primary sensorimotor cortex active with motor imagery? The first experiment used unilateral movements and unilateral motor imagery. For two reasons it was followed by a second experiment involving only bilateral symmetrical activity. Firstly, possible effects merely related to unilaterality and not to movement/imagery per se should be analysed. Secondly, cognitive influences on lateralizations should be analysed by keeping the motor demands symmetrical. The following concept was used in order to approach the points of interest: (1) A change of the pattern of cortical activity between imagination and execution of the task should be associated with a change of the spatial pattern of the task-related DC potentials. A conservative testing procedure based on data normalized within conditions and subjects was used (McCarthy and Wood, 1985). (2) Hemispheric asymmetries and the putative functional significance of the left hemisphere for motor imagery was tested by comparing recordings at corresponding sites of the two hemispheres. The sensitivity of DC potentials to detect hemispheric asymmetries has been proved in previous studies (Lang et al., 1988; Altenmüller et al., 1993). (3) It has been shown in previous experiments that the topography of DC potentials associated with the execution of manual sequence tasks (Lang et al., 1989, 1991b; Lindinger et al., 1990) or visuomotor manual tracking (Grünwald-Zuberbier and Grünwald, 1978; Lang et al., 1984) vary with the side of the performing hand. These variations are localized in the scalp area located over the sensorimotor hand area (C3, C4 and sites in the close vicinity) with movements of the right hand causing a relative increase of DC potentials in C3 and movements of the left hand causing a relative increase of DC potentials in C4. If the sensorimotor hand area is active with motor imagery there should be a differential effect on recordings in C3 and C4, depending on the side of the hand performing the task.

2. Methods and materials

Subjects

Twenty-seven right-handed subjects (12 females, 15 males), ranging in age from 19 to 30 years, participated in experiment I. Nineteen right-handed subjects (5 females, 14 males), ranging in age from 21 to 30 years, participated in experiment II. Hand dominance was assessed with a modified version of the Edinburgh Inventory. All subjects were paid for completing the experiment.

Conditions

Movements had to be performed by the hand or fingers. Tempo and sequence of directions of the movements were defined by a target sequence (see Fig. 1).

Experiment I. In condition 1, subjects had to move a joystick according to the target sequence with their right hand (rH-E; right Hand, Execution of the movement). In

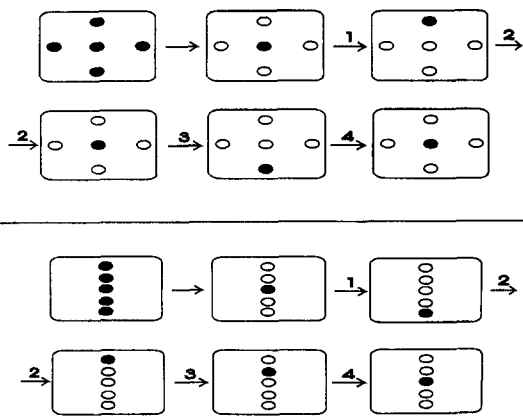


Fig. 1. Examples of visually cued sequences running from left to right. Upper part: a sequence used in experiment I. Subjects had to move a joystick with the same speed and in the same directions as the sequence ran. Lower part: a sequence used in experiment II. Subjects had to move both index fingers simultaneously with the same speed and in the same directions as the sequence ran.

condition 2, they had to imagine moving their right hand (rH-I; right Hand Imagery). In condition 3, they were instructed to move their left hand (lH-E) and in condition 4 they had to imagine moving their left hand (lH-I).

Experiment II. In condition 1, subjects had to move both index fingers simultaneously according to the target sequence (bH-E; bilateral Hand, Execution of the movement). In condition 2, they had to imagine moving both index fingers (bH-I; bilateral Hand Imagery) and in condition 3 they were instructed to imagine a picture which consisted of the 5 positions on the screen being illuminated (i.e., imagine the warning stimulus). This served as a control condition to clarify possible effects merely due to visual imagination.

Paradigm, stimuli

By pressing buttons (experiment I) or lifting both index fingers (experiment II) a sequence of positions was illuminated on a computer screen (Fig. 1). Subjects had to memorize this sequence. Then, by pressing buttons/lifting fingers again, subjects were informed about the task which had to be performed. The time schedule of events is displayed in Fig. 2: the presentation of the sequence of positions lasted 5 sec. After a period of time which lasted more than 10 sec, subjects could start the task by pressing the buttons/lifting fingers again. Then they immediately received the task information on the screen for 2 sec. DC potentials were recorded for a period of 18 sec (4 sec prior to button pressing, 2 sec of task information and 12 sec of task performance).

Sequence of positions (see Fig. 1) in experiment I there were 5 circles on the computer screen. One of them was located in the centre, the others at equal distance to the left, the right, above and below (being empty). A sequence was produced by successively illuminating 1 of the 5 circles with red colour for 1 sec, thus generating a se-

quence of jumping illuminated circles indicating direction and *relative* amplitude of the movements. Before starting the sequence a warning stimulus was presented consisting of all 5 circles being simultaneously illuminated. Within one sequence either horizontal or vertical jumps were allowed but not a combination of them. All possible directions (right vs. left, up vs. down) were balanced across the experiment. The visual display subtended an angle of 5° in the horizontal and 5° in the vertical plane.

With experiment II the course of stimulation was similar to experiment I, with the exception that all circles were arranged in a vertical line. The directions (up vs. down) were balanced across the experiment. The visual display subtended an angle of 5° only in the vertical plane.

Task information (see Fig. 2): after having seen the sequence, subjects received the instruction about the forthcoming task (single word on the screen) by button pressing/lifting fingers. The area of this visual display subtended an angle of 2° in the horizontal plane and 0.5° in the vertical plane.

Visual information during performance (either imagination or movement): after ending the sequence the centre circle was constantly illuminated and served as a fixation point. The other 4 circles remained empty.

Button pressing: subjects held joysticks in their hands. Buttons were mounted at the top of the joysticks and could easily be pressed by the thumbs. Button pressing was always bimanually performed in order to prevent any lateralization of brain activity caused by unilateral performance.

Lifting index fingers: immediately above both index fingers, a light barrier was positioned. By lifting the fingers the barrier was broken and a connected computer started the next event. Starting was always done bimanually to avoid lateralization.

Sequence of trials: conditions were completely randomized across the experiment. Subjects were “blind” about the condition until the visual information about the task appeared. Since the baseline for the measurements of DC

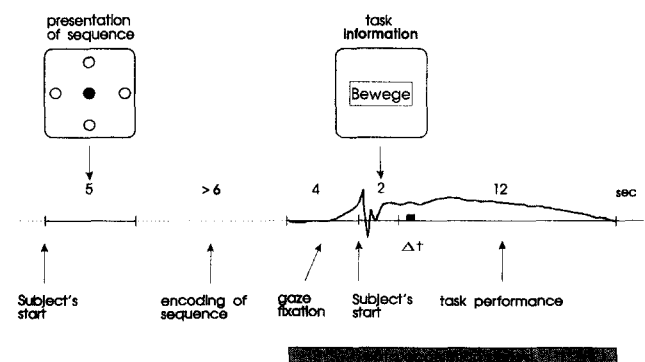


Fig. 2. Run of events for one trial as used in both experiments; “ Δt ” represents the time interval within which the mean amplitude of DC potentials was calculated. Dashed lines indicate free time choice for subjects.

potentials was taken prior to the presentation of the task information, baseline was independent of the conditions under study. In each condition at least 40 trials free of artifacts were collected.

Training session

Before starting each experiment subjects had a training session within which they got acquainted with the task requirements. The training session included 20 trials for each condition. Within that session subjects learned to perform hand movements corresponding to the visual target display. We did not train them to move their hands over particular distances but instructed them to remain constant within their individual coordinate system.

The performance of movements according to the target sequence lasted about 4 sec (4 steps with an inter-movement latency of 1 sec). Subjects were instructed to (either actually or mentally) perform the whole cycle of movements twice (i.e., about 8 sec performance).

Recording of EEG and EOG

The methods for reducing skin potential and for stabilizing electrode potentials, as introduced by Bauer et al. (1989), were used in the present study: non-polarizable Ag/AgCl electrodes were connected to the recording sites via salt bridges (silicon rubber tubes filled with electrode gel). Thus drifts of electrode potentials were lower than 3 μ V within 1 min. Scratching of recording sites reduced electrode impedance at 10 Hz to less than 1 k Ω . In experiment I the EEG was recorded in F3, F4, C3, Cz, C4, T5, P3, P4, T6 and Oz. In experiment II EEG was recorded in 28 channels: F7, F3, Fz, F4, F8, FC5 (half-way between F7 and C5), FC1 (half-way between Fz and C3), FC2 (half-way between Fz and C2), FC6 (half-way between F8 and C6), T3, C5 (half-way between T3 and C3), C3, C1 (half-way between C3 and Cz), Cz, C2 (half-way between Cz and C4), C4, C6 (half-way between C4 and T4), T4, CP5 (half-way between C5 and T5), CP1 (half-way between C1 and Pz), CP2 (half-way between C2 and Pz), CP6 (half-way between C6 and T6), P3, Pz, P4, T5, T6, Oz. Resistor (5 k Ω) linked ear-lobe electrodes served as a reference. The EEG was amplified using DC amplifiers. Horizontal EOG (lateral orbital rim of the right eye vs. lateral orbital rim of the left eye) and vertical EOG (upper vs. lower orbital rim of the right eye) were amplified using a bandpass ranging from DC to 70 Hz. Data were digitized at a rate of 200 samples/sec.

Behavioural analyses

The absence of overt movements with motor imagery was controlled by measuring hand movements by deflections of the joysticks (experiment I). In experiment II the index fingers were connected to a special splint (goniometer), which allowed the exact registration of flexions and extensions of the index fingers. In addition eye movements

were controlled by use of an Infrared-System (IRIS, Skalar Medical Inc.). We did not measure the EMG since occurrence of muscular activity with motor imagery is well known in the literature (e.g., Jacobson, 1932; Wehner et al., 1984). During the off-line analysis the absence of task-related fast, vertically or horizontally oriented movements of eyes and hands with the imagery tasks was controlled.

Analysis of DC potentials and measurements

Baseline was calculated from the first 2 sec of the data acquisition period (see Fig. 2). All data were visually controlled for artifacts and affected epochs were excluded. A linear regression was applied during off-line analysis in order to remove artifacts in the EEG resulting from eye blinks, after identifying these in the vertical EOG by means of a Woods filter. We measured the mean DC potential within a 1 sec lasting interval starting 2 sec after the onset of the task (8th to 9th sec of the analysis epoch, see Figs. 2, 3, 6 and 8). The term N-P is used to describe the amplitude of the performance-related negativity. In the two experiments the points of interest are based on the existence of systematic changes of the topography of DC potentials between the different conditions. In order to reduce the likelihood of false-positive results we used a conservative testing procedure: (1) Within each condition and subject N-P was normalized using an algorithm suggested by McCarthy and Wood (1985). This procedure results in normalized values of N-P (nN-P) which range between 0 (minimum value at a certain recording position) and 1 (maximum value). (2) For correction of violation of the sphericity assumption the Greenhouse-Geisser epsilon was used. (3) In order to reduce testing procedures only those effects were tested in detail which had significant main effects or interactions in the first-level global MANOVA.

Experiment I. The global MANOVA used the within-subject factors Task (2 levels: imagery, movement), Hand (2 levels: right, left), Electrode (10 levels). For the evaluation of hemispheric differences the within-subject factors were Task (2), Hand (2), Hemisphere (2 levels: right hemisphere, left hemisphere), and Region (4 levels: frontal, F3/F4; central, C3/C4; temporal, T5/T6; parietal, P3/P4).

Experiment II. For comparison of imagination and movement the global MANOVA used the within-subject factors Task (2 levels: motor imagery, movement) and Electrode (28 levels). To approach the question of sensorimotor cortex activity with imagination the global MANOVA used the within-subject factors Task (2 levels: motor imagery, picture imagery) and Electrode (28 levels). For the evaluation of hemispheric differences the within-subject factors were Task (3 levels: imagery, movement, picture), Hemisphere (2 levels: right, left) and Region (12 levels: frontal, F7/F8, F3/F4; fronto-central, FC5/FC6, FC1/FC2; central, C5/C6, C3/C4, C1/C2; centro-

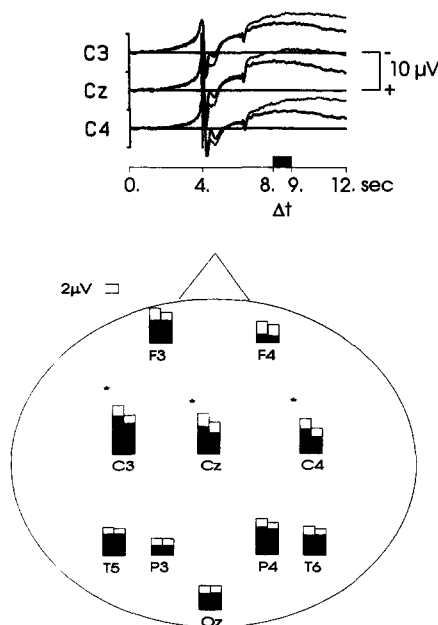


Fig. 3. Experiment I. Lower part, left column: hand movement, right column: hand imagery (left and right hand together). Negative is up. Solid blocks give mean amplitudes across subjects, empty blocks indicate standard error. * = $P < 0.05$. Upper part: course of DC potentials for recordings showing significant effects (C3, Cz, C4). Solid line: hand imagery; dotted line: hand movement. Negative is up. “ Δt ” indicates the period of statistical analysis.

parietal, CP5/CP6, CP1/CP2; temporal, T3/T4, T5/T6; parietal, P3/P4).

In the following all df and P values given are Greenhouse-Geisser corrected when necessary. On condition that

the first-level tests were significant, subsequent tests were employed in order to test the points of interest.

3. Results of experiment I

Imagination vs. movement

The significant interaction Task \times Electrode ($df = 4, 116, F = 3.18, P < 0.05$) proves that the pattern of DC potentials changes between imagination and execution of the tasks. Subsequent within-subject paired t tests demonstrate that Task effects are caused by local variations in C3, Cz and C4 (Fig. 3). Here, N-P is larger with moving than with imagery. Frontal, temporal, parietal and occipital recordings are not affected by Task.

The first-level analysis did not produce a significant Hand \times Task \times Electrode interaction ($df = 5, 128, F = 1.42$). This means that N-P increase with movement execution as compared to imagery is comparable for movements of either side.

Hemispheric asymmetries

The mean differences between recordings at corresponding sites of the two hemispheres (F3/F4, C3/C4, T5/T6 and P3/P4) are given in Fig. 4. There is a general lateralization of DC potentials with larger amplitudes in the left hemisphere (effect of the within-subject factor Hemisphere across all regions and conditions: $df = 1, 26, F = 37.10, P < 0.001$). In central recordings (C3/C4) this general lateralization of N-P to the left is modulated by the side of the hand which performs the task (Hand \times

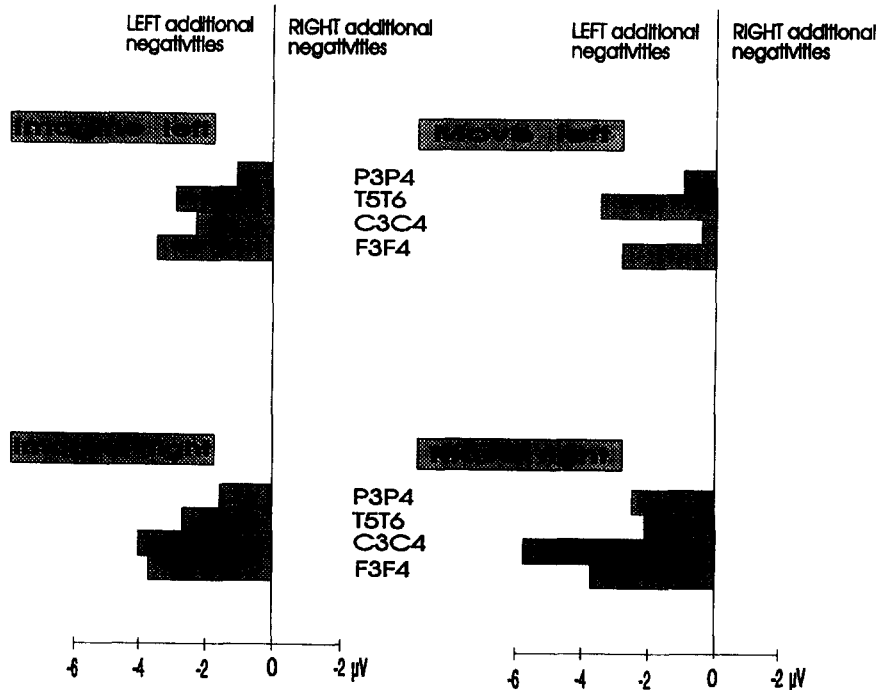


Fig. 4. Lateralizations with experiment I. Differences of mean amplitudes of DC potentials between recordings of corresponding sites of the two hemispheres.

Hemisphere \times Region: $df = 3, 66, F = 27.19, P < 0.001$; Hand \times Hemisphere for C3/C4: $df = 1, 26, F = 39.47, P < 0.001$. Performance (imagination and execution) with the right hand increases the lateralization to the left (C3 \gg C4), performance with the left side reduces the superiority of the left hemisphere (C3 $>$ C4).

Hemispheric asymmetries due to the side of the performing hand did not only exist in central recordings (C3/C4) as described above but also in temporal recordings (Hand \times Hemisphere at T5/T6: $df = 1, 26, F = 4.68, P < 0.05$). In contrast to central recordings, left hemispheric superiority in temporal recordings was larger with the performance of the left hand as compared to performance of the right hand (compare Fig. 4).

Concerning task-specific differences of lateralization no Task \times Hemisphere ($df = 1, 26, F = 0.28$) and no Task \times Hemisphere \times Region ($df = 2, 64, F = 0.9$) effects were found indicating that the contribution of the left hemisphere does not differ between imagery and movement.

Involvement of the sensorimotor cortex in motor imagery

As deduced in the Introduction, systematic changes of N-P in recordings located above the sensorimotor hand area (C3, C4), which are depending on the side of the imagined motor sequence, would indicate an activity of the sensorimotor cortex with motor imagery.

The interaction Hand \times Task \times Electrode ($df = 5, 128, F = 1.42$) was not significant but the interaction Hand \times Electrode was significant ($df = 5, 128, F = 6.38, P < 0.001$). This indicates that the pattern of DC potentials indeed changes depending on the side which performs (either executes or imagines) the task. There is no difference between movement and imagery which means that there is a specific pattern of cortical activity with unilateral execution and imagination of the movement. Concerning the location of this hand-specific effect, analyses of variances selectively done for each recording position (F3 to Oz) show that the side of the performing does only affect DC potentials (N-P) in C3 ($df = 1, 26, F = 8.43, P < 0.01$)

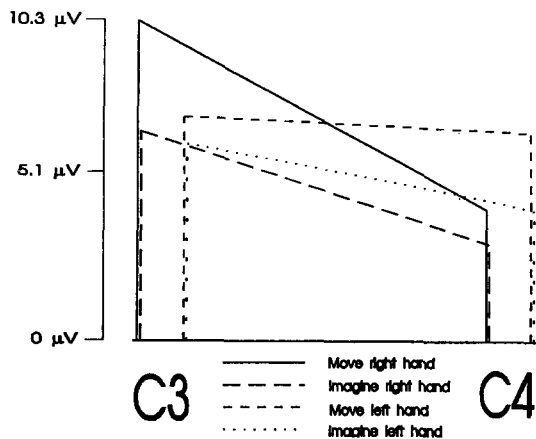


Fig. 5. Experiment I. Pattern of DC potentials in the central region. Corresponding amplitudes of DC potentials at left and right central recordings are connected with each other.

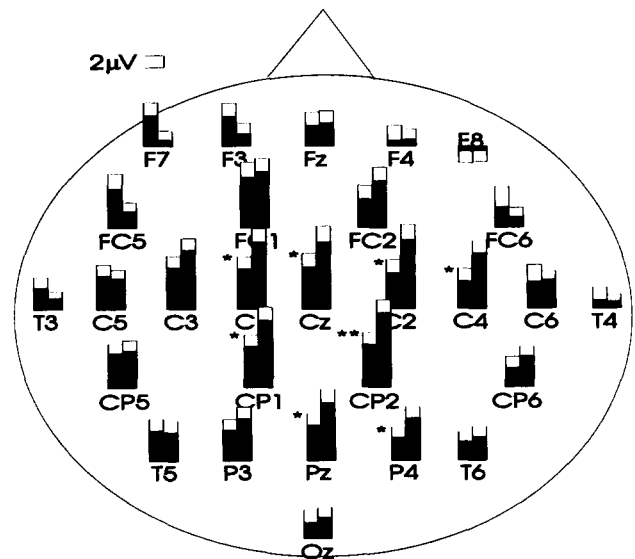
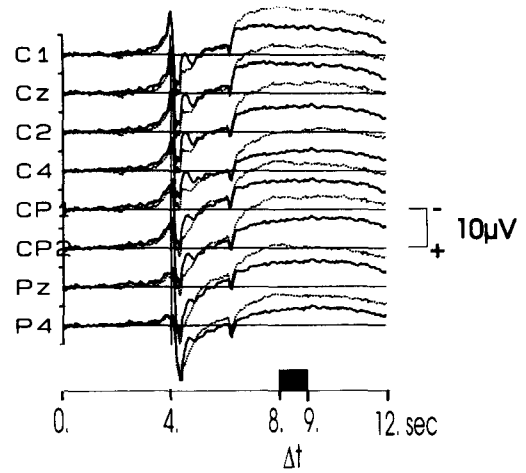


Fig. 6. Experiment II. Lower part, left column: hand imagery, right column: hand movement. Negative is up. Solid blocks give mean amplitudes across subjects, empty blocks indicate standard error. * = $P < 0.05$, ** = $P < 0.01$. Upper area: course of DC potentials for recordings showing significant effects. Solid line: hand imagery; dotted line: hand movement. Negative is up. “Dt” indicates the period of statistical analysis.

and C4 ($df = 1, 26, F = 12.43, P < 0.01$) which are located above the sensorimotor hand area but does not affect N-P in all other recordings (F3, F4, Cz, T5, T6, P3, P4 and Oz). At C3 performing (= moving and imagery) of the right hand was associated with larger amplitudes than performing of the left hand, at C4 it was vice versa. Note, that this was true for both tasks. Results are summarized in Fig. 5.

4. Results of experiment II

Imagination vs. movement

The global level of DC potentials did not differ between the execution and imagination of the movements ($df = 1, 18, F = 0.63$). However, the pattern of DC potentials

significantly changed (Task (imagination, movement) \times Electrode: $df = 4, 76, F = 7.93, P < 0.001$). The change of the spatial pattern of DC potentials is based on significant differences of DC potentials in C1, Cz, C2, C4, CP1, CP2, Pz and P4 with larger amplitudes with movement than with imagery (paired t tests: $P < 0.05$; Fig. 6).

Hemispheric asymmetries

As displayed in Fig. 7, DC potentials are larger above the left hemisphere than above the right one with both tasks. Exceptions of this rule are C1/C2 and CP1/CP2, respectively. These recordings are close to the midline and lateralization to the contralateral hemisphere (so-called “paradoxical lateralization”) due to neural activity in the mesial wall of the predominant ipsilateral cortex might exist as shown for hemifield visual stimulation (cf., Barrett et al., 1976) and for foot movements (Boschert and Deecke, 1986). Lateralization to the left hemisphere is larger with imagery than with moving (Hemisphere \times Task: $df = 2, 27, F = 4.83, P < 0.05$). The degree of this task-specific lateralization varies between the regions (Hemisphere \times Task \times Region: $df = 6, 106, F = 2.65, P < 0.05$). As displayed in Fig. 7, the main source for the left hemispheric increase with motor imagery are fronto-central regions ($F7 \gg F8, F3 \gg F4, FC1 \gg FC2$).

Involvement of the sensorimotor cortex in motor imagery

Concerning our third question, a direct comparison of motor imagery with a control condition was possible here. The global level as well as the spatial distribution of DC potentials significantly changes between motor imagery and picture imagery (Task (motor imagery, picture imagery): $df = 1, 18, F = 8.48, P < 0.01$; Task (motor im-

agery, picture imagery) by Electrode: $df = 4, 71, F = 5.88, P < 0.001$). As displayed in Fig. 8, DC potentials are always more negative with motor imagery as compared to visual imagery with differences being most pronounced in central recordings.

5. Discussion

Different patterns of DC potentials with imagination and movement

In experiment I, the right-handed movement was associated with larger negative DC potentials in central recordings (C3, Cz, C4) as compared to the corresponding imagery task. What can be deduced about the sources in the cortex which contribute to these differences? Movement-related activity of the sensorimotor hand area causes a radial current flow with a surface-negative field potential close to positions C3 or C4, respectively (Neshige et al., 1988). Movement-related potentials in Cz are either assumed to be caused by activity of the two hand motor areas (e.g. Bötzel et al., 1993) or, at least to a major part, by activity of the mesial, fronto-central cortex (e.g. Kornhuber et al., 1989). Thus, the differences of brain potentials in central recordings are likely to reflect differential activity of the sensorimotor hand area and the mesial fronto-central cortex. Another question is whether this difference may be “sensory” or “motoric” in nature? Overt movements cause peripheral stimulation of receptors which is absent with covert movements. While natural stimulation of peripheral receptors (passive movements, perturbations during active movements) provide an effective input with discharges of a high proportion of neurones

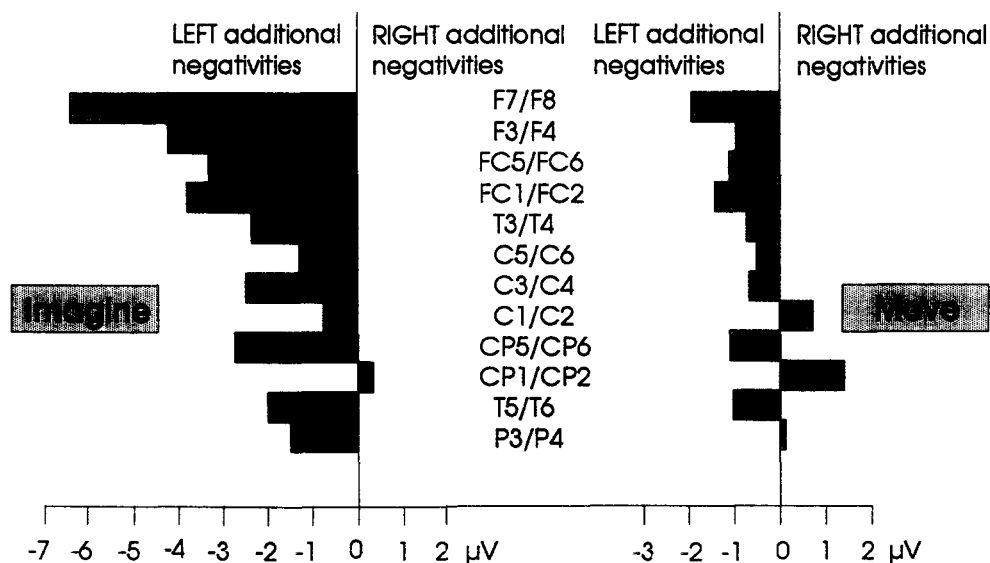


Fig. 7. Lateralizations with experiment II. Differences of mean amplitudes of DC potentials between recordings of corresponding sites of the two hemispheres.

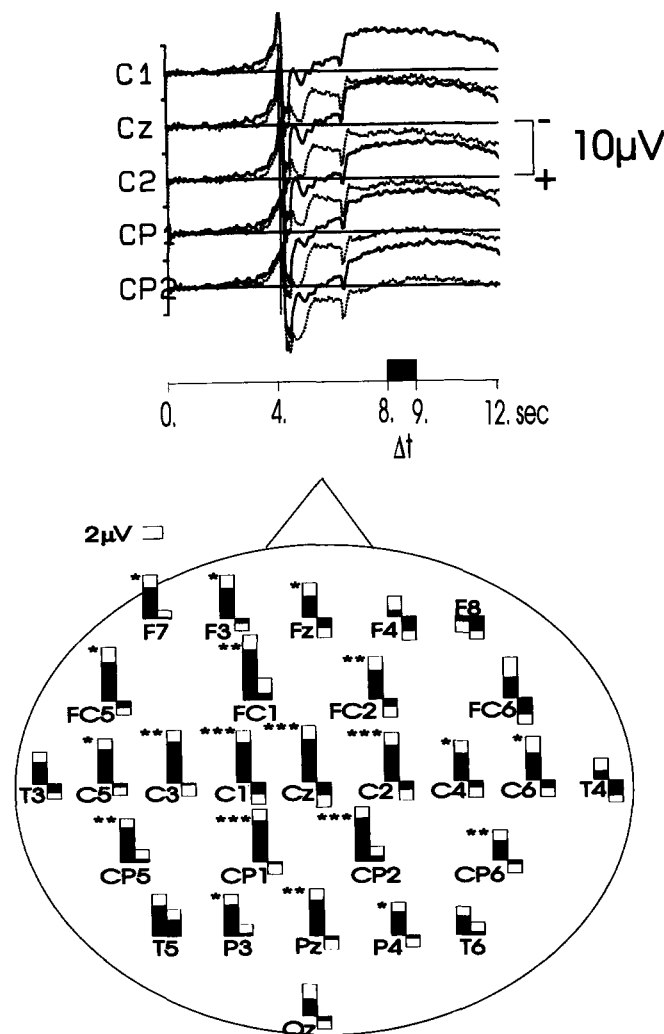


Fig. 8. Experiment II. Lower area, left column: hand imagery, right column: picture imagery. Negative is up. Solid blocks give mean amplitudes across subjects, empty blocks indicate standard error. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Upper area: course of DC potentials for recordings showing significant effects. Solid line = hand imagery; dotted line = picture imagery. Negative is up. " Δt " indicates the period of statistical analysis. Note that the amplitudes for picture imagery are found around the zero level.

of the primary motor cortex, such natural activation of peripheral receptors activate only a small proportion of neurones of the SMA (review: Porter and Lemon, 1993). Ipsilateral receptive fields have been reported in area 5 and the second somatic sensory area (SII) which project to the SMA. Thus, stimulation of peripheral receptors may contribute to the increase of DC potentials during movements as compared to imagination. However, one would expect an asymmetry depending on the performing hand because of the strong projection of sensory input to the contralateral sensorimotor cortex. On the other hand, it is established now that the two primary motor cortices, although to different degrees, are active prior and during unilateral finger movements (Neshige et al., 1988; Kristeva et al., 1991; Lang et al., 1991b). Thus, a different level of activation of the cortico-motoneuronal system may exist and

account for the difference of DC potentials between executed and imagined movements.

Experiment II substantiates these results by showing larger negative DC potentials in central recordings when executing than when imagining the bimanual motor task. In addition, the difference was also present in recordings posterior to the sulcus centralis (CP5, CP6, Pz and P4). This may support the activity of the parietal cortex when executing the bimanual task as compared to motor imagery.

Hemispheric asymmetry

Experiment I. DC potentials with the execution and imagination of the motor sequence were strongly lateralized to the left hemisphere. This lateralization was even present with movements of the left hand. As displayed in Fig. 5, the side of the performing hand either diminished (left hand) or increased (right hand) this lateralization in central recordings (C3/C4). The functional meaning of the lateralization is not unequivocal: the necessity to internally maintain and transform a series of visuo-spatial patterns into a sequence of movements may critically involve the left hemisphere (Goldenberg, 1992). The "articulatory loop" of the working memory might be involved and the superiority of the left hemisphere with language-related processes in right-handed subjects is well established. Finally, the sequential and analytic structure of the task may be an independent cause of the left hemispheric dominance in the present task (cf. Moscovitch, 1979).

Hemispheric asymmetry does qualitatively not differ between execution and imagination of the movements. At least for the particular task employed, there is no evidence that left hemispheric dominance is larger with imagination than with execution of movements.

An unexpected finding deserves to be pointed out although its functional significance cannot presently be specified. In recordings above the parieto-temporal junction (T5/T6) left hemispheric dominance was larger with performance of the left hand than with those of the right hand (imagination and execution). One line of explanation for this unexpected finding is the following: right-handed subjects are more skilled for movements of the right hand than for those of the left hand. If we assume a critical involvement of the left inferior parietal cortex in maintaining and transforming spatial cues into a sequence of movements (Goldenberg, 1992) and if we assume that the load imposed on the task is larger with performance of the left hand than with performance of the right hand, an additional activation of the left inferior parietal cortex might exist and account for the phenomenon.

Experiment II. Imagination of a bilateral movement is significantly more lateralized to the left than the execution of the movement. This finding is surprising since the first experiment which employed unilateral movements did not show differences of lateralization between imagination and movement. The common feature of both experiments was

that subjects were required to move or imagine to move according to a memorized sequence of positions. There are two differences between the two experiments. Experiment II restricted movements to the vertical direction and required to perform the task with the two hands. A conclusion concerning the factor which is relevant for the lateralization effect in experiment II can be made in context with an unpublished experiment of our laboratory where the same sequence of movements was used but where the subjects were instructed to perform memorized saccades or to imagine to do so. Hemispheric lateralization of DC potentials did not differ between memorized saccades and oculomotor imagery. Considering these data we conclude that bimanual motor imagery of memorized sequences may critically involve the left hemisphere. This possibly is due to the larger demands concerning imagination of spatial coordination when using the limbs.

Involvement of the primary motor area in motor imagery

Experiment I. It is established that the side of the hand which executes a movement has significant and selective effects on brain potentials at C3/C4 and adjacent recordings (e.g. C1/C2). This holds for brain potentials preceding (Kornhuber and Deecke, 1965; Deecke et al., 1976) and accompanying the movement (see Introduction) and is reproduced in experiment I where brain potentials in C3 and C4 were shown to vary with the side of the hand executing the movement. The present study adds to that current knowledge by demonstrating that the same phenomenon is also present with imagination of the movement. In fact, statistics proved that with imagery this phenomenon is even present to a comparable extent. For that reason, present data indicate the involvement of the sensorimotor hand area in motor imagery. Spatial sampling was not sufficient to specify whether the primary motor, adjacent parts of the non-primary motor cortex (so-called premotor cortex) or the primary sensory hand area is activated by motor imagery. Because of the lack of tactile or kinaesthetic input during motor imagery (besides that of the small muscular activity accompanying it), it seems reasonable to assume that neural activity of the primary motor cortex alone or together with adjacent parts of the premotor cortex is the main source of variation of DC potentials in C3/C4 with motor imagery of either side.

Present findings do not support the concept that the primary motor cortex is not involved in motor imagery which is based on several SPECT studies (Ingvar and Philipson, 1977; Roland et al., 1980; Decety et al., 1988). Those negative findings might have been caused by an insensitivity of the methods applied (cf. Fox et al., 1985). Our findings are consistent with previous clinical EEG studies which have shown a blocking of the central “mu rhythm” with motor imagery (see Introduction).

Experiment II. The second experiment which compared motor imagery with a visual imagery control showed an increase of the performance-related negative DC potentials

in motor imagery as compared to the control. The difference negativity was widespread across the scalp and with maxima in central recordings. Thus, the data are consistent with the assumption that the sensorimotor hand area is active with motor imagery. However, the spatial extent of the difference negativity indicates that other parts of the cortex are active with that particular task of motor imagery as well.

In conclusion, the theory that motor planning is not channeled to the sensorimotor cortex and to descending motor pathways during motor imagery (Roland et al., 1980) is not supported by the present study. We would propose that the same structures may be involved in the two tasks and that some gating occurs at the subcortical level.

General remarks

The field of functional neuro-imaging is presently developing very fast. The main advantage of neurophysiological tools, such as EEG and MEG, is temporal resolution as compared to the spatial resolution of PET and functional magnetic resonance imaging. The present study and previous observations of the mu rhythm indicate the activity of the sensorimotor cortex with the imagination of a manual motor sequence task. This activity has not been observed by PET and SPECT (see Introduction) which may reflect a superiority of sensitivity of the EEG as compared to rCBF measurements. This superiority has also been turned out in a different physiological model: Neshige et al. (1988) used epicortical recordings to measure the brain potentials associated with unilateral movements and reported that the ipsilateral primary motor cortex is active with a unilateral hand movement. Functional activation studies using PET did not detect ipsilateral activity of the motor cortex during hand movements (Roland et al., 1982; Colebatch et al., 1991). Topographic analysis of scalp-recorded EEG with unilateral movements indicates the contribution of the ipsilateral motor cortex (Lang et al., 1991b; Bötzel et al., 1993) and MEG succeeded to quantify the extent of ipsilateral activity (Kristeva et al., 1991). Recently, functional MRI succeeded to detect the ipsilateral activity of the motor cortex as well (Kim et al., 1993).

There is a long-standing discussion in motor physiology whether the motor cortex commands the generation of forces or movements of the limb through space (see Wise, 1993). Motor imagery is not associated with overt movements. The present study indicates that the activity of the sensorimotor cortex is not necessarily associated with moving the limb through space.

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References

- Altenmüller, E., Thomas, C., Hornung, T., Kahrs, J. and Dichgans, J. Funktionelle Topographie von Sprachleistungen und höheren visuellen Funktionen mit Gleichspannungspotentialen. In: L. Deecke and W. Lang (Eds.), *Topographische Diagnostik des Gehirns*. Deutsch-Österreichischer Neurologenkongress, Vienna, 16–18 September, 1993: Abst. 22.
- Barrett, G., Blumhardt, L., Halliday, A.M., Halliday, E. and Kriss, A. A paradox in the lateralisation of the visual evoked response. *Nature*, 1976, 261: 253–255.
- Bauer, H., Korunka, C. and Leodolter, M. Technical requirements for high-quality scalp DC recordings. *Electroenceph. clin. Neurophysiol.*, 1989, 72: 545–547.
- Boschert, J. and Deecke, L. Cerebral potentials preceding voluntary toe, knee and hip movements and their vectors in human precentral gyrus. *Brain Res.*, 1986, 376: 175–179.
- Bötzel, K., Plendl, H., Paulus, W. and Scherg, M. Bereitschaftspotential: is there a contribution of the supplementary motor area? *Electroenceph. clin. Neurophysiol.*, 1993, 89: 187–196.
- Caspers, H., Speckmann, E.J. and Lehmenkühler, A. Electrogenesis of cortical DC potentials. In: H.H. Kornhuber and L. Deecke (Eds.), *Progress in Brain Research*, Vol. 54, Elsevier, Amsterdam, 1980: 3–16.
- Chatrian, G.E., Petersen, M.C. and Lazarte, J.A. The blocking of the rolandic wicket rhythm and some central changes related to movement. *Electroenceph. clin. Neurophysiol.*, 1959, 11: 497–510.
- Colebatch, J.G., Deiber, M.P., Passingham, R.E., Friston, K.J. and Frackowiak, R.S.J. Regional cerebral blood flow during voluntary arm and hand movements in human subjects. *J. Neurophysiol.*, 1991, 65: 1392–1401.
- Decety, J. and Ingvar, D.H. Brain structures participating in mental simulation of motor behaviour: a neuropsychological interpretation. *Acta Psychol. (Amst.)*, 1990, 73: 13–34.
- Decety, J. and Michel, F. Comparative analysis of actual and mental movement times in two graphic tasks. *Brain Cogn.*, 1989, 11: 87–97.
- Decety, J., Philippon, B. and Ingvar, D.H. RCBF landscapes during motor performance and motor ideation of a graphic gesture. *Eur. Arch. Psychiat. Neurol. Sci.*, 1988, 238: 33–38.
- Decety, J., Jeannerod, M. and Prablanc, C. The timing of mentally represented actions. *Behav. Brain Res.*, 1989, 34: 35–42.
- Decety, J., Jeannerod, M., Germain, M. and Pastene, J. Vegetative response during imagined movement is proportional to mental effort. *Behav. Brain Res.*, 1991, 42: 1–5.
- Deecke, L., Grözinger, B. and Kornhuber, H.H. Voluntary finger movement in man: cerebral potentials and theory. *Biol. Cybern.*, 1976, 23: 99–119.
- Farah, M. The neurological basis of mental imagery: a componential analysis. *Cognition*, 1984, 18: 245–272.
- Fox, P.T., Fox, J.M., Raichle, M.E. and Burde, R.M. The role of cerebral cortex in the generation of voluntary saccades: a positron emission tomography study. *J. Neurophysiol.*, 1985, 54: 348–369.
- Gastaut, H., Naquet, R. and Gastaut, Y. Etude d'une activité électroencéphalographique méconnue: "le rythme rolandique en arceau." *Marseille Méd.*, 1965, 18: 720–721.
- Goldenberg, G. The riddle of apraxia. In: J. Annett (Ed.), *International Workshop on Imagery and Motor Processes*. University of Leicester, 1992.
- Grünewald, G. and Grünewald-Zuberbier, E. Cerebral potentials during voluntary ramp movements in aiming tasks. In: A.W.K. Gaillard and W. Ritter (Eds.), *Tutorials in ERP Research: Endogenous Components*. Elsevier, Amsterdam, 1983: 311–327.
- Grünewald-Zuberbier, E. and Grünewald, G. Goal-directed movement potentials of human cerebral cortex. *Exp. Brain Res.*, 1978, 33: 135–138.
- Ingvar, D.H. and Philipson, L. Distribution of cerebral blood flow in the dominant hemisphere during motor ideation and motor performance. *Ann. Neurol.*, 1977, 2: 230–237.
- Jacobson, E. *Electrophysiology of mental activities*. *Am. J. Physiol.*, 1932, 44: 677–694.
- Jasper, H.H. and Andrews, H.L. *Electroencephalography*. III. Normal differentiation of occipital and precentral regions in man. *Arch. Neurol. Psychiat.*, 1938, 39: 96–115.
- Kim, S.G., Ashe, J., Georgopoulos, A.P., Merkle, H., Ellermann, J.M., Menon, R.S., Ogawa, S. and Ugurbil, K. Functional imaging of motor cortex at high magnetic field. *J. Neurophysiol.*, 1993, 69: 279–302.
- Klass, D. and Bickford, R.G. Observations on the rolandic arceau rhythm. *Electroenceph. clin. Neurophysiol.*, 1957, 9: 570.
- Kornhuber, H.H. and Deecke, L. Hirnpotentialänderung bei Willkürbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und reafferente Potentiale. *Pflügers Arch. Ges. Physiol.*, 1965, 284: 1–17.
- Kornhuber, H.H., Deecke, L., Lang, W., Lang, M. and Kornhuber, A. Will, volitional action, attention and cerebral potentials in man: Bereitschaftspotential, performance-related potentials, directed attention potential, EEG spectrum changes. In: W. Hershberger (Ed.), *Advances in Psychology. Volitional Actions*. Elsevier, Amsterdam, 1989: 107–168.
- Kristeva, R., Cheyne, D. and Deecke, L. Neuromagnetic fields accompanying unilateral and bilateral voluntary movements: topography and analysis of cortical sources. *Electroenceph. clin. Neurophysiol.*, 1991, 81: 284–298.
- Lang, W., Lang, M., Heise, B., Deecke, L. and Kornhuber, H.H. Brain potentials related to voluntary hand tracking, motivation and attention. *Hum. Neurobiol.*, 1984, 3: 235–240.
- Lang, W., Lang, M., Uhl, F., Kornhuber, A., Deecke, L. and Kornhuber, H.H. Left frontal lobe in verbal associative learning: a slow potential study. *Exp. Brain Res.*, 1988, 70: 99–108.
- Lang, W., Zilch, O., Koska, C., Lindinger, G. and Deecke, L. Negative cortical DC shifts preceding and accompanying simple and complex sequential movements. *Exp. Brain Res.*, 1989, 74: 99–104.
- Lang, W., Cheyne, D., Kristeva, R., Beisteiner, R., Lindinger, G. and Deecke, L. Three-dimensional localization of SMA activity preceding voluntary movement. *Exp. Brain Res.*, 1991a, 87: 688–695.
- Lang, W., Cheyne, D., Kristeva, R., Lindinger, G. and Deecke, L. Functional localisation of motor processes in the human cortex. *Electroenceph. clin. Neurophysiol.*, 1991b, Suppl. 42: 97–115.
- Lang, W., Beisteiner, R., Lindinger, G. and Deecke, L. Changes of cortical activity when executing learned motor sequences. *Exp. Brain Res.*, 1992, 89: 435–440.
- Lindinger, G., Lang, W., Obrig, H. and Deecke, L. Current-source density analysis of scalp potentials – topographical analysis of movement-related DC-shifts. In: *Psychophysiological Brain Research*, Vol. 1. Tilburg University Press, Tilburg, 1990: 142–145.
- McCarthy, G. and Wood, C.C. Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. *Electroenceph. clin. Neurophysiol.*, 1985, 62: 203–208.
- Mendoza, D. and Wichman, H. Inner darts: effects of mental practice on performance of dart throwing. *Percept. Motor Skills*, 1978, 47: 1195–1199.
- Moscovitch, M. Information processing and the cerebral hemispheres. In: M.S. Gazzaniga (Ed.), *Handbook of Behavioral Neurobiology*, Vol. 2 (Neuropsychology). Plenum Press, New York, 1979.
- Neshige, R., Lüders, H. and Shibasaki, H. Recording of movement-related potentials from scalp and cortex in man. *Brain*, 1988, 3: 719–736.
- Niedermeyer, E. The normal EEG of the waking adult. In: E. Niedermeyer and F. Lopes da Silva (Eds.), *Electroencephalography*. Urban and Schwarzenberg, Baltimore, MD, 1987: 97–117.
- Pfurtscheller, G. and Aranibar, A. Änderungen in der spontanen EEG Aktivität vor Willkürbewegungen. Neue Wege bei der Untersuchung der zentralen μ -Aktivität. *Z. EEG-EMG*, 1978, 9: 18–23.
- Pfurtscheller, G. and Berghold, A. Patterns of cortical activation during

- planning of voluntary movement. *Electroenceph. clin. Neurophysiol.*, 1989, 72: 250–258.
- Porter, R. and Lemon, R. *Corticospinal Function and Voluntary Movement*. Oxford University Press, Oxford, 1993.
- Rockstroh, B., Elbert, T., Canavan, A., Lutzenberger, W. and Birbaumer, N. (Eds.). *Slow Cortical Potentials and Behaviour*. Urban and Schwarzenberg, Baltimore, MD, 1989.
- Roland, P.E., Larsen, B., Lassen, N.A. and Skinhøj, E. Supplementary motor area and other cortical areas in organization of voluntary movements in man. *J. Neurophysiol.*, 1980, 43: 118–136.
- Roland, P.E., Meyer, E., Shibasaki, T., Yanamoto, Y.L. and Thompson, C.J. Regional cerebral blood flow changes in cortex and basal ganglia during voluntary movements in normal human volunteers. *J. Neurophysiol.*, 1982, 48: 467–480.
- Speckmann, E.J. and Elger, C.E. Introduction to the neurophysiological basis of the EEG and DC potentials. In: E. Niedermeyer and F. Lopes da Silva (Eds.), *Electroencephalography*. Urban and Schwarzenberg, Baltimore, MD, 1987: 1–15.
- Stephan, K.M., Fink, G.R., Frith, C.D. and Frackowiak, R.S.J. Funktionelle Anatomie der Vorstellung von Handbewegungen. In: L. Deecke and W. Lang (Eds.), *Topographische Diagnostik des Gehirns*. Deutsch-Österreichischer Neurologenkongress, Vienna, 16–18 September, 1993: Abst. 116.
- Uhl, F., Goldenberg, G., Lang, W., Lindinger, G., Steiner, M. and Deecke, L. Cerebral correlates of imagining colours, faces and a map. II. Negative cortical DC potentials. *Neuropsychologia*, 1990, 28: 81–93.
- Wehner, T., Vogt, S. and Stadler, M. Task-specific EMG characteristics during mental practice. *Psychol. Res.*, 1984, 46: 369–401.
- Wise, S.P. Monkey motor cortex: movements, muscles, motoneurons and metrics. *Trends Neurosci.*, 1993, 16: 46–49.