

EEG-Correlates of Coordinate Processing During Intermanual Transfer

Dissertation

der Fakultät für Informations- und Kognitionswissenschaften
der Eberhard-Karls-Universität Tübingen
zur Erlangung des Grades eines
Doktors der Naturwissenschaften
(Dr. rer. nat.)

vorgelegt von
Dr. med. Regine Kerstin Lange
aus Hamburg

**Tübingen
2004**

Tag der mündlichen Qualifikation: 29.7.2004

Dekan: Prof. Dr. Ulrich Güntzer

1. Berichterstatter: Prof. Dr. Bruno Preilowski

2. Berichterstatter: Priv.-Doz. Dr. Christoph Braun

Contents

1 Introduction

1.1 Behavioural Research.....	6
1.2 Current Models of Intermanual Transfer.....	7
1.2.1 Cross Activation Model.....	7
1.2.2 Callosal Access Model.....	9
1.2.3 Model of Coordinate Processing.....	10
1.3 Hypotheses and Aims of Present Study.....	12
1.4 Logic of Data Analysis.....	14

2 Subjects and Methods

2.1 Subjects.....	16
2.2 Methods.....	16
2.2.1 The Task.....	16
2.2.2 Experimental Design.....	17
2.2.3 EEG-Recording.....	18

3 Data Analysis

3.1 Behavioural Parameters.....	20
3.2 Neurophysiological Parameters.....	21
3.2.1 Movement-Related Potentials.....	21
3.2.2 EEG-Power.....	21
3.2.1 EEG-Coherence.....	22
3.3 Statistics.....	23

4 Results

4.1 Right-to-Left Hand Transfer.....	24
4.1.1 Behavioural Data.....	24
4.1.2 Neurophysiological Data.....	26
4.1.2.1 Movement-Related Potentials.....	26
4.1.2.2 EEG-Power.....	28
4.1.2.3 EEG-Coherence.....	29
4.2 Left-to-Right Hand Transfer.....	32
4.2.1 Behavioural Data.....	32

4.2.2 Neurophysiological Data.....	33
------------------------------------	----

5 Discussion

5.1 Remarks on Data Interpretation.....	35
5.2 Right-to-Left Hand Transfer.....	37
5.2.1 Task Performance.....	37
5.2.2 Interpretation of Neurophysiological Data.....	37
5.2.2.1 Reference Frame Used During Intermanual Transfer.....	37
5.2.2.2 Period of Coordinate Processing.....	38
5.2.2.3 Internal Representation of the Learned-Task.....	38
5.2.2.4 Coordinate Processing During the Normal-Task.....	39
5.2.2.5 Coordinate Processing During the Mirror-Task.....	42
5.2.2.6 Interhemispheric Communication.....	43
5.2.3 Neurophysiological Data Under the Aspect of Performance.....	43
5.2.4 Conclusions of the Right-to-Left hand Transfer.....	44
5.3 Left-to-Right Hand Transfer.....	45
5.3.1 Task Performance.....	45
5.3.2 Interpretation of Neurophysiological Data.....	46
5.3.2.1 Reference Frame Used During Intermanual Transfer.....	46
5.3.2.2 Period of Coordinate Processing.....	46
5.3.2.3 Internal Representation of the Learned-Task.....	47
5.3.2.4 Coordinate Processing During the Normal-Task.....	47
5.3.2.5 Coordinate Processing During the Mirror-Task.....	48
5.3.2.6 Interhemispheric Communication.....	48
5.3.3 Neurophysiological Data Under the Aspect of Performance.....	49
5.3.4 Conclusions of the Left-to-Right Hand Transfer.....	51
5.4 Comparison of the Right-to-Left Hand with the Left-to-Right Hand Transfer.....	52
5.4.1 Task Performance.....	52
5.4.2 Neural Systems of Coordinate Processing.....	53
5.4.3 Neurophysiological Data Under the Aspect of Task Performance.....	55
5.5 Coordinate Processing under the Aspect of Models of Intermanual Transfer.....	56

5.5.1 Cross Activation Model.....	56
5.5.2 Callosal Access Model.....	56
5.6 General Conclusions.....	58
6 Summary.....	59
Zusammenfassung	60
7 References.....	61
8 Acknowledgements.....	69
9 Curriculum Vitae.....	70

Abbreviations

Learned-task: performance of the task with the hand used during acquisition

Normal-task: performance of the task in the original-oriented version with the untrained hand

Mirror-task: performance of the task in the mirror-reversed version with the untrained hand

1 Introduction

1.1 Behavioural Research

It is well known that practice of novel movements with one arm affects subsequent performance with the other arm. So-called intermanual transfer has been demonstrated for a number of tasks, such as finger tapping (Laszlo et al., 1970), keyboard pressing (Taylor and Heilman, 1980), inverted or reversed writing (Hicks, 1970; Vaid and Stiles-Davis, 1989; Parlow and Kinsbourne, 1989 and 1990; Yang, 1997; Latash, 1999), figure drawing (Halsband, 1992; Thut et al., 1996) and reaching during Coriolis force perturbations (Dizio and Lackner, 1995) or during visuomotor displacements (Elliott and Roy, 1981; Imamizu and Shimojo, 1996; Imamizu and Kawato, 1998).

There is ample evidence that the effect of opposite hand training on the performance of the untrained hand depends on the hand used during initial learning. The transfer direction reported most often is the transfer from the dominant right to the non-dominant left hand (Laszlo et al., 1970; Halsband, 1992; Dizio and Lackner, 1995; Thut et al., 1996; Criscimagna-Hemminger, 2002). In contrast, there are only few reports of superior transfer effect from left to the dominant right hand as compared to the transfer from the right towards the left hand (Hicks, 1970; Yang, 1997).

Furthermore, there is evidence that patterns of intermanual transfer differ for different features of the movement. For instance, Thut et al. (1996) who investigated a figure drawing task reported that speed transferred best from the right to left hand, spatial accuracy in the opposite direction. Sainburg and Wang (2002) showed, for a visuomotor rotation task, prominent transfer effects for initial movement direction during the right-to-left hand transfer (as compared to left-to-right-hand transfer), whereas final hand position revealed positive transfer effects in the opposite direction.

Importantly, behavioural studies strongly suggest that the benefit of acquired motor skills for actions executed with the opposite hand depends on whether the initially trained task, called here as Learned-task, is repeated by the untrained hand in its original orientation, in the following referred to as Normal-task, or in the mirror-oriented version, in the following referred to as Mirror-task.

There exists evidence that motor learning with the right hand facilitates predominantly the Mirror-task rather than the Normal-task performed by the left hand. For instance, it is known for over 100 years that 'mirror writing with the left hand is easier done than left-handed writing in the regular form' (Orton, 1928), an observation that has been confirmed in more recent studies (Vaid et al., 1989; Yang, 1997).

Concerning the left-to-right hand transfer, it has been demonstrated that left-handed training improves the Normal-task, but not the Mirror-task with the right hand. Interestingly, there are reports (Thut et al., 1996 and 1997) that left-handed training leads to a decrease of velocity in relearning the right-handed Mirror-task. That is, subjects performed the right-handed task slower after than without left-handed motor learning

1.2 Current Models of Intermanual Transfer

A number of models have been put forward to explain the dependence of intermanual transfer performance on the hand used at acquisition and the orientation of the transfer task.

Asymmetric transfer effects are described in the so-called cross activation model and callosal access model. Prominent transfer effects from the right towards the left hand are explained by the cross activation model. The callosal access model is appropriate to describe positive transfer from the left to the right hand. The so-called model of coordinate processing explains the specific control of the Normal-task and Mirror-task

2.2.1 Cross Activation Model

The cross activation model proposes that during training with the right arm a duplicate engram is stored in the right cerebral hemisphere (see figure 1). This information is then directly accessible to the left arm controller during subsequent movements (Parlow and Kinsbourne, 1989). By contrary, sensorimotor skill acquired during training with the left arm is restricted to the contralateral right hemisphere. Consequently, to permit the control of the right hand, learned left-handed information must be transferred from the right to the left hemisphere.

Cross Activation Model

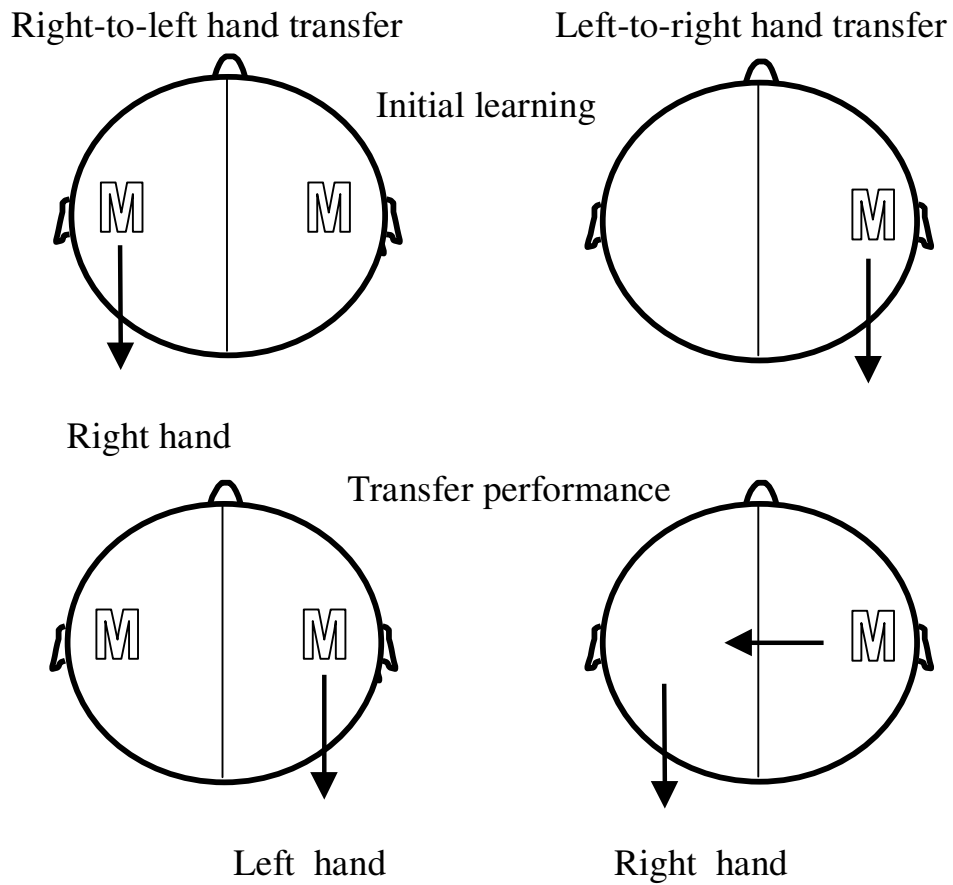


Figure 1. Cross Activation Model. Motor engrams are indicated by 'M'. After right-handed training, motor engrams are stored in both hemispheres, after left-handed training in the right hemisphere only. Hence, interhemispheric information transfer is needed during the left-to-right hand transfer, but not during the right-to-left hand transfer.

2.2.2 Callosal Access Model

The callosal access model was derived from findings showing that the right hand benefits more from opposite hand training than did the left hand (Taylor and Heilamn, 1980). The idea of this model is that during initial training motor engrams are stored in the left hemisphere, regardless of the hand used during motor training. Thus, the right arm may benefit from the initial training with the left arm because the learned information is stored in the hemisphere that controls the right arm. As a result, interhemispheric connections are involved during the repetition of a learned task with the left hand, but not during subsequent transfer to the right hand (see figure 2).

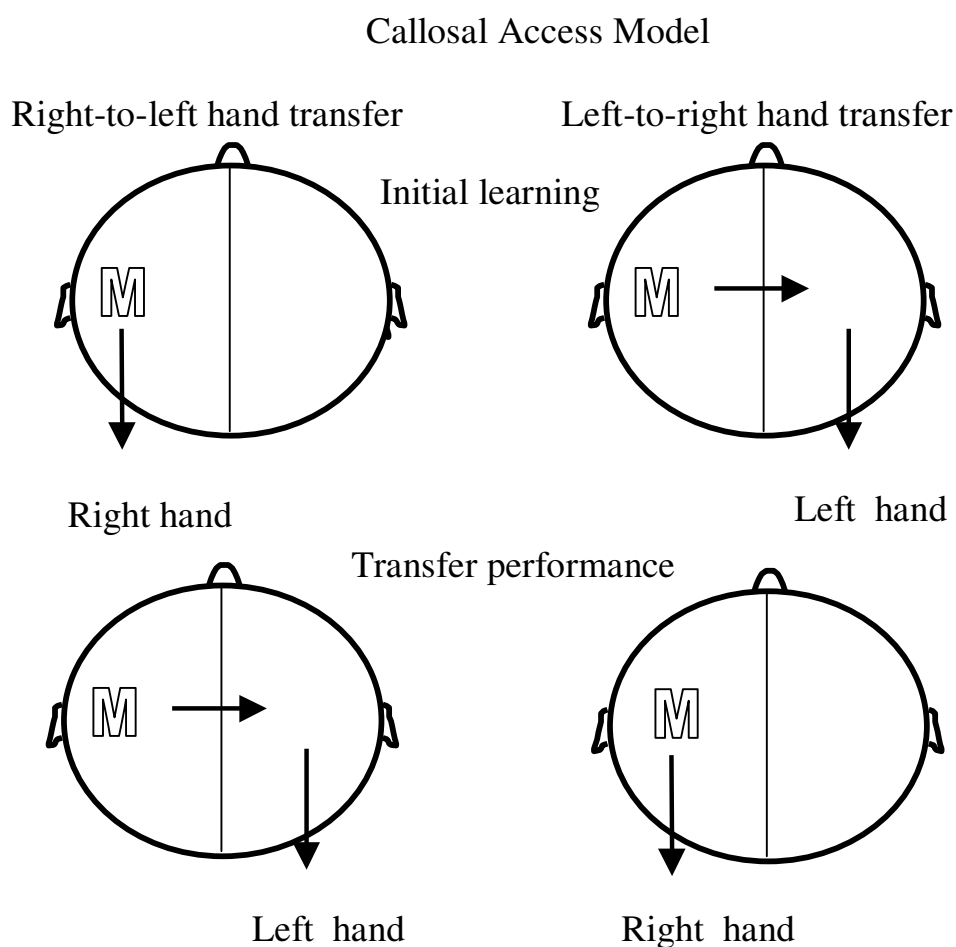


Figure 2 Callosal Access Model. Motor engrams ('M') are stored in the left hemisphere, independently on the hand used during training. Consequently, interhemispheric information transfer is required during intermanual transfer from the right to the left hand, but not from the left to the right hand.

1.2.3 Model of Coordinate Processing

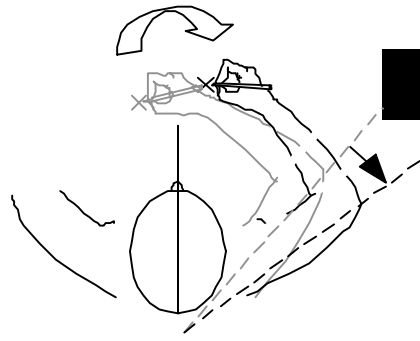
This model describes intermanual transfer performance of the Normal-task and Mirror-task and considers the representation of learned information in different frames of reference.

During visuomotor integration, visually derived representations of the target are transformed into appropriate motor patterns (Soetching and Flanders, 1989; Wolpert et al., 1995). The translation between coordinates of different reference frames is essential for these processes (Kawato et al., 1988; Atkeson, 1989; Andersen et al., 1993). The location of the movement target is initially coded in an external, eye-centered reference frame and is mapped into a body-centered frame used for motor output. In the following, coordinates that describe the location of an object extrinsic to the subjects - as mediated by vision – are referred to as extrinsic coordinates. In contrast, intrinsic coordinates describe the orientation of ‘body segments with reference to the body-midline (Soetching and Flanders, 1989).

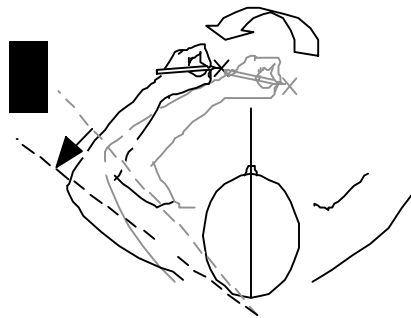
Recall of acquired Coordinates During Intermanual Transfer

Intermanual transfer of movements learned previously with one hand and executed with the other hand either in the original orientation or in mirror orientation can be explained by specific coordinates established during the learning period (Imamizu and Kawato, 1998; Malfait et al., 2002; Criscimagna-Hemminger et al., 2003). During the control of the Normal-task, extrinsic coordinates are similar to those during the repetition of the Learned-task. In contrast, during the movement execution of the Mirror-task, intrinsic coordinates are preserved. Thus, a benefit of the untrained hand from opposite hand training may be due to the recall of intrinsic coordinates during the Mirror-task and due to the access to learned extrinsic coordinates during the Normal-task (see figure 3).

Learned-task



Mirror-task



Normal-task

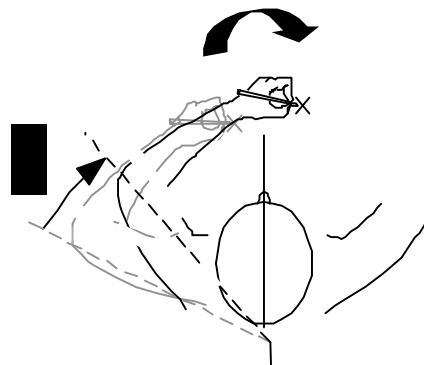


Figure 3. Model of Coordinate Processing. Extrinsic coordinates are indicated by the thick arcuated arrows representing the direction of the movement in extra-personal space. Intrinsic coordinates are indicated by angles $\Delta\alpha$ and $\Delta\beta$ which represent the angles between shoulder and upper arm during the movement. Initial arm and pen position (cross) are indicated in gray. The position after finishing the movement is presented in black. During the Mirror-task, intrinsic coordinates are the same as in the Learned-task ($\Delta\alpha$), whereas extrinsic coordinates have to be modified. During the Normal-task, intrinsic coordinates need modification ($\Delta\beta$), while extrinsic coordinates are recalled in their unchanged form.

Modification of Coordinates During Intermanual Transfer

It seems likely that both extrinsic and intrinsic coordinates are accessed in any transfer task. First, in ventral premotor cortex (Kurata and Hishi, 2002) and superior parietal cortex (Lacquanati et al., 1995; Scott et al., 1997; Buneo et al., 2002), a significant proportion of neurons is modulated by changes of both visual and motor parameters. Such cells presumably code both extrinsic and intrinsic coordinates during the control of the transfer hand in intermanual transfer tasks. Furthermore, visual information stored in extrinsic coordinates is generally essential for the planning of visually-guided movements (Flanagan and Rao, 1995; Rossetti et al., 1995) and their online control (Servos and Goodale, 1994). Thus, accurate performance of movements transferred from the trained to the untrained hand depends on information encoded in both reference frames and, consequently, intermanual transfer requires not only recall of coordinates acquired during training, but also involves processes of modification. Both the recall of extrinsic and the modification of intrinsic coordinates are necessary during the Normal-task and likewise the recall of intrinsic and the modification of extrinsic coordinates are required during the Mirror-task.

1.3 Hypotheses and Aims of Present Study

The cross activation model explains greater transfer effects of right-handed skill as compared with left-handed acquired skill. Since right-hand training effects are superior on the Mirror-task relatively to the Normal-task, the cross activation model might be appropriate to explain intermanual transfer performance of the Mirror-task. This model suggests that stored information of the right hemisphere is accessed during transfer in both directions. Thus, one may argue that the right hemisphere provides information which is specifically accessed in the Mirror-task.

The callosal access model has been derived from reports of higher transfer effects after left-handed than after right-handed skill acquisition. Considering of reports that of superior left-hand training effects on the Normal-task as compared to the Mirror-task, mechanisms underlying the performance of the Normal-task might be explained by the callosal access model. The view of this model that learned information of the *left* hemisphere controls the opposite hand leads to the assumption that the left hemisphere plays a dominant role in the control of the Normal-task.

Therefore, one might assume that the left hemisphere is responsible for coordinate processing in the Normal-task, and the right hemisphere for coordinate processing in the Mirror-task.

Following the view of the model of coordinate processing, both the recall and the modification of acquired coordinates might be responsible for an assumed specific role of right and left hemisphere in the control of the Normal-task and Mirror-task (see table 1).

Table 1: Coordinate Processing During Intermanual Transfer and Assumed Hemisphere Specialisation.

	Intrinsic coordinates	Extrinsic coordinates	Hemisphere specialisation
Normal-task	Modification	Recall	Left
Mirror-task	Recall unchanged	Modification	Right

Assuming that the role of each hemisphere is due to the *recall* of learned information, the right hemisphere might be specific in the presentation of intrinsic information, the left for extrinsic representations. In contrast, taken that each hemisphere is specifically engaged in the *modification* of acquired coordinates, the role of the left hemisphere in the control of the Normal-task might be due to the transformation of acquired intrinsic coordinates. Correspondingly, the modification of learned extrinsic coordinates might be encoded predominantly in the right hemisphere.

Previous findings from behavioural and clinical research are compatible with each of these possibilities.

Concerning the role of the left hemisphere in the control of the Normal-task, Wards and co-workers (1989) suggested that the left hemisphere uses a strategy of motor learning that codes movements ‘relative to a neutral reference point’. This view is in accord with a left-hemispheric specialisation in the recall of extrinsic coordinates. On the contrary, there are also reports which are more compatible with a dominant role of the left hemisphere in the modification of intrinsic coordinates. Rodriguez and co-workers (1989 and 19991) analysed patterns of spontaneous mirror writing in patients with left hemispheric lesions and interpreted their findings as a failure to reverse the right-hand writing motor patterns.

There are also different interpretations with respect to the role of the right hemisphere in the control of the Mirror-task. Wards and colleagues (1984) proposed ‘a right-hemisphere based motoric strategy in skill acquisition, which rely on cues derived from limb movement direction, i.e. movements directed toward or away from the body midline’. This idea is

equivalent with the view of a right-hemispheric feature in the recall of intrinsic coordinates. On the other hand, there are a number of studies that showed a dominant role of the right hemisphere in the adaptation to novel extrinsic visual cues (e.g. Deiber et al., 1997; Inoue et al., 1997). According to these reports, the role of the right hemisphere in the Mirror-task might be due to the modification of learned extrinsic information.

The main goal of the present study was to identify topography and time-course of coordinate processing during the Normal-task and Mirror-task. In particular, it was intended to investigate whether and how the left and right hemisphere are specifically involved in the processing of acquired intrinsic and extrinsic information.

1.4 Logic of Data Analysis

EEG-recordings in combination with different analytical techniques were used to study when (with respect to movement onset) and where (with respect to brain regions) recall and modification of extrinsic and intrinsic coordinates occurs during intermanual transfer.

First, movement-related potentials including movement-preceding potentials, which reflect cortical activation during movement preparation and execution (Kornhuber and Deecke, 1965; Deecke et al., 1969; Deecke and Kornhuber, 1976; Kristeva, 1977) were used to assess activation of specific cortical brain regions. Second, task-related power, and third, task-related coherence were calculated in the frequency domain. Decreases in power both in the alpha-band ranging from 8 to 13 Hz and in the beta-band between 13 and 20 Hz are assumed to reflect cortical activation. In contrast, increases of task-related power are associated with cortical areas of idling state (Pfurtscheller, 1991; Pfurtscheller and Neuper, 1992; Leocini et al., 1997). EEG-coherence is an indicator of functional connectivity between different cortical areas and reflects network-like activation (Rappelsberger et al., 1994; Andrew and Pfurtscheller, 1996; Classen et al., 1998; Leoconi et al., 1997; Manganotti et al., 1998; Gerloff et al., 1998; Andres et al., 1999).

In the present experiment the analysis of EEG parameters was based on the following considerations: If learned representations remain unchanged during intermanual transfer, EEG-activation associated with the transfer task is assumed to be identical with the Learned-task. However, if learned representations are modified during transfer, EEG-activation during intermanual transfer will reveal changes in EEG-activity as compared to the Learned-task.

Since transfer tasks were performed with the non-dominant left hand and since they have been trained less than the Learned-task, one might object that the observed differences in EEG-

patterns between the transfer tasks and the Learned-task and reflect higher processing demands in the Normal-task and Mirror-task as compared to the Learned-task. In order not to intermingle specific processes of coordinate recall and modification with these types of general transfer effects, in a first step of the analysis differences between EEG parameters of the Normal-task and the Mirror-task were identified. In a second step of the analysis EEG patterns of the Normal-task and the Mirror-task were separately compared to the Learned-task in order to identify differences and similarities between the transfer-tasks and the Learned-task that indicate processes of coordinate modification and recall, respectively.

In summary, the comparison of the two transfer tasks (Normal-task and Mirror-task) with the Learned-task may reveal two possible patterns:

First, EEG-patterns of the Normal-task, but not of the Mirror-task differ from those of the Learned-task , which indicates processing of extrinsic coordinates (recall during the Normal-task and modification during the Mirror-task). Second, EEG-parameters of the Mirror-task, but not of the Normal-task differ from those of the Learned-task. This possibility is compatible with the processing of intrinsic coordinates.

2 Subjects and Methods

2.1 Subjects

A total of 44 subjects (20 male) aging from 21 to 44 years participated in the study after having given informed consent in accordance to the declaration of Helsinki. This study was performed in full accordance with the local ethic policies. All subjects were right-handed according to the Edinburgh handedness inventory (Oldfield, 1971). 18 subjects (10 males) participated in the first part of the experiment which investigated the right-to-left hand transfer, 16 subjects aging from 23 to 38 years (10 males) took part in the second part which addressed the left-to-right hand transfer. In each group, half of the subjects were assigned to an experimental group that first trained the drawing of a figure using one hand. Subsequently, they underwent EEG recordings while repeating the Learned-task and while performing the figure drawing in its normal and mirror version by the opposite untrained hand. The remaining subjects served as a control group for the behavioural task, executing the right-handed movement and the left-handed normal and mirror movement without previous opposite hand training.

2.2 Methods

2.2.1 The Task

The motor task performed by all subjects required the drawing of a complex meaningless figure with a pen on a writing pad. The figure consisted of two different geometric regular and asymmetric geometric forms (figure 4). Subjects had full visual control over their drawing hand. However, the pen used was inkless and produced no visual trace. Since positive effects of intermanual transfer, studied in the experimental group have been reported to be more consistent for proximal actions than for distal movements (Thut et al., 1996) the involvement of proximal muscles during movement execution was assured by fixating the subjects' wrist by hand cuffs.

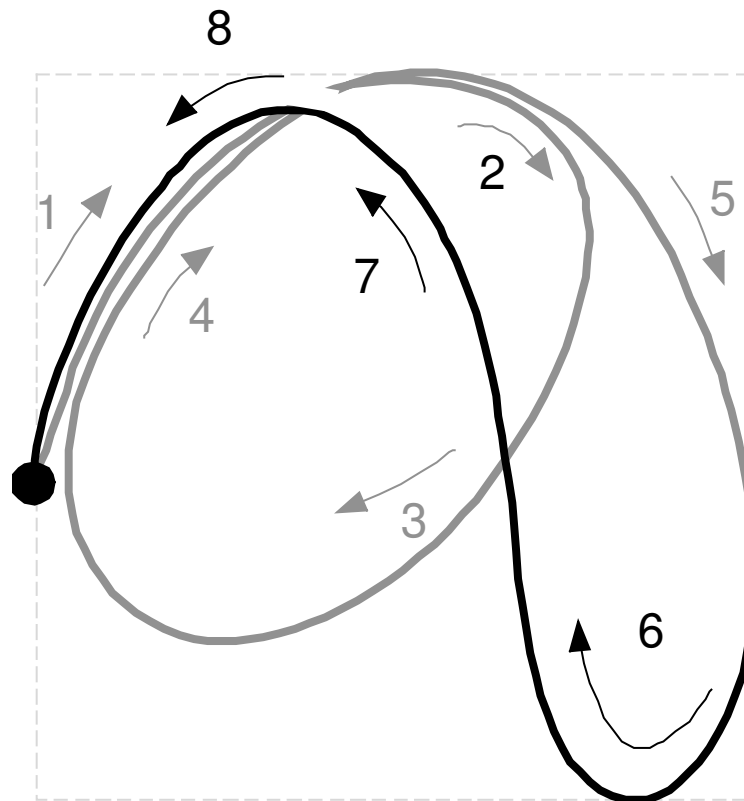


Figure 4. Template of Figure Drawing. Numbers and arrows indicate the course of the movement. For easier learning, the trajectory was introduced subsequently in two segments (grey: first segment, black: second segment. Total size of the figure was 10 x 10 cm².

2.2.2 Experimental Design

Prior to the EEG-measurement subjects of the experimental group practised figure drawing with either their right or left hands. The figure had to be performed within a frame of 10 cm x 10 cm in size. The starting point of the movement was indicated by a small circle. Initially, the required drawing was demonstrated to the subjects. In order to facilitate the learning of the complex figure, the two segments of the figure were presented separately, one after the other (Figure 4). Subjects were instructed to redraw each of the segments 5 times. Thereafter, subjects had to reproduce the whole figure. Each trial consisted of a movement execution phase of three seconds duration where subjects had to perform the whole figure without interruption (corresponding to a velocity of about 20 cm/sec). Figure performance was paced by a metronome (1 bps) and a voice informing subjects about onset and requested end of task execution. No synchronisation of individual figure elements with metronome beats was

requested. Each trial was followed by a resting interval of about 5 seconds. The training phase comprised 5 blocks of 10 trials each with a pause of half a minute between blocks.

After training, EEG-activity was recorded in the experimental group while subjects reproduced the acquired movement under different conditions. During the first task (Learned-task) subjects reproduced the previously trained figure with the right hand. In the second and third tasks which were performed during subsequent blocks, subjects were asked to redraw the learned figure with the left hand in normal (Normal-task) and mirror orientations (Mirror-task), respectively. Pacing was the same as under the training phase. However, unlike the training phase, subjects had to perform the movement trajectories without a given frame. They were asked to draw figures at approximately the same size as they had done during the training phase. To avoid blinking, subjects were instructed to gaze at a cross in front of the writing pad. The control group had to perform the same tasks as the experimental group, however without any right-previous contralateral hand training. Control subjects were requested to perform only one block of each movement condition. The sequence of conditions, first Mirror-task and subsequently Normal-task or vice versa was balanced across subjects.

EEG was recorded in the experimental group during the Learned-task in 10 blocks of 5 trials each. In the following blocks subjects had to draw the figure in normal and mirror fashion with their untrained left hands. These intermanual transfer phases consisted of 10 blocks for each transfer task resulting in a total of 20 blocks of 5 trials each. To reduce systematic effects of time on motor performance, e.g. learning effects and changes in attention, subjects were requested to perform the Normal-task and the Mirror-task in alternating blocks. Therefore, after completion of each block, subjects were instructed to change the orientation of the movement.

2.2.3 EEG-Recording

During reproduction and transfer phase, EEG was recorded using Ag/AgCl electrodes placed on the skull at nine scalp positions (F3, C3, P3, Fz, Cz, Pz, F4, C4 and P4) according to the 10-20 system (Jasper, 1958). Electrically linked earlobes were used as reference. The ground electrode was placed on the forehead. Electrode impedances were kept below 7 k Ω . To record the electro-oculogram, additional Ag/AgCl electrodes were placed supra- and suborbitally to the right eye and 2 cm external to the outer canthus of each eye. One bipolar EMG channel was recorded from surface electrodes located at the distal tendon and the belly (15 cm apart)

of the biceps of the arm used for the execution of the actually requested motor task. A programmable DC coupled SynAmps amplifier (NeuroScan 4.0; gain 2,500) was used to record EEG continuously in DC-mode. Sampling rate was set to 500 Hz with a lowpass filter of 80 Hz.

3 Data Analysis

3.1 Behavioural Parameters

Since training effects during task performance have to be considered, the analysis of motor performance was done for the last of the 10 blocks for the Learned-task and for the first block of each transfer task. In order to quantify changes in figure size and form for the different tasks, a rectangular frame that was vertically and horizontally adjusted to the figure of each trial was determined. Figure size was determined by the product of width and height and related to the ideal figure size of 100 cm². Figure form was defined as ratio of height to width. Of these 'size and form coefficients', a value close to 1 indicated no change in the layout of the trajectory, whereas changes are reflected by values different from 1.

Considering that a decrease of inter-trial variance of drawings results in an increased overlap, variability of figure drawings across trials was assessed by estimating the area covered by the drawing lines within a selected block. Consequently, low variability would result in a smaller area than high variability. In a first step of the analysis, line thickness of figures of each block was set to 1 cm. Then, figures were adjusted to the size of the ideal figure that had been presented to the subjects. Adjustment was done by magnification or reduction in vertical and horizontal dimension. Then, figures of different trials within one block were overlaid and the pixel area which was covered by the lines was determined and related to the area which was associated with the ideal figure.

In order to assess transfer, performance of the same task (either the Normal-task and the Mirror-task) *after* opposite hand *training* (in the experimental group) were compared with those of subjects who did *not* undergo a previous *training* phase (i.e. subjects of the control group). If transfer of previously acquired capabilities occurs, task performance of the untrained hand – that is used during transfer (during the control of the Normal-task and Mirror-task) – will be significantly different after as compared with action performance without opposite hand training. In case of absent transfer effects, performance of the transfer tasks will not reveal any significant differences between the experimental and the control group.

3.2 Neurophysiological Parameters

Ocular artefacts were marked by visual inspection and corresponding trials were discarded from further analysis. A minimum of 30 trials was requested for each task and each subject. In order to detect the onset of figure drawing EMG-bursts were marked by visual inspection of highpass filtered EMG (30 Hz). The onset was defined by the time point where the EMG-activity reached 30 % of the maximal amplitude for the first time. Although this method has only limited accuracy in defining movement onset, it was regarded sufficient for the study of movement preparation processes like early and late Bereitschaftspotential that revealed time constants of more than 300 ms. Additionally, the actual duration of task performance within the given three seconds interval was determined by analysing EMG-activity.

For EEG analysis, the average reference was calculated. EEG-data were analysed using three approaches, i.e. movement-related cortical potentials, power and coherence analyses.

3.2.1 Movement-Related Potentials

To study movement-evoked potentials, epochs of 100 ms duration were defined ranging from 1200 ms before to 3800 ms after onset of the EMG-burst. Baseline correction was done by subtracting the mean amplitude of the time interval from -1200 ms to -800 ms. For each condition, single sweeps were averaged across trials. Subsequently, data were bandpass filtered between 0.5 Hz to 5 Hz. Since pre-movement negativity emerges within 200 to 500 ms prior movement onset, filtering between 0.5 and 5 Hz was optimal to depict changes in EEG-potential. The course of activity was characterised by calculating the mean activity of 100 ms time intervals. For the pre-movement period 8 values were obtained per subject, condition and electrode.

3.2.2 EEG- Power

For the analysis of task-related power, EEG-signals were digitally bandpass filtered off-line (1-50 Hz, slope 24 dB/octave) and segmented into five non-overlapping epochs of 1024 ms duration. Thus, frequency resolution was 0.977 Hz. The first epoch corresponded to the period 4024 ms to 3000 ms prior movement onset and was chosen as resting condition, the second epoch corresponded to the pre-motor phase, namely from 1024 ms to movement onset. The further three epochs were related to the movement execution phase. For each electrode and each trial, power spectral densities were computed using the fast Fourier transform algorithm. To reduce the effects of inter-subject and inter-electrode variations in absolute spectral power, task-related power at an electrode i was calculated by subtracting the absolute

power during the resting interval $Power_{rest_i}$ from the power of the activation condition ($Power_{activation_i}$) according to the equation: $Power_i = Power_{activation_i} - Power_{rest_i}$. Therefore, power increases are expressed as positive values, power decreases reflecting cerebral activation are expressed as negative values (Leocani et al., 1997; Manganotti et al. 1998). Broad-band power changes for the theta- (4-8 Hz), alpha (9-12 Hz) and beta-(18-22 Hz) frequency bands were obtained by averaging the power of the respective frequency bins.

3.2.3 EEG-Coherence

Because parieto-frontal connections are known to be critical in coordinate transformation, electrode pairs of interest were determined as pairs including parietal and frontal electrodes. Coherence was calculated for electrode pairs F3-F4, F3-P3, F3-P4, F4-P3, F4-P4 and P3-P4 according to the following equation, implemented in commercial software (Vision Analyzer, BrainVision, Munich, Germany).

$$Co(\lambda) = \frac{\left| \sum_k f_{ik}(\lambda) f_{jk}^*(\lambda) \right|^2}{\sum_k |f_{ik}(\lambda)|^2 \sum_k |f_{jk}(\lambda)|^2}$$

where $f_{ik}(\lambda)$ and $f_{jk}(\lambda)$ are the complex spectra of the EEG activity for frequency λ at electrode i and j and for trial k . f_{jk}^* denotes the complex conjugate of f_{jk} . Intervals were of 1024 ms duration corresponding to 512 sampling points. Time segments were windowed by a Hamming window. To reduce the effect of inter-subject variability and variations between electrode pairs of absolute coherence, task-related coherence (Coh_{ij}) was obtained by subtracting the coherence during rest ($Coh_{rest_{ij}}$) from the activation condition ($Coh_{activation_{ij}}$): $Coh_{ij} = Coh_{activation_{ij}} - Coh_{rest_{ij}}$.

Therefore, increments in coherence were expressed as positive and decrements as negative coherence values. Broad-band analyses were performed for theta- (4-8Hz), alpha- (9-12Hz) and beta-bands (18-22Hz) by averaging coherences of corresponding frequency bins.

3.3 Statistics

To test the statistical significance of task differences, ANOVAs including the repeated measurement factor TASK with levels “Normal-task”, “Mirror-task“ and “Learned-task” were applied (SuperANOVA, Abacus Concepts, Berkley USA). In order to assess differences in topography of motor related potentials, power and coherence an additional factor either ELECTRODES or ELECTRODE PAIRS was introduced. Finally, comparing behavioural effects of movement performance between the experimental group and the control group a factor GROUP was introduced. In case of more than two levels of within factors the Huyn-Feldt correction for violations of the sphericity assumption of variances was applied. Statistical significance level was set to $\alpha = 0.05$. To characterise the results in more detail, post-hoc analyses were done in two steps. First, means of Normal-task and Mirror-task were compared to identify effects of coordinate processing. Second, to distinguish between processes of modification and recall, both Normal-task and Mirror-task were compared to the Learned-task in separate analyses.

4 Results

4.1 Right-to-left Hand Transfer

4.1.1 Behavioural Data

To assess effects of right-handed training on motor performance, figure drawings of the experimental group were compared to that of a control group that had experienced no training. For the statistical analysis a two-factorial design was calculated, using the factors GROUP (control versus experimental group) and figure SIZE (ideal size versus reproduced figure size). In additional analysis figure FORM (ideal form versus reproduced form in the right-handed task) and inter-trial VARIABILITY (area covered by the ideal figure versus area covered by the right-handed task) was examined. For figure size, no differences between groups could be found (figure 5A). Concerning figure FORM, the analysis yielded a significant GROUP x FORM interaction [$p = 0.001$; $F(1, 16) = 14.8$]. Post-hoc ANOVA of repeated measures revealed that drawing of figure size of the untrained control group differed highly significantly from the ideal value of 1.0 [$p < 0.0001$; $F(1, 8) = 50.9$]. By contrast, figure performance of the experimental group did not significantly differ from the ideal form (figure 5B).

Concerning inter-trial variability in the drawing performance, a highly significant interaction of VARIABILITY x GROUP indicated that the experimental and the control group deviated differently from a perfect figure copying that is indicated by a value of 1.0 [$p < 0.001$; $F(1,16) = 721$]. The untrained control group revealed a larger variability [$p < 0.001$; $F(1, 16) = 416$] as compared to the experimental group [$p < 0.001$; $F(1,16) = 160$; see figure 5C].

To estimate whether acquired motor skill with the right hand is used during the transfer tasks, additional analyses comparing motor performance between the transfer tasks were performed. Figure form and variability differed highly significantly between the experimental and the control group [$p = 0.005$; $F(1, 16) = 10.6$ and $p = 0.0001$; $F(1, 16) = 38.28$, for form and variability, respectively]. For both parameters, no significant GROUP x TASK interactions were found which would have been expected if training only affected the Learned-task in the experimental group but not the tasks of intermanual transfer.

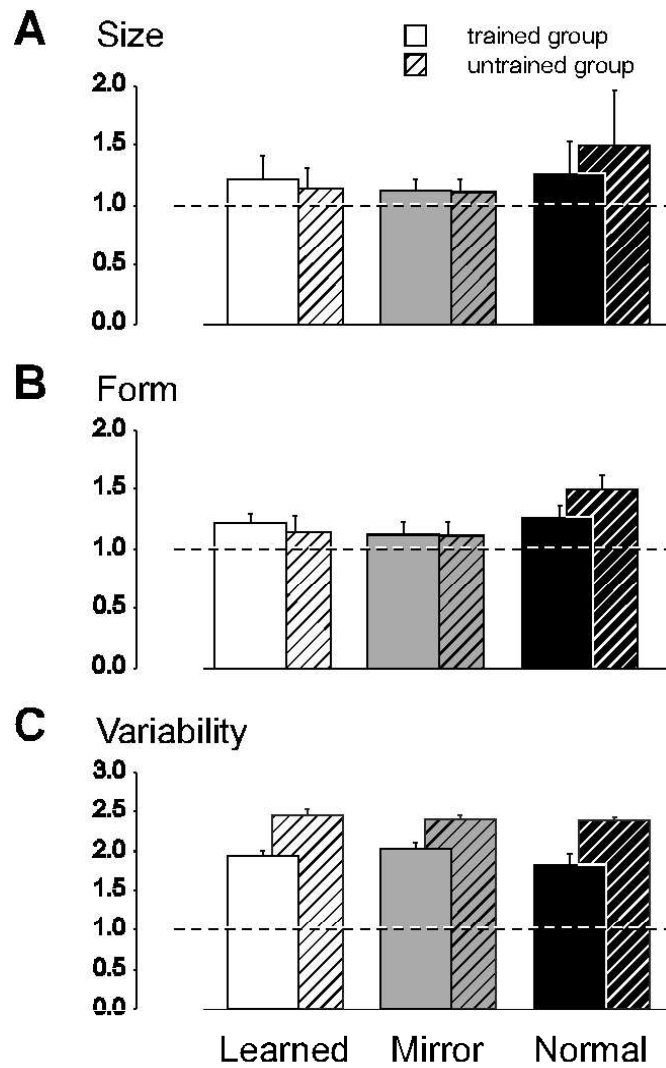


Figure 5. Behavioural Performance of the Right-to-Left Hand Transfer. Behavioural measures were taken from 5 selected subsequent trials (see Experimental Procedures). Bars indicate group means and mean standard error. The ideal values of 1.0 (dashed line) represents ideal figure performance (see Data analysis).

A. Figure size as estimated by width x height.

B. Distortion of performed figure form with reference to the ideal figure. Figure form was calculated as ratio of height to width. Positive values indicate a horizontal, negative values a vertical squeezing.

C. Inter-trial variability of figure drawing. The pixel area which was covered by the figures drawn was determined and related to the area covered by the ideal figure. Prior to the overlay, figures were adjusted in height and width to the size of the ideal figure.

4.1.2 Neurophysiological Data

4.1.2.1 Movement-Related Potentials

As observed in figure 6A, cerebral responses revealed a steadily developing negativity for the Normal-task preceding the movement-onset at about 400 ms. In the Mirror-task and Learned-task, by contrast, no such negative wave was apparent. Moreover, the Mirror-task revealed even a pre-movement positivity, particularly at the left frontal electrode (F3). ANOVA analysing effects of tasks and topography on the amplitude of the motor potential showed a significant ELECTRODE x TASK-interaction for the interval ranging from -300 ms to -200 ms [$p = 0.04$; $\epsilon = 0.29$; $F(16, 128) = 2.67$] and for the interval from -200 ms to -100 ms [$p = 0.050$; $\epsilon = 0.29$; $F(16, 128) = 2.39$]. Post-hoc analyses for the first interval revealed that amplitudes of the Normal-task differed from Mirror-task at frontal (F3, Fz and F4) and left and mid-central (C3 and Cz) electrodes (see figure 6B). This effect was highly significant for all frontal electrodes, however, more pronounced at left-frontal [F3: $p = 0.0002$; $F(1, 16) = 43.39$] and midline electrodes [Fz: $p = 0.002$; $F(1, 16) = 25.04$] as compared to the right frontal electrode [F4: $p = 0.009$; $F(1, 16) = 14.67$]. For central electrodes, negativity was larger for the Normal-task as compared to the Mirror-task over the left hemisphere [C3: $p = 0.02$; $F(1, 16) = 8.88$] and at the midline [Cz: $p = 0.04$; $F(1, 16) = 6.91$]. The comparison between the Normal-task and the Learned-task revealed a stronger negativity for the Normal-task at mid-frontal [Fz: $p = 0.0009$; $F(1, 16) = 30.01$] and latero-frontal electrodes [F3: $p = 0.004$; $F(1, 16) = 20.73$ and F4: $p = 0.003$; $F(1, 16) = 21.08$] and also at the left central and midline electrodes [C3: $p = 0.01$; $F(1, 16) = 12.59$; Cz: $p = 0.007$; $F(1, 16) = 16.11$]. No significant differences were found between amplitudes of the Mirror-task and the Learned-task. The positive deflection seen in the Mirror-task did not differ significantly from the Learned-task ($p = 0.07$).

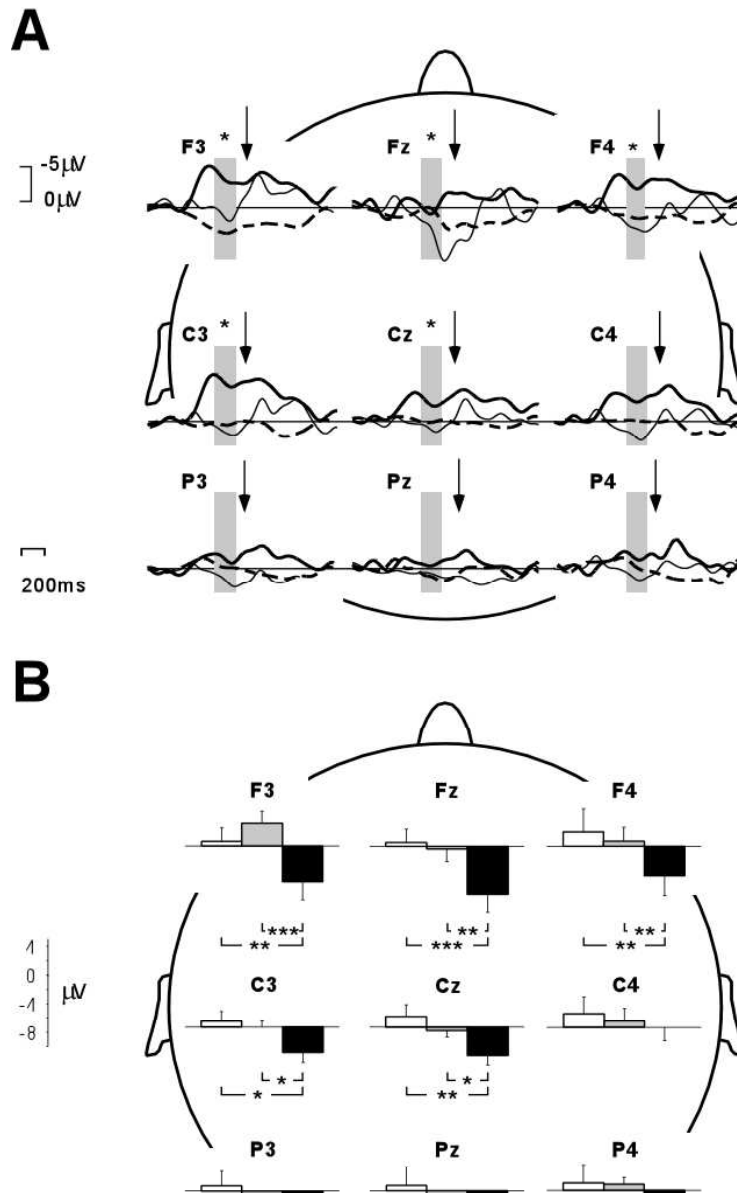


Figure 6. Movement-Related Potentials.

A. Grand-average slopes for the interval ranging from 800ms prior to 1200ms after movement onset (movement onset is indicated by the *vertical arrow*) are shown for the Learned-task (*thin line*), the Mirror-task (*dashed line*) and the Normal-task (*thick line*). Significant task effects observed in the interval from -300 ms to -100 ms before movement initiation (grey hatched area) are marked by asterisks.

B. Mean amplitude and standard error of the movement-related potentials for the Learned-task (white), the Mirror-task (grey) and the Normal-task (black) in the time interval between -300 ms to -200 ms before movement onset. Asterisks indicate the level of significance of differences between tasks. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

4.1.2.2 EEG-Power

Significant differences of EEG-power between tasks were found only in the beta-band (18-22 Hz) for the interval prior to movement onset [$p = 0.0008$, $\epsilon = 0.6$; $F(2, 16) = 21.4$]. Contrast analysis revealed that beta-power in the Normal-task was lower as compared to the Mirror-task [$p = 0.002$; $F(1, 16) = 24.76$] and as compared to the Learned-task [$p = 0.0004$; $F(1, 16) = 38.04$]. Additionally, a significant TASK x ELECTRODE-interaction for beta-power [$p = 0.0001$; $\epsilon = 0.17$; $F(16, 128) = 12.97$] was found. Post-hoc analyses indicated that beta power in the Normal-task was significantly lower as compared to the Learned-task at parietal, right central and latero-frontal electrodes [$p < 0.001$, $F(1, 64) > 55$; for all these electrodes; see figure 7). Furthermore, the beta-power in the Normal-task differed significantly from that in the Mirror-task at right central and at latero-frontal sites [$p < 0.001$; $F(1, 64) > 55$]. The comparison of beta-power between the Normal-task and the Learned-task revealed significant differences at the same sites [$p < 0.0001$; $F(1, 64) > 58$].

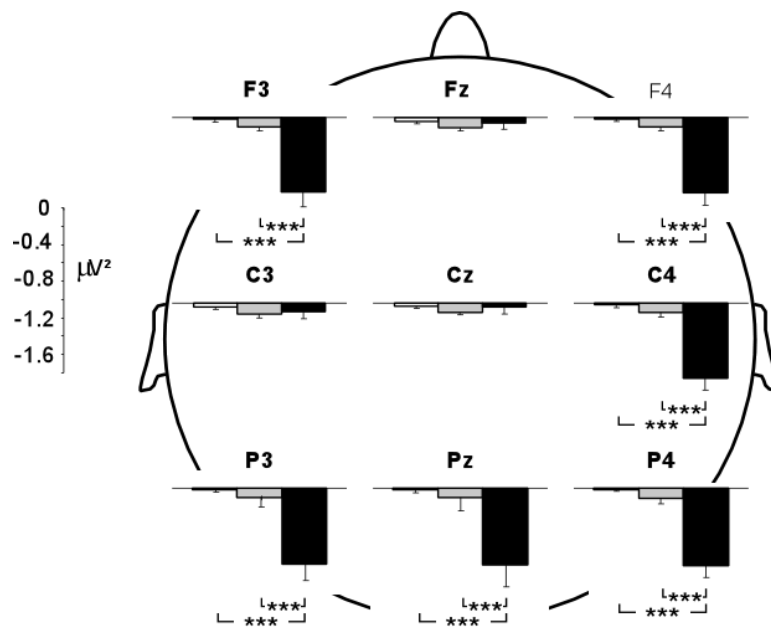


Figure 7. EEG-Power. Average changes in power in the pre-movement period (-1024 ms to 0 ms) in the beta-range (18 - 22 Hz) with respect to the baseline interval (-4024 ms to -3000 ms). Error bars indicate standard errors. EEG power is shown for the Learned-task (white), the Mirror-task (grey) and the Normal-task (black) at the 9 electrode positions defined by 10/20 system. Asterisks indicate the level of significance of differences between tasks. *** = $p < 0.0001$.

4.1.2.3 EEG-Coherence

Alpha-band (8-12Hz)

The ANOVA of inter-electrode coherence showed a general TASK effect for the period prior to movement onset for the alpha-band [$p = 0.047$; $\epsilon = 0.80$; $F(2, 16) = 4.16$, see figure 6A]. Post-hoc analysis revealed a strongly decreased coherence associated with the Normal-task as compared to the Mirror-task [$p = 0.02$; $F(1, 16) = 4.16$]. Additionally, there was a significant ELECTRODE PAIR x TASK effect [$p = 0.04$; $\epsilon = 0.80$; $F(10, 80) = 2.19$]. Contrast analysis showed that the coherence in the Normal-task as compared to the Learned-task decreased significantly for all electrode pairs [$p < 0.01$; $F(1, 80) > 5.9$]. A significant increase of coherence was found for the Mirror-task as compared to the Learned-task for all fronto-parietal electrode-pairs except F4-P4 [$p < 0.05$; $F(1, 80) > 4.1$, see figure 8A].

Beta-band (18-22 Hz)

A significant TASK effect was found for the pre-movement period [$p = 0.03$; $\epsilon = 0.98$; $F(2, 16) = 8.7$]. Coherence in the Normal-task was generally lower as compared to the Mirror-task [$p = 0.001$; $F(1, 16) = 15.97$] and to the Learned-task [$p = 0.008$, $F(1, 16) = 9.35$]. Furthermore, the ANOVA showed a significant ELECTRODE PAIR x TASK effect [$p = 0.004$; $\epsilon = 0.82$; $F(1, 80) = 3.17$]. Coherences in the Mirror-task were significantly higher as compared to the Learned-task for F3-P3 [$p = 0.003$; $F(1, 80) = 10.7$], F3-P4 [$p = 0.006$; $F(1, 80) = 9.1$] and F4-P3 [$p = 0.007$; $F(1, 80) = 8.5$] (see figure 8B).

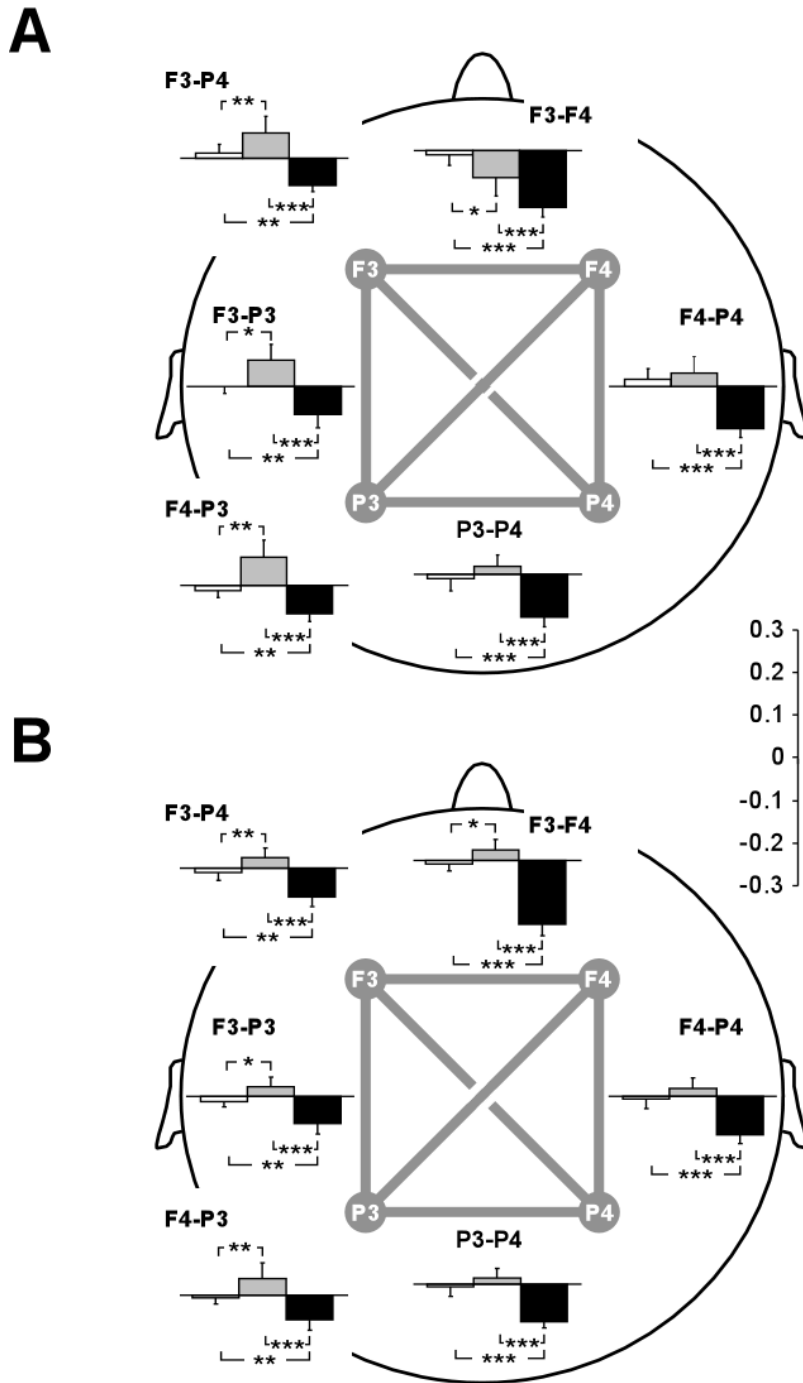


Figure 8. EEG-Coherence of the Right-to-Left Hand Transfer. Coherence in the pre-movement period (-1024 ms to 0 ms) between frontal and parietal electrode sites in the alpha- (8 - 12 Hz) (A) and beta-band (18-22 Hz)(B) for the Learned-task (white), the Mirror-task (grey) and the Normal-task (black). Bars indicate group means and standard errors for the different conditions. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

4.2 Left-to-Right Hand Transfer

4.2.1 Behavioural Data

ANOVA of repeated measurements revealed a significant TASK effect for both figure size [$p = 0.001$; $\epsilon = 0.88$; $F(2, 14) = 12.7$] and inter-trial variance [$p = 0.47$; $\epsilon = 0.58$; $F(2, 14) = 5.03$]. Neither for figure size nor for inter-trial variance, significant differences were observed between Normal-task and Mirror-task. Concerning the figure form, the analysis showed a significant GROUP x FORM interaction [$p = 0.05$; $F(1, 14) = 4.3$] Post-hoc ANOVA of repeated measures revealed that figure form of the untrained control group differed highly significantly from the ideal value of 1 [$p < 0.0001$; $F(1, 7) = 13.9$]. By contrast, figure performance of the experimental group did not significantly differ from the ideal form (figure 9A).

Concerning the figure size, the analysis showed a significant GROUP x SIZE interaction [$p = 0.02$; $F(1, 14) = 6.1$]. Post-hoc ANOVA of repeated measures revealed that figure size of the trained control group decreased highly significantly from the ideal value of 1 during the Mirror-task [$p = 0.01$; $F(1, 7) = 11.6$] (figure size of trained group: mean 0.7; SE = 0.06 versus value of 1 of ideal size) and differed also significantly from figure size of the Learned-task (mean: 1.01, SE = 0.06) [$p = 0.01$; $F(1, 7) = 10.7$]. By contrast, figure form of the *control* group did not significantly differ from the ideal form in any task (figure 9B).

Concerning inter-trial variability, a highly significant interaction of VARIABILITY x GROUP indicated that the experimental and the control group deviated differently from a perfect figure copying that is indicated by a value of one [$p = 0.04$; $F(1, 14) = 5.0$]. The untrained control group revealed a larger variability [$p < 0.001$; $F(1, 14) = 403$] as compared to the experimental group [$p < 0.001$; $F(1, 14) = 115$; see figure 9C].

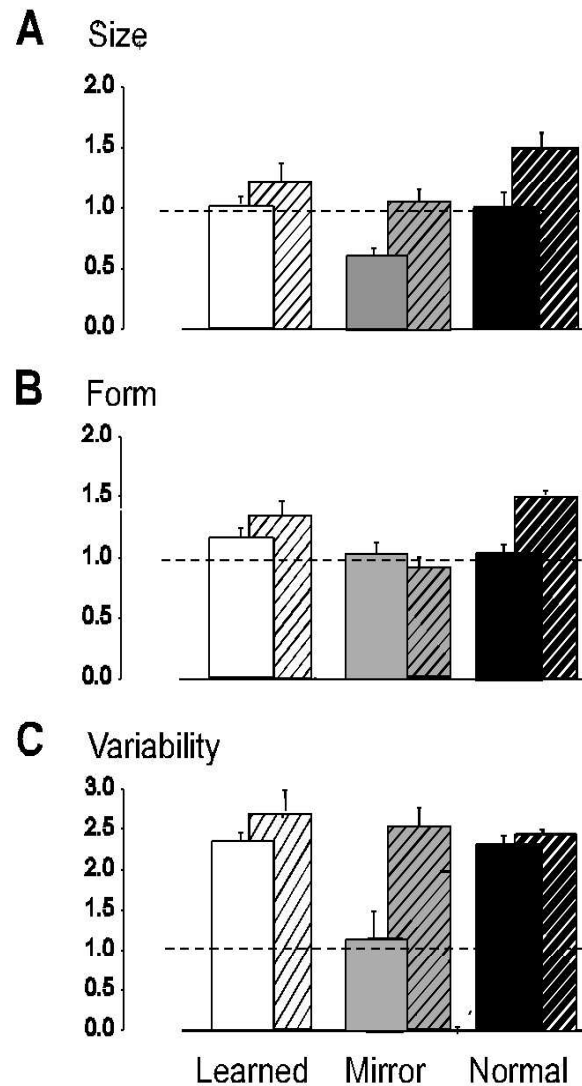


Figure 9. Behavioural Performance of the Left-to-Right Hand Transfer. Behavioural measures were taken from 5 selected subsequent trials (see Experimental Procedures). Bars indicate group means and mean standard error. The ideal values of 1.0 (dashed line) represents ideal figure performance (see Data analysis).

A. Figure size as estimated by width x height.

B. Distortion of performed figure form with reference to the ideal figure. Figure form was calculated as ratio of height to width. Positive values indicate a horizontal, negative values a vertical squeezing.

C. Inter-trial variability of figure drawing. The pixel area which was covered by the figures drawn was determined and related to the area covered by the ideal figure. Prior to the overlay, figures were adjusted in height and width to the size of the ideal figure.

4.2.2 Neurophysiological Data

EEG-values did not reveal any significant differences between tasks in movement-related potentials, power and alpha-coherence.

EEG-Coherence

Beta-band (18-22Hz)

A general TASK effect for the period 1000ms to 1200ms after movement onset [$p = 0.017$, $\epsilon = 0.57$; $F(2, 14) = 5.5$]. Beta-coherence in the Mirror-task increased significantly as compared to the Normal-task [$p = 0.001$; $F(1, 14) = 4.4$] as well as to the Learned-task [$p = 0.001$; $F(1, 14) = 3.9$]. Additionally, there was a significant ELECTRODE PAIR x TASK effect of inter-electrode coherence [$p = 0.001$; $\epsilon = 1.0$; $F(10, 70) = 4.57$]. The Mirror-task showed significant increases of coherence in comparison to the Normal-task as well as to the Learned-task in F4-P4 ($p = 0.001$; $F(1,70) = 20.7$), F4-P3 [$p = 0.001$; $F(1,70)$] and F3-P3 [$p = 0.0001$; $F(1,70) = 17.7$]. Additionally, highly significant increases were determined for the electrode pairs between frontal sites of the right and left side (F3-F4)[$p = 0.001$, $F(1,70) = 106.7$] and parietal sites [$p=0.001$; $F(1,70)=34.1$] (see figure 10).

ANOVA of repeated measures revealed also a significant ELECTRODE PAIR x BASELINE effect [$p = 0.001$; $\epsilon = 0.9$; $F(15,105) = 3.9$]. Post-hoc one sample t-test showed that coherence increased significantly compared to the baseline in the Learned-task in parieto-frontal pairs of the right site (F4-P4) [$t = 2.64$; $p = 0.03$], between left frontal and right parietal site (F3-P4) [$t = 2.68$; $p = 0.03$], and reached significance for the left-sided parieto-frontal electrode pair [$t = 2.15$; $p = 0.06$].

For parieto-frontal electrode pairs, significant increases of beta-coherence were observed in the Mirror-task in electrode pairs between parieto-frontal sites of the right hemisphere (F4-P4) [$t = 2.24$; $p = 0.01$] and between left and right parietal sites (P3-P4) [$t = 2.72$; $p = 0.03$]. Beta-coherence values associated with the Normal-task did not differ from baseline.

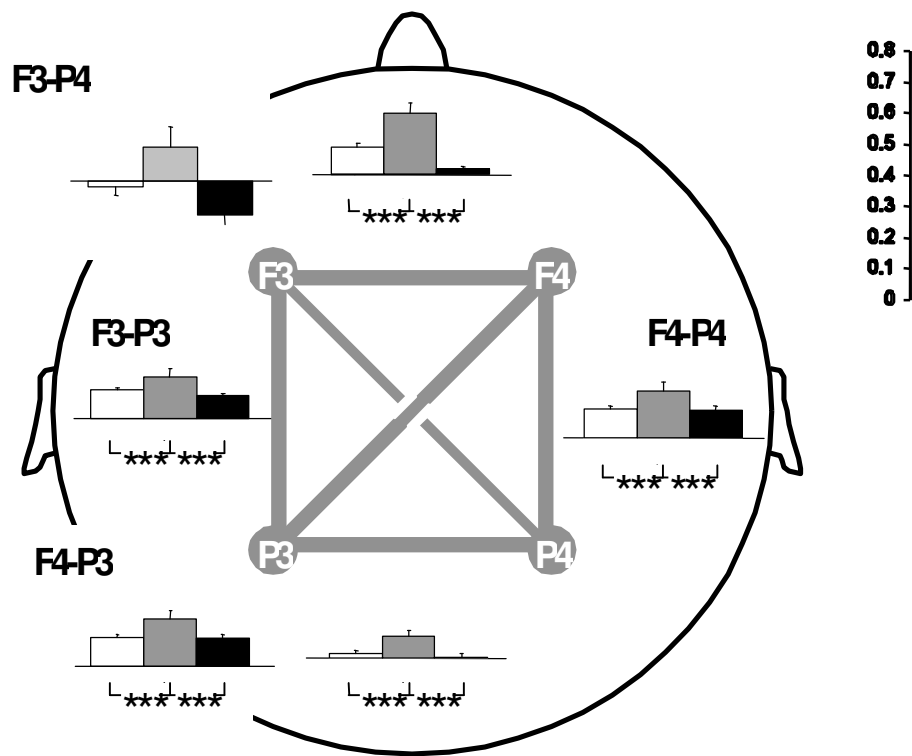


Figure 10. Beta-Coherence of the Left-to-Right Hand Transfer. Coherence in the interval ranging from 1024 ms to 2048 ms after movement onset between frontal and parietal electrode sites for the Learned-task (white), the Mirror-task (grey) and the Normal-task (black). Bars indicate group means and standard errors for the different conditions. *** = $p < 0.001$.

5 Discussion

5.1 Remarks on Data Interpretation

To investigate the reference frame that is used for intermanual transfer, the neural activity in Mirror-task and Normal-task was compared with each other and with the Learned-task. The use of extrinsic coordinates during intermanual transfer is assumed to be reflected in similar EEG-data during Learned-task and Normal-task, but not during Learned-task and Mirror-task. The coding by intrinsic coordinates during intermanual transfer is assumed to be paralleled in EEG-patterns which reveal similar results in Learned-task and Mirror-task, but not in Learned-task and Normal-task.

Moreover, it is assumed that the processing of acquired coordinates during intermanual transfer concerns not only on the recall of acquired coordinates in their original unchanged form, but also processes of coordinate modification. These processes of coordinate modification are attributed to be reflected in observed changes between transfer task and Learned-task.

To interpreted patterns of EEG activity and coherence as processes of recall and modification of coordinates, one must be sure that changes in EEG-data between Learned-task and transfer tasks do not result from general differences due to the processing of right and left hand actions. One such unspecific effect is for example the more bilateral representation of left-hand than of right-hand movements (Kim et al., 1993; for review: see Haaland and Harrington, 1996). To exclude such unspecific effects not related to the modification of coordinates only significant differences of EEG-patterns between the Normal-task and the Mirror-task were considered. Differences between the Normal-task and the Mirror-task unambiguously reflect task-specific modes of coordinate processing. In a subsequent step, more detailed information about processes involved in coordinate processing is obtained if brain responses of transfer tasks are compared to the Learned-task during which the movement trajectory was reproduced in original orientation using the right hand. While similar EEG-data during one of both transfer tasks and the Learned-task are assumed to reflect the retrieval of unchanged coordinates, differences in EEG patterns between a transfer task and the Learned-task may correlate with different modes of coordinate processing during transfer tasks as compared to the Learned-task. Such different processes might involve modification of previously stored coordinates, or alternatively the acquisition and encoding of novel movement representations.

To verify whether specific EEG-data that are associated with the Normal-task and Mirror-task reflect the processing of acquired coordinates, one must consider behavioural data.

In case of a de novo acquisition of coordinates during transfer motor control would be like a novel learned task. In this case, opposite hand training would not affect performance of the transfer tasks. Behavioural data showed that right-handed as well as left-handed training influenced the performance during both the Mirror-task and the Normal-task: control subjects not having experienced a training of the figure drawing did perform worse in the transfer tasks as compared to the experimental group. This finding indicates that subjects of the experimental group must have had access to visuomotor information which had been acquired during training of the figure drawing. Thus EEG-patterns of the Mirror-task and the Normal-task that diverge from the Learned-task reflect processing of already *established* coordinates.

5.2 Right-to-Left-Hand Transfer

5.2.1 Task Performance

As compared to the control group, subjects who underwent right-hand training revealed better accuracy of figure performance a smaller inter-trial variance and a higher accuracy with respect to the ideal figure during the Learned-task as well as during both transfer tasks. Thus, it is evident that the untrained left hand profits from motor skill that has been acquired with the opposite right hand. The pronounced effect (better performance) of right-handed training with respect to inter-trial variability suggests that during intermanual transfer, acquired motor commands are accessed.

5.2.2 Interpretation of Neurophysiological Data

5.2.2.1 Reference Frame used during Intermanual Transfer

EEG results showed profound differences in amplitude, power, and coherence for the alpha and beta frequency bands between the Normal-task and the Learned-task. The Mirror-task, however, differed significantly from the Learned-task only in alpha- and beta- coherence between distinct brain sites. Extensive differences in EEG-parameters between the Normal-task and the Learned-task imply that additional computations are necessary during the Normal-task as compared to the Learned-task. Few differences in EEG-parameters between the Mirror-task and the Learned-task were taken as index that the access to acquired motor skill is quite similar for both tasks.

These results suggest that the processing of intrinsic coordinates is mainly recorded during transfer tasks. Similar EEG-patterns in the Mirror-task and the Learned-task reflect the recall of intrinsic representations which can be assessed in their unchanged form. During the Normal-task, by contrast, acquired intrinsic coordinates have to be modified and these processes are responsible for the differences in EEG-results between Normal-task and Learned-task.

Preferred storage and control of visuomotor tasks by use of intrinsic coordinates has also been shown by psychophysical research (Imamizu and Kawato, 1998; McIntyre et al., 1998; Malfait et al., 2002). In these studies reference frames used to store learned motor skills were concluded from subjects' behaviour. For instance, investigating intermanual transfer of hand displacements, Imamizu and Kawato (1998) reported better performance for a mirror than a normal transfer condition by the hand opposite to the trained hand, and interpreted the results as evidence for representations of the initial learned task in intrinsic coordinates.

In the present study, indication that right-handed skill is transferred by use of an intrinsic reference frame comes only from neurophysiological results, but not from behavioural data. Considering that the Mirror task is controlled predominantly by *unchanged*, the Normal-task by *modified* intrinsic information, one might expect greater transfer effects in the former than in the latter task because it is plausible that learned information in its unchanged form permits better motor control than in its modified form. Surprisingly, subjects exhibited a similar benefit for both the Mirror-task and the Normal-task. Hence, cerebral mechanisms of intrinsic coordinate modification are capable of managing the Normal-task successfully.

5.2.2.2 Period of Coordinate Processing

Having in mind the long duration of task execution of three seconds, it is an intriguing finding that task-specific effects during right-left hand transfer were observed only prior to movement onset. This observation indicates that the processing of intrinsic coordinates can be attributed to the planning of the ongoing movement.

Significant differences between tasks occur only in the late pre-motor period phase of movement preparation, namely –300 ms to –100 ms prior movement onset. Movement-evoked potentials in this period had been assumed to reflect the final stages of motor programming, the scaling of ‘control signal to excitatory impulse’ (Slobounov et al., 2000). Therefore, task-specific alterations of potentials indicate that coordinate modification affects the final right handed learned motor program.

Behavioural results are in accordance with this assumption. Learning-related changes were observed in figure size and form, but were prominent with regards to inter-trial variability. Since improvement of figure and form was rather low (relatively to the decrease of inter-trial variance), the changes of inter-trial variability might be interpreted as reflecting the availability of acquired motor information (i.e. stable patterns of outputs to the muscles. rather than as a consequence of acquired spatial knowledge).

5.2.2.3 Internal Representation of the Learned-Task

Neurophysiological data of each parameter obtained in the Learned-task did not differ from baseline in any parameter which was investigated. This is surprising in particular in movement-related potentials. The well-known pre-movement negativity, usually denoted as Bereitschaftspotential (Kornhuber and Deecke, 1965; Kristeva et al., 1990) was absent.

It is known that effects of practice of motor skill is paralleled by a decrease of negative amplitudes, presumably due to an automatic task performance (Taylor et al., 1978; Fetz et al., 1996). With respect to this finding, absent negativity of the Learned-task should be due to the number of repetitions before scanning which led to an almost automatic task reproduction and which demands only low cortical activity.

5.2.2.4 Coordinate Processing During the Normal-Task

Movement-Related Potentials

Movement-related potentials revealed task-specific differences in the period ranging from -300 ms to -100 ms prior movement onset. A negative potential starting about 500 ms prior to the onset of muscle contraction is known as Bereitschaftspotential (Kornhuber and Deecke, 1965; Kristeva et al., 1990) and is usually observed over the supplementary motor area (Neshige et al., 1988; Bötzel et al., 1993) and primary motor area contralateral to the intended action (Kristeva et al., 1990; Slobounov and Ray, 1998). With respect to these notes of research, present data of movement-related potentials reveal several striking findings.

First, the negativity observed in the Normal-task was lateralized at central and frontal electrodes to the left hemisphere, that is ipsilateral to the hand actually performing the movement. Furthermore, stronger frontal activation during performance of the Normal-task as compared to the Learned-task is apparently in conflict to reports of functional imaging studies showing the reverse, i. e. enhanced activity in frontal areas during a learned task and reduced activity in an untrained task (Grafton et al., 1992; Deiber et al., 1997; Seitz et al., 1997; Grafton et al., 2002). However, in these functional imaging studies, activation was associated with skill acquisition. Thus, stronger frontal activation during skill training as compared to an untrained task might be attributed to the formation of internal representation of the trained movements. The critical difference between these imaging studies and the present study is that in the actual experiment EEG-data of the tasks executed with the trained and untrained hand were measured after subjects had acquired the relevant motor skills, and therefore stored information is available for the control of both tasks. Consequently, compared to the Learned-task, increased negativity over SMA and left-frontal cortex during the Normal-task presumably reflects specific processing related to the access of acquired skills, namely the modification of learned intrinsic representations.

Following the view that negativity of the Normal-task reflects the modification of acquired intrinsic coordinates, it is concluded that fronto-central areas of the left hemisphere as well as

the supplementary motor area are critically involved in processes of modification of intrinsic coordinates. This interpretation gains support from clinical reports. Patients suffering from lesions in parieto-frontal areas of the left hemisphere and the supplementary motor area often fail to write in the correct orientation with their non-dominant left hand, while writing in mirror fashion with the left hand is still possible. It has been suggested that the impairment results from the disability of reversal of right-handed motor patterns (Chan and Ross, 1988; Rodriguez *et al.* 1989; Rodriguez, 1991; Buxbaum *et al.*, 1993).

EEG-Power

Further evidence for modification of intrinsic coordinates in the Normal-task comes from changes of EEG-power in the beta frequency band which was lower than during the Learned-task at multiple sites. Decrease of beta power is an indicator of cortical activation related to movement preparation and execution and has been attributed to processing of motor information (Manganotti *et al.*, 1998; Andres *et al.*, 1999).

Topography of beta-power changes differed considerably from changes in negativity in movement-related potentials, supporting the assumption that these events are generated independently from each other and represent different aspects of cortical activation (Toro *et al.*, 1993). In contrast to the pronounced left-sided fronto-central negativity of potentials, beta-power decreased at central as well as latero-frontal and parietal electrodes. Increases of negativity were observed in the interval ranging from -300 to -100 ms prior to movement onset. However, changes in power were found for the whole one second pre-movement period. Considering of notes of experimental research that movement planning begins in parietal areas (Graziano and Gross, 1998), the most obvious explanation for the different spatial distribution of beta-power and brain potentials is that changes of beta power in parietal areas might reflect early stages of movement planning while brain potentials in fronto-central premotor regions are associated with later processes of movement programming.

According to the results for movement-related potentials, significant increases of negativity were observed in the Normal-task only. However, whereas negative waves in cortical potentials were predominantly observed over frontal sites, EEG-power revealed increased activity prominently over the parietal cortex. A possible explanation for this observation arises from the notion that changes of potentials were observed shortly (300 ms) before movement onset, whereas EEG-power was associated with the pre-motor period beginning 1

sec prior to movement onset. Present results support that the early stages of movement planning begin in parietal areas (Gross and Graziano, 1998).

EEG-Coherence

Task-specific effects were also obtained for EEG-coherence in the alpha and beta band. EEG-coherence is a measure of inter-regional functional coupling (Rappelsberger et al., 1994; Andrew and Pfurtscheller, 1996; Classen et al., 1998). Increases in coherence between pairs of electrodes are regarded as intensified neural communication between cortical areas (Manganotti et al., 1998; Gerloff et al., 1998; Andres et al., 1999). Decreased coherence can be conceived as functional 'disconnection' (Singer, 1992; Bullock et al., 1995).

Coherence did not only differ between both transfer tasks, but also differed differentially from the Learned-task. The Normal-task revealed a decrease of coherence in comparison to the Learned-task. Taken that acquired intrinsic coordinates cannot be used in their original form for the control of the Normal-task, decreased coherence during this task can be conceived as neurophysiological correlate of suppressed interregional information flow relevant for intrinsic representation of movements.

Interestingly, the decrease of beta-coherence was not restricted to frontal and central electrodes that cover typical motor and pre-motor brain areas, but could also be observed at parietal sites. According to the present analysis, this finding suggests a contribution of parietal cortex to the transformation of intrinsic coordinates. This assumption fits the critical involvement of lateral premotor cortex and posterior parietal cortex in the storage of trajectories and in coordinate transformation. As shown by functional imaging, posterior parietal cortex as well as lateral premotor cortex are essential for the storage of trajectories (Shadmehr and Holcomb, 1996; Seitz et al., 1997; Sakai et al., 1998). Furthermore, the parietal cortex is well known to be concerned with the transformation of coordinates and recent data have shown that this transformation occurs also in the premotor cortex (Graziano and Gross 1998; Kurata and Hoshi, 2003). Thus, the transformation (modification) of motor patterns which are stored in lateral premotor cortex and parietal areas might be responsible for the decrease of power at latero-frontal and parietal electrodes.

Furthermore, it is notable that the increased activity of brain areas was accompanied with a suppression of network activity. This association provide evidence that an inhibition of cortical networks occurs even when these areas are strongly involved in task performance. Taking the strong benefit of right-handed training, the suppression of information flow within

neural circuits might be conceived as an efficient strategy in motor control during intermanual transfer.

5.2.2.5 Coordinate Processing During the Mirror-Task

Movement-Related Potentials

Similar to the Learned-task, negative amplitudes (Bereitschaftspotential) were absent in the Mirror-task – an observation which indicates that the recall of learned intrinsic information permits a similarly automated task performance as with the trained right hand.

The positive wave over left frontal cortex which was visible only in the Mirror-task calls for further explanations. Positive shifts of EEG amplitudes are known to reflect suppression of cortical activation (Shibasaki et al., 1980; Pfefferbaum et al., 1985; Natio and Matsumara, 1994 and 1996). Because acquired extrinsic coordinates are not appropriate to control the Mirror-task, the inhibited recall of learned extrinsic coordinate information might underlie the observed positivity .

EEG-Coherence

In contrast to the decrease of coherence in the Normal-task with respect to the Learned-task, coherence in the Mirror-task increased in parieto-frontal electrode pairs on the left hemisphere. Taking that the acquired extrinsic coordinates need to be transformed during the performance of the Mirror-task, increases of coherence in this task can be conceived as the neurophysiological correlate of the modification of extrinsic representations. This assumption is consistent with previous reported data in mental rotation tasks. Like in the Mirror-task, extrinsic coordinates of an observed figure have to be transformed during mental rotation. The coherence pattern between parietal and frontal sites (Silberstein et al., 1999; Rescher et al., 1999) as well as the left-hemispheric involvement reported for mental rotation tasks (Voyer, 1995; Milivojevic et al., 2003) agree with the left-sided increase of coherence in the Mirror-task and therefore support the conclusion that the modification of extrinsic coordinates induces activation of cortical connections, predominantly in the left hemisphere.

Values of alpha- and beta-coherence in electrode pairs of the right hemisphere did not differ between the Mirror-task and the Learned-task. This finding suggests that the processing of acquired coordinates in the right hemisphere is similar in these tasks. Since it is the recall of acquired intrinsic information which is in common in the Learned-task and the Mirror-task, the connections of the right hemisphere might be particularly involved in the retrieval of intrinsic representations.

5.2.2.5 Interhemispheric Communication

As indicated by results of movement-related potentials, the left hemisphere is critically involved in the preparation of the Normal-task. Given that this task is executed by the left hand, it seems logical that interhemispheric projections are activated in the Normal-task because left-hemispheric information must be transferred to the right hemisphere (which controls the contralateral left hand). Indeed, a negative wave over the central electrode of the left side observed in left-handed tasks indicates that the left hemisphere assists the movements of the left hand via ipsilateral pathways.

However, this assumption does not explain the finding that coherence in the Normal-task decreased as compared to the Learned-task. This paradox is explained best with the interpretation that observed interhemispheric information exchanges reflect the cortical mechanisms of coordinate processing. The modification of intrinsic information- as required in the Normal-task- induces decreases of network-like activity and this reduction of information flow concerns cortical connections not only between parietal and frontal sites, but also between hemispheres.

5.2.6 Neurophysiological Data Under the Aspect of Task Performance

Since it is evident that the planning of the Normal-task depends on the modification of acquired information, one may expect low transfer effects in the Normal-task. However, subjects profit from right-handed training for the Normal-task with respect to each movement feature. Therefore, the modification of intrinsic information in the left hemisphere permits adequate for the control of the Normal-task with the ipsilateral left hand.

Neurophysiological results provided evidence that the Mirror-task is controlled by original right-handed intrinsic information. This finding fits well with behavioural data that demonstrates a similar benefit of right-handed training for the performance of the Mirror-task and the Learned-task. Nevertheless, it is worth mentioning that the Mirror-task profits not only with respect to inter-trial variability, but also with respect to figure size and form from opposite hand training. This observation leads to the conclusion that the left hemisphere is capable to modify acquired extrinsic representations in order to control the Mirror-task with the left hand.

5.2.5 Conclusions of the Right-to-Left Hand Transfer

1. The transfer of visuomotor skill acquired with the right towards the left hand is associated with movement preparation and is coded mainly by use of intrinsic coordinates.
2. The role of the left hemisphere in the control of the Normal-task is due to the modification of acquired intrinsic representations. These processes induce increased activity of cortical areas and a decrease of information flow within intra- and interhemispheric connections.
3. The left hemisphere is also responsible for the modification of extrinsic coordinates in the Mirror-task. However, this process is regulated by increased activation of network activity.
4. The specific role of the right hemisphere in the control of the Mirror-task can be attributed to a right hemispheric specialisation in storage and recall of intrinsic information.
5. High transfer effects in both the Normal-task and the Mirror-task reflect efficient modifications of coordinates in the left hemisphere.

5.3 Left-to-Right Hand Transfer

5.3.1 Task Performance

Behavioural results demonstrate that left-handed training affected performance of the Normal-task and Mirror-task differently. An unambiguous profit of left-handed training was only observed in the Normal-task. Better task performance in each parameter was determined in subjects who underwent left-handed training as compared to subjects who performed the task without previous opposite hand training. In contrast, left-handed training improved performance of the Mirror-task only with regards to inter-trial variability.

The observation of a greater benefit from left-handed skill for the right-handed Normal-task than for the right-handed Mirror-task indicates that transfer occurs in extrinsic coordinates. Acquired extrinsic representations can be recalled in their unchanged form in the control of the Normal-task, whereas they have to be transformed in the Mirror-task.

It is an interesting finding that the effects of left-handed training for the Mirror-task were different for inter-trial variance and figure size. Contrasting to the positive effect in inter-trial variability, acquired left-handed visuomotor skill influenced accuracy of figure size in the Mirror task negatively. That is, subjects of the experimental group (who underwent left-handed training) drew the mirror figure in a significant smaller form as requested, whereas such a figure size reduction was not observed in the control group. The finding of a negative influence of left-handed training on transfer performance on the Mirror-task fits in with reports of Thut and co-workers (1996 and 1997). These authors investigated transfer of a similar drawing task and demonstrated that left-handed training induced a decrease of velocity in the performance of the right-handed mirror figure. In present study, however, it was the parameter of figure size which was negatively influenced from left-hand training. This observation might be interpreted as a failure in spatial processing, resulting from the required reversal of the internal image of the figure. Alternatively, the reduction of figure size might be interpreted in terms of Thut's reports. One must consider that each trial of figure performance was executed to pacing of a metronome. Hence, a decrease of figure size is equivalent with a decrease of velocity and the reduction of figure size might be conceived as an indirect effect of reduced speed.

5.3.2 Interpretation of Neurophysiological Data

5.3.2.1 Reference Frame Used During Intermanual Transfer

As compared to the Learned-task, a strong increase of beta-coherence was observed in the Mirror-task. The Normal-task, by contrary, did not reveal any significant differences from corresponding values of the Learned-task. These patterns of EEG-coherence suggest that mainly the processing of extrinsic coordinates were recorded during transfer tasks: Similar EEG-patterns in the Normal-task and the Learned-task reflect the recall of extrinsic representations which can be assessed in their unchanged form. During the Mirror-task, by contrast, acquired extrinsic coordinates have to be modified and these processes are reflected in increased values of coherence in the Mirror-task in comparison to the Learned-task. Thus, the interpretation of behavioural data that transfer occurs in extrinsic coordinates fits exactly with patterns of the neurophysiological results.

Taking that the beta-band reflects motor information processes (Leoconi et al., 1997; Manganotti et al., 1998; Andres et al., 1999), processing of extrinsic coordinates might be attributed to neural circuits which code learned information of the motor domain. This interpretation calls for further explanation because motor commands and the precise patterns of motor output to the muscles have to be encoded coded by intrinsic coordinates (which reflect the mirror-symmetry of the body). To understand the transfer in extrinsic representations, it is important to consider the period which is associated with transfer (as explained in the following).

5.3.2.2 Period of Coordinate Processing

Task-specific effects were associated with the period ranging from 1 to 2 seconds after movement onset. Hence, the processing of extrinsic coordinates is associated with control strategies of on-line monitoring, such as feedback processing, detection and corrections of errors. The coding of motor processes in an extrinsic reference frame might be attributed to higher level movement parameters, such as the coding of the distance and direction of the movements (Buneo et al., 2000).

The use of eye-centred, i.e. so-called extrinsic coordinates during an actually executed task has been well documented by experimental research (Carozzo et al., 1996; McIntyre et al., 1997). Results of these studies strongly suggested that it is the *actually* perceived target that is encoded by extrinsic coordinates. In the present study, however, extrinsic processing were determined during intermanual transfer and it must be stressed out that these processes reflect

coordinates *acquired* by the opposite hand. In other words, extrinsic coordinates can be attributed to the *stored* extrinsic representations.

5.3.2.3 Internal Representation of the Learned-Task

In the period ranging from 1 to 2 sec after movement onset, beta-coherence in the Learned-task increased significantly versus baseline. Thereby, coherence increased significantly between parietal and frontal sites of the right hemisphere as well as in parieto-frontal pairs that connected right and left hemispheres. Further, the increase of coherence between left-sided parietal and frontal sites reached significance.

Increases of beta-coherence in the left-handed Learned-task indicates that information exchanges via distinct motor connections are critical in the storage of left-handed visuomotor skill. Present data indicates that connections predominantly of the right hemisphere are activated. However, the increases between hemispheres lead to the assumption that the left hemisphere is also involved in the repetition of this left-handed task.

A critical role of the left hemisphere in the control of the left hand has been well demonstrated in experimental and clinical studies. Using PET (positron emission tomography), acquisition of visuomotor skill by the left hand has been shown to be paralleled by increases of activation in frontal and parietal areas of the left hemisphere (Frustiger et al, 2000; Grafton et al., 2002). Furthermore, Halsband and Freund (1990) demonstrated that patients with lesions in the left frontal cortex were impaired in visuomotor association learning regardless of the hand used. These findings were interpreted as reflecting the dominant role of the left hemisphere in motor information processing. The increase of beta-coherence in electrode pairs including left-sided electrodes fits in with this view. In addition, present data suggest that learned left-handed motor information is associated with the monitoring of the actually executed task.

5.3.2.4 Coordinate Processing During the Normal-Task

In the period between 1 to 2 sec after movement onset, coherence in the Normal-task did not differ significantly from corresponding values of the Learned-task in any electrode pair.

With respect to coordinate processing, absent differences between Normal-task and Learned-task can be interpreted as an index of similar processing of learned extrinsic coordinates, namely as a recall of learned visuomotor skill that is encoded in extrinsic coordinates. Under

the topographical aspect, these results suggest that parieto-frontal connections which represent left-handed learned information are engaged similarly during the repetition of the left-handed Learned-task as during the control of the Normal-task with the opposite right hand.

5.3.2.5 Coordinate Processing During the Mirror-Task

With regards to coordinate processing, changes of coherence in the Mirror-task can be conceived as an indicator of changes in acquired coordinates, i.e. as a neurophysiological correlate of the modification of acquired extrinsic coordinates.

It is an interesting finding that only beta-coherence, but not alpha-coherence increased in the Mirror-task as compared to the Learned-task. These results can be conceived as support for the notion that alpha- and beta-coherence reflect different networks (i.e. sensory and motor networks) and indicate that motor, but not sensory networks are activated.

5.3.2.6 Interhemispheric Communication

The Normal-Task

Taken the preferred right hemispheric representation of left-handed skill, one might expect that interhemispheric information flow increased as compared to the Learned-task during execution of the right-handed Normal-task. Surprisingly, changes of interhemispheric coherence between Normal-task and Learned-task were absent. There are two possible explanations. First, one must have in mind that interhemispheric projections are engaged in the left-handed learned task. Learned information of the right to the left hemisphere- as it might be requested in the Normal-task - might be transferred via these projections. Alternatively, it seems possible that subcortical pathways serve for the transfer of learned right-hemispheric information to the left side during the Normal-task (Velay and Benoit-Dubrocard, 1999).

The Mirror-Task

A critical finding of the present study is the dramatic increase of beta-coherence between homologous sites in the Mirror-task. Increases of coherence between homologous sites have been attributed to reflect interhemispheric information transfer as mediated by the corpus callosum (Andres et al., 1999). Under this consideration, strong interhemispheric increases of

beta-coherence demonstrate a critical role of callosal fibres in the mediation of motor information. This finding adds to experimental findings that intact callosal fibres are essential for intermanual transfer from the left to the right hand (Thut et al., 1996 and 1997).

It is an intriguing finding that the contribution of interhemispheric connections depends on the orientation of the transfer task. Coherence increased in comparison to the Learned-task in the Mirror-task only, an observation which indicates that interhemispheric connections are specifically involved in the Mirror-task. Therefore, interhemispheric connections are likely to be responsible for the specific processes of coordinates. Since patterns of coherence strongly suggest that left-to-right hand transfer occurs in extrinsic coordinates, the process of extrinsic modification might be reflected in the critical role of callosal interconnections in the Mirror-task.

It is worth to note that determined patterns of interhemispheric coherence fit with the prediction of hemisphere-based differences. The hypothesis that the right hemisphere plays a specific role in the control of the Mirror-task, the left hemisphere for the Normal-task predicts stronger interhemispheric information transfer in the former as compared with the latter task. Patterns of coherence fit in with this view. However, expected hemisphere-differences in transfer tasks could not be determined here. The right as well as the left hemisphere revealed increases of coherence in the Mirror-task (in comparison with the Learned-task and the Normal-task). Thus, both hemispheres are involved in the modification of spatial information. The strong interhemispheric increases of coherence suggest that information exchanges between hemispheres play a critical role in these transformation processes.

5.3.3 Neurophysiological Data Under the Aspect of Task Performance

The Normal-Task

The improvement of the Normal-task from opposite hand training did not significantly differ from the determined benefit for the Learned-task. This is well compatible with the observation that activation of cortical connections did not differ between these tasks.

The Mirror-Task

The Mirror-task was characterised by a strong learning-related reduction of figure size. The negative effect of left-handed training on figure size in the Mirror-task suggests that the access and use of acquired left-hand skill during the Mirror-task is responsible for this

finding. This means, because of the processing of extrinsic coordinates during intermanual transfer performance, figure size reduction presumably results from the modifications of these extrinsic representations.

As indicated by the pronounced increase of coherence between right and left sides, interhemispheric information exchanges are critically involved in the modification of extrinsic representations. Since the corpus callosum is known to mediate the communication between hemispheres, present data suggests an important role of callosal interconnections in the Mirror-task. In this context, observation of Thut and co-workers (1997) who investigated intermanual transfer in patients with callosal damage are of particular interest. Compared with healthy subjects, patients with callosal damage showed a superiority for left-to-right hand transfer. This observation was interpreted to reflect missing callosal inhibition. With respect to these findings, one might speculate that the negative effect of left-hand acquisition on the Mirror-task is due to engagement of callosal fibres, namely due to callosal effects of inhibition.

5.3.4 Conclusions of the Left-to-Right Hand Transfer

1. The transfer of acquired visuomotor skill with the left hand is coded by use of extrinsic coordinates that are associated with on-line monitoring of the actually performed task.
2. Both hemispheres are involved in the recall of extrinsic information in the Normal-task and the modification of these learned extrinsic representations in the Mirror-task.
3. In the Mirror-task, the modification of acquired extrinsic coordinates induces an increase of information flow in motor circuits. Interhemispheric projections are critically involved in the modification of extrinsic motor information.
4. Learning-related negative effects (i.e. a reduction of figure size) in the Mirror-task might be due to a failure in sensorimotor translation or due to callosal inhibitory effects.

5.4 Comparison of the Right-to-left Hand with the Left-to-right hand Transfer

The comparison of results obtained during the transfer tasks after right-handed training with data observed in tasks after left-handed training yields several interesting aspects that are not evident when viewing data of one transfer direction alone.

5.4.1 Task Performance

Behavioural data showed that practice of right-handed as well as left-handed training led to changes in task performance by the opposite untrained hand. However, different features of movement transferred in different directions: Opposite hand training improved inter-trial variability of the left hand, but affects predominantly accuracy of figure size of the untrained right hand. Moreover, transfer revealed different patterns with respect to the performance of the Normal-task and Mirror-task. A profit from right-handed training was found for both the Normal-task and the Mirror-task, left-handed training, however, influenced task performance negatively in the Mirror-task.

The observation of different patterns of opposite hand training for transfer performance with the right and left hand demonstrates that transfer of training is not due to unspecific training effects, such as a general familiarisation of experimental design, since such effects should influence either hand equally. Furthermore, results demonstrate that each hand has access to information learned during opposite arm training. Since different movement features are transferred after right-handed and left-handed training, each hand uses apparently specific strategies for learning the visuomotor task.

As indicated by the decrease of inter-trial variability during the right-to-left hand transfer, the computation of the final motor output might be crucially employed during motor learning with the right hand. In contrary, strong transfer effects with respect to figure size during the left-to-right hand transfer suggest that spatial processes play a critical role during motor learning by use of the left hand.

EEG-results revealed that transfer of acquired left-handed skill differed from the transfer of learned right-handed skill with respect to the reference frame that codes for transfer and with respect to the period of motor control. An intrinsic reference frame codes for the transfer of acquired right-handed skill towards the left hand. Extrinsic coordinates are processed during the transfer from the left to the right hand. With regards to the period of motor control, intrinsic processing during the right-to-left hand transfer are associated with movement

programming, extrinsic coordinates during left-to-right hand transfer control the actually executed task.

Present results are in accordance with notes of experimental research that movement preparation is closely related with body-related (intrinsic) coordinates, whereas eye-centred (extrinsic) coordinates play the dominant role in motor control of the actually performed task (McIntyre et al., 1996; Carozzo et al., 1996).

One must have in mind that the control strategy (movement programming and on-line monitoring) as well as the processing of coordinates during intermanual transfer reflect the *storage* of acquired skill. This means, right-handed skill is internally represented in intrinsic coordinates which code for the motor plan, learned left-handed visuomotor information is stored in a control strategy which is associated with the up-dating of the executed movement.

The storage of acquired skill in extrinsic coordinates is an intriguing finding: Eye-centred (extrinsic) coordinates have been frequently shown to code visual information which is *actually perceived* (Carozzo et al., 1996, McIntyre et al., 1998). In the present study, behavioural as well as neurophysiological results in the left-to-right hand transfer are in accord with the notion that extrinsic coordinates code for motor control strategies during movement execution. However, these extrinsic coordinates do not code for actually perceived information, but reflect information that has been *previously* acquired during left-handed training.

Last but not least, it is worth to mention that each hand makes use of established control strategies of the opposite hand. This means, the left hand benefits from established strategies of movement preparation (learned by the right hand), although the left hand favours apparently on-line control strategies without opposite hand training. The right hand, in turn, is controlled by left-handed feedback processes, although movement planning is a favoured strategy of right-handed control.

5.4.2 Neural Systems of Coordinate Processing

The combined view of EEG-parameters permit insight into activation of cortical brain areas (indicated by movement-related potentials and EEG-power) and activity of neural networks (measured by EEG-coherence). Results suggest that networks and regional areas are specifically activated in the processing of extrinsic and intrinsic coordinates

Modification of extrinsic coordinates are required during the Mirror-task. Both the right-handed and the left handed Mirror-task revealed increases of coherence versus the Learned-task. Neither the right-handed nor the left-handed Mirror-task were associated with changes in

values of power or movement-related potentials. These results lead to the suggestion that the modification of extrinsic coordinates - as it is required in the Mirror-task- is processed by an increase of information flow within cortical connections. Furthermore, significant increases of coherence versus baseline were determined in the left-handed Learned-task. Since left-handed skill is obviously encoded in extrinsic coordinates, the communication between areas play the critical role in the representation and the modification of extrinsic coordinates.

Modification of intrinsic information are presumably reflected in changes of EEG-data between Learned-task and Normal-task. Differences between these two tasks were observed only during right-to-left hand transfer and in each parameter. However, whereas the decrease of coherence indicates a *deactivation* of neural circuits, increased negativity in movement-preceding potentials and beta-power demonstrates *activation* of cortical brain area. Thus, it is likely that the modification of intrinsic coordinates are processed on the level of regional brain activation.

5.4.3 Neurophysiological Data Under the Aspect to Task Performance

Different patterns were observed with respect to the effect of opposite hand training for the Normal-task and Mirror-task. Right-handed skill affected both these transfer tasks positively; left-handed training improved only the Normal-task, whereas the Mirror-task was negatively influenced (namely by a reduction of figure size). These observations show that negative effects during transfer occur apparently only in the left-to-right hand direction (but not in the right-to-left hand direction) and only during the Mirror-task (but not during the Normal-task). This finding replicates the reports of Thut and co-workers (1996 and 1997) who investigated transfer effects in similar drawing tasks. In those studies, left-handed training results in a decrease of velocity in relearning the mirror reversed task with the right hand.

Thut and co-workers (1997) demonstrated such learning-related negative influences only in healthy subjects, but not in patients with callosal damage. On the other hand, healthy subjects were superior to those 'callosal' patients in performance of the left-handed mirror reversed task after skill acquisition with the right hand. These authors concluded that inhibitory callosal effects are responsible for the disadvantage of the right-handed mirror reversed task after left-handed skill acquisition, whereas callosal connections might facilitate intermanual transfer of right-handed skill.

Present results are compatible with these views. Interhemispheric coherence increased prominently in the right-handed Mirror-task, but reached also significance between parietal and frontal sites during the left-handed Mirror-task. Hence, interhemispheric callosal connections are engaged in the access and use of acquired skill in both transfer directions. With regards to performance, however, the left-handed Mirror-task revealed a benefit of opposite hand, the right-handed Mirror-task was negatively influenced- an observation which adds to the hypothesis that callosal inhibitory effects occur during the left-to-right hand transfer, but not in the opposite transfer direction.

5.5 Coordinate Processing Under the Aspect of Models of Intermanual Transfer

The present results are compatible with distinct aspects of both the cross activation model and the callosal access model.

5.5.1 Cross Activation Model

The cross activation model explains greater transfer effects from the right to the left hand than in the opposite direction. This model suggests that right-handed skill is represented in both hemispheres, whereas information acquired by left-handed training is thought to be represented in the right hemisphere only. As a result, interhemispheric information flow is requested during the left-to-right hand transfer, but not during the right-to-left hand transfer. In the present study, greater transfer effects in the right-to-left hand as compared to the left-to-right hand direction were determined with respect to performance of the Mirror-task. Neurophysiological results indicate that visuomotor skill is represented bilaterally not only after right-handed motor learning, but also when the left hand is used during skill acquisition. Nevertheless, patterns of coherence in the Mirror-task fit in with the prediction of the cross activation model: The Mirror-task of the untrained right hand yielded highly significant increases of beta-coherence between hemispheres in each electrode pair. The left-handed Mirror-task increased significantly in comparison to the Learned-task only between parietal and frontal sites. These results are in accord with the view that interhemispheric projections are more critically involved during intermanual transfer of the untrained right hand than the left hand. It must be stressed that interhemispheric communication in the right-handed Mirror-task reflect the modification of acquired extrinsic representations rather than the mere transfer of learned information from the right to the left hemisphere (as it is assumed in the cross activation model).

5.5.2 Callosal Access Model

According to this model, the storage of learned information in the left hemisphere. As a result, interhemispheric projections during the repetition of a left-handed learned task by use of the trained left hand, but not during subsequent transfer to the right hand. Here, behavioural data demonstrated a benefit of left-handed training for the Normal-task of the right hand. Again, results of interhemispheric coherence in Learned-task and Normal-task associated with the left-to-right hand transfer fit exactly with the prediction of the callosal access model.

Significant interhemispheric increases of coherence (versus baseline) were found in the Learned-task, but not in the Normal-task.

Summed up, the present proposed mechanisms of intermanual transfer are in agreement with the current models under the aspect of interhemispheric projections. Transfer mechanisms for the Mirror-task fit with the cross activation model, the control of the Normal-task with the transcallosal model. Whereas these models suggest that interhemispheric exchanges result from hemisphere-differences in the storage of skill, it is assumed here that the need of information flow between right and left hemisphere is due to the modification of acquired coordinates.

5.6 General Conclusions

1. The transfer of right-handed skill towards the left hand is encoded mainly by intrinsic coordinates which are associated with movement preparation. Visuomotor skill acquired with the left hand, in contrast, is transferred in extrinsic coordinates that code for on-line monitoring of the task.
2. A hemispheric specialisation in coordinate processing is observed only in the transfer of right-handed skill towards the left hand. The right hemisphere is specifically engaged in the recall of learned intrinsic coordinates, the left hemisphere is dominant in the modification of learned coordinates of both extrinsic and intrinsic coordinates.
3. Modification of intrinsic coordinates (as required in the Normal-task) induces increased activation of cortical brain areas. Modification of extrinsic coordinates- as required in the Mirror-task- induces activation of cortical networks.
4. Callosal fibres are involved most critically in the Mirror-task after left-handed training. Information flow between hemispheres is due to the modification of extrinsic coordinates. Callosal inhibitory effects are likely to be responsible for negative effects of left-handed motor skill on relearning the right-handed Mirror-task

6 Summary

Acquisition of sensorimotor skill facilitates performance of the identical and mirror reversed task with the opposite hand (Normal-task and Mirror-task). The specific control of the Normal-task and Mirror-task can be conceived as a specific use of learned information in different coordinate systems. Intrinsic, body-related coordinates are preserved in the Mirror-task, but must be transformed in the Normal-task. Extrinsic, object-centred coordinates are modified in the Mirror-task, but not in the Normal-task.

To identify the neuronal correlates of coordinate processing during intermanual transfer, EEG-recordings were obtained during the repetition of a trained drawing task (Learned-task) and the performance of the Normal-task and Mirror-task with the opposite hand.

Behavioural data showed transfer effects in each task. As compared to the right-handed Learned-task, the left-handed Normal-task revealed increases of negativity in movement-related potentials and EEG-power and a decrease of EEG-coherence prior to movement onset. The Mirror-task did not differ in general from the Learned-task. After left-handed training, beta-coherence increased in the Mirror-task relatively to the Learned-task after movement onset, whereas the Normal-task did not differ from the Learned-task.

The results indicate that right-handed skill is transferred in intrinsic coordinates which code for movement preparation. The transfer of left-handed skill occurs in extrinsic coordinates which control the actually executed task. The modification of intrinsic coordinates induces increased activity of cortical areas and a decrease of inter-regional communication. Increases of inter-regional information exchanges, in contrast, can be conceived as the neural correlate of the transformation of extrinsic coordinates.

Concluding, different coordinate systems encode the intermanual transfer of right-handed and left-handed skill. On the other hand, distinct brain mechanisms are engaged in the modification of acquired extrinsic and intrinsic coordinates.

Zusammenfassung

Motorisches Training erleichtert die Ausführung der gelernten Aufgaben in spiegelbildlicher sowie originaler Orientierung der gegenüberliegenden Hand (Spiegel- bzw. Normalaufgabe). Die Kontrolle dieser beiden Transferaufgaben läßt sich als spezifische Verarbeitung erlernter Koordinaten auffassen. Intrinsische, körperbezogene Koordinaten können in unveränderter Form die Spiegelaufgabe kontrollieren, müssen jedoch während der Normalaufgabe modifiziert werden. Demgegenüber werden extrinsische, objekt-zentrierte Koordinaten bei der Spiegelaufgabe, nicht aber bei der Normalaufgabe transformiert.

Um die neuronalen Korrelate der Koordinatenprozessierung während des intermanuellen Transfers zu erfassen, wurden EEG-Messungen bei der Wiederholung einer erlernten Zeichenaufgabe (Lernaufgabe) und der Normal- und der Spiegelaufgabe der kontralateralen Hand durchgeführt.

Die Verhaltensdaten ließen auf Transfereffekte in jeder Aufgabe schließen. Im Vergleich zur rechtshändigen Lernaufgabe wurden Negativitätsanstiege der motorisch-evozierter Potentiale und der EEG-Power sowie ein Abfall der Kohärenz bei der Normalaufgabe vor Bewegungsbeginn beobachtet. Die Spiegelaufgabe unterschied sich nicht generell von der Lernbewegung. Nach linkshändigem Training wurde ein genereller Kohärenzanstieg in der Beta-Bande bei Spiegelaufgabe nach Bewegungsbeginn gefunden, während sich die Normalaufgabe nicht von der Lernaufgabe unterschied.

Diese Ergebnisse deuten an, dass nach rechtshändigem Training intrinsische Koordinaten, die die Bewegungsvorbereitung kontrollieren, den intermanuellen Transfer kodieren. Der Transfer nach linkshändigem Training wird durch extrinsische Koordinaten kodiert, die mit der Bewegungsausführung assoziiert sind.

Die Modifikation intrinsischer Koordinaten induziert verstärkte Aktivität kortikaler Areale sowie eine Verminderung der inter-regionalen cerebralen Kommunikation. Demgegenüber kann ein Anstieg des inter-regionalen Informationsflusses als neuronales Korrelat der Transformation extrinsischer Koordinaten aufgefaßt werden.

Es wird gefolgert, dass einerseits unterschiedliche Koordinatensysteme den Transfer nach rechtshändigem und linkshändigem Training kodieren, andererseits die Modifikation extrinsischer und intrinsischer Koordinaten durch unterschiedliche neuronale Systeme kodiert wird.

7 References

Andersen, R. A., Snyder, L. H., Li, C. S., & Stricanne, B. (1993). Coordinate transformations in the representation of spatial information. *Current Opinion in Neurobiology*, 3, 171-176.

Andres, F. G., Mima, T., Schulman, A. E., Dichgans, J., Hallett, M., & Gerloff, C. (1999). Functional coupling of human cortical sensorimotor areas during bimanual skill acquisition. *Brain*, 122, 855-870.

Andrew, C., & Pfurtscheller, G. (1996). Event-related coherence as a tool for studying dynamic interaction of brain regions. *Electroencephalography and Clinical Neurophysiology*, 98, 144-148.

Atkeson, C. G. (1989). Learning arm kinematics and dynamics. *Annual Reviews in Neuroscience*, 3, 171-176.

Bötzel, K., Plendl, H., Paulus, W., & Scherg, M. (1993). Bereitschaftspotential: Is there a contribution of the supplementary motor area? *Electroencephalography and Clinical Neurophysiology*, 89, 187-196.

Bullock, T. H. (1992). Introduction to induced rhythms: a widespread heterogeneous call of oscillations. In Basar, E. & Bullock, T.H. (eds.), *Induced rhythms of the brain*. Birkhauser: Boston, pp. 1-26.

Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen R. A. (2002). Direct visuomotor transformation for reaching. *Nature*, 416, 632-636.

Buxbaum, L. J., Coslett, H. B., Schall, R. R., McNally, B., & Goldberg, G. (1994). Hemispatial factors in mirror writing. *Neuropsychologia*, 37, 1317-1421.

Carozzo, M., McIntyre, J., Zago, M. & Lacquanati, F. (1999). Viewer-centered and body-centered frames of reference in direct visuomotor transformations. *Experimental Brain Research*, 129, 201-210.

Chan, J. L., & Ross, E. D. (1988). Left-handed mirror writing following right anterior cerebral artery infarction: Evidence for nonmirror transformation of motor programs by the right supplementary motor area. *Journal of Neurology*, 38, 59-62.

Classen, J., Gerloff, C., Honda, M., & Hallett, M. (1998). Integrative visuomotor behavior is associated with interregionally coherence oscillations in the human brain. *Journal of Neurophysiology*, *79*, 1567-1573.

Criscimagna-Hemminger, S. E., Donchin, O., Gazzaniga, M. S., & Shadmehr, R. (2003). Learned Dynamics of Reaching Movements Generalize From Dominant to Nondominant Arm. *Journal of Neurophysiology*, *89*, 168-176.

Deecke, L., Scheid, P., Kornhuber, H. H. (1969). Distribution of readiness potential, pre-movement positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements. *Experimental Brain Research*, *7*, 158-168.

Deecke, L., & Kornhuber, H. H. (1976). Voluntary finger movement in man: Cerebral potentials and theory. *Biological Cybernetics*, *23*, 99-119.

Deiber, M. P., Wise, S. P., Honda, M., Catalan, M. J., Grafman, J., & Hallett, M. (1997). Frontal and parietal networks for conditional motor learning: a positron emission tomography study. *Journal of Neurophysiology*, *78*, 977-991.

Dizio, P., & Lackner, J. R. (1995). Motor adaptation to Coriolis force perturbations of reaching movements: endpoint but not trajectory adaptation transfers to the nonexposed arm. *Journal of Neurophysiology*, *74*, 1787-1792.

Elliott, D., & Roy, E. A. (1981). Interlimb transfer after adaptation to visual displacement: patterns predicted from the functional closeness of limb neural control centres. *Perception*, *10*, 383-389.

Fettaposta, F., Amabile, G., Cordischi, M. V., Di Venanzio, D., Foti, A., Pierelli, F., D'Alessio, C., Pigozzi, F., Parisi, A., & Morrocutti, C. (1996). Long-term practice effects on a new skilled motor learning: An electrophysiological study. *Electroencephalography and Clinical Neurophysiology*, *99*, 495-507.

Flanagan, J. R., & Rao, A. K. (1995). Trajectory adaptation to a non-linear visuomotor transformation: evidence of motion planning in visually perceived space. *Journal of Neurophysiology* *74*, 2175-2178.

Frustiger, S. A., Strother, S. C., Anderson, J. R., Sidtis, J. J., Arnold, K. B., & Rottenberg, D. A. (2000). Multivariate Predictive Relationship between Kinematic and Functional Activation Patterns in a PET Study of Visuomotor Learning. *NeuroImage*, *10*, 515-528.

- Gerloff, C., Richard, J., Hadley, K., Schulman, A. E., Honda, M., & Hallett, M. (1998). Functional coupling and regional activation of human cortical motor areas during simple internally paced and externally paced finger movement. *Brain*, *121*, 1513-1531.
- Grafton, S. T., Hazeltine, E., & Ivry, I. B. (2002). Motor sequence learning with the nondominant hand. *Experimental Brain Research*, *146*, 369-378.
- Graziano, M. S., & Gross, C. G. (1998). Spatial maps for the control of movement. *Current Opinion in Neurobiology*, *8*, 195-201.
- Haaland, K. Y., & Harrington, D. L. (1996). Hemispheric asymmetry of movement. *Current Opinion in Neurobiology*, *6*, 796-800.
- Halsband, U., & Freund, H. J. (1990). Premotor cortex and conditional motor learning in man. *Brain*, *113*, 207-222.
- Halsband, U. (1992). Left hemisphere preponderance in trajectorial learning. *Neuroreport*, *3*, 397-400.
- Hicks, R. E. (1974). Asymmetry of bilateral transfer. *American Journal of Psychology*, *87*, 667-674.
- Imamizu, H., & Shimojo, S. (1996). The locus of visual-motor learning at the task or manipulator level: implications from intermanual transfer. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 719-733.
- Imamizu, H., & Kawato, M. (1998). Adaptive Internal Models of Kinematics Involved in Learning an Aiming Task. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 812-829.
- Inoue, K., Kawashima, R., Satoh, K., Kinomura, I., Goto, R., Sigiura, M., Ito, M., & Fukuda, H. (1997). Activity in the parietal area during visuomotor learning with optical rotation. *Neuroreport*, *8*, 3979-3983.
- Jasper, H. H. (1958). The ten-twenty electrode system of the international federation of electroencephalography and clinical neurophysiology. *Electroencephalography and Clinical Neurophysiology*, *183*, 321-375.

Kawato, M., Isobe, M., Maeda, Y., & Suzuki, R. (1988). Coordinates transformation and learning control for visually guided voluntary movement with iteration: A Newton-like method in a function space. *Biological Cybernetics*, 59, 161-177.

Kornhuber, H. H., & Deecke, L. (1965). Hirnpotentialänderungen bei Willkürbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und Reafferente Potentiale. *Pflügers Archiv der Gesamten Physiologie*, 284, 1-17.

Kristeva, R., Cheyne, D., Lang, W., Lindinger, G., & Deecke, L. (1990). Movement-related potentials with different inertial loads. *Electroencephalography and Clinical Neurophysiology*, 75, 410-418.

Kurata, K., & Hoshi, E. (2002). Movement-Related Neuronal Activity Reflecting the Transformation of Coordinates in the Ventral Premotor Cortex of Monkeys. *Journal of Neurophysiology*, 88, 3118-3132.

Kutas, M., & Donchin, E. (1974). Studies squeezing: The effect of handedness. The responding hand and response force on the contralateral dominance of readiness potential. *Science*, 186, 545-548.

Lacquanati, F., Guignon, E., Bianchi, L., Ferraina, S., & Caminiti, R. (1995). Representing spatial information for limb movement: role of area 5 in the monkey. *Cerebral Cortex*, 5, 410-428.

Laszlo, J. I., Baynley, R. A., & Bairstow, P. J. (1970). Bilateral transfer of tapping skill in the absence of peripheral information. *Journal of Motor Behaviour*, 2, 261-271.

Latash, M. L. (1999). Mirror writing: learning, transfer and implications for internal inverse models. *Journal of Motor Behaviour*, 31, 107-111.

Leocani, L., Toro, C., Manganotti, P., Zhuang, P., & Hallett, M. (1997). Event-related coherence and event-related desynchronization/synchronization in the 10 Hz and 20 Hz EEG during self-paced movements. *Electroencephalography and Clinical Neurophysiology*, 104, 199-206.

Malfait, N., Shiller, D. M., & Ostry, D. J. (2002). Transfer of Motor Learning across Arm Configurations. *Journal of Neuroscience*, 22, 9656-9669.

Manganotti, P., Gerloff, C., Toro, C., Katsuta, H., Sadato, N., Zhuang, P., Leoconi, L., & Hallett, M. (1998). Task-related coherence and task-related spectral power changes during sequential finger movements. *Electroencephalography and Clinical Neurophysiology*, *109*, 50-62.

McIntyre., J., Stratta, F., & Lacquanati, F. (1997). Viewer-Centered Frame of Reference for Pointing to Memorized Targets in Three-Dimensional Space. *Journal of Neurophysiology*, *78*, 1601-1618.

McIntyre., J., Stratta, F., & Lacquanati, F. (1998). Short-Term Memory for Reaching to Visual Targets: Psychophysical Evidence For Body-Centered Reference Frames. *Journal of Neuroscience*, *18*, 8423-8435.

Milivojevic, B., Johnson, B. W., Hamm, J. P., & Corballis, M. C. (2003). Non-identical neural mechanisms for two types of mental transformation: event-related potentials during mental rotation and mental paper folding. *Neuropsychologia*, *41*, 1345-1356.

Natio, E., & Matsumara, M. (1994). Movement-related potentials associated with motor inhibition as determined by use of a stop signal paradigm in humans. *Cognitive Brain Research*, *2*, 139-146.

Natio, E., & Matsumara, M. (1996). Movement-related potentials associated with motor inhibition under different preparatory states during performance of two visual stop signal paradigms in humans. *Neuropsychologia*, *43*, 565-573.

Neshige, R., Lüders, H., Friedman, L., & Shibasaki, H. (1988). Recording of movement-related potentials from the human cortex. *Annals of Neurology*, *24*, 439-445.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97-113.

Orton, S. T. (1928). Specific reading disability- strephosymbolia. *Journal of the American Medical Association*, *90*, 1095-1099.

Parlow, S. E., & Kinsbourne, M. (1989.) Asymmetrical transfer of training between hands: implications for interhemispheric communication in normal brain. *Brain and Cognition*, *11*, 98-113.

- Parlow, S. E. , & Kinsbourne, M. (1990). Asymmetrical transfer of braille acquisition between hands. *Brain and Language*, *39*, 319-330.
- Pfefferbaum, A., Ford, J. M., Weller, B. J., & Kopell, B. S. (1985). ERP to response production and inhibition. *Electroencephalography Clinical Neurophysiology*, *60*, 423-434.
- Pfurtscheller, G., & Neuper, C. (1992). Simultaneous EEG 10 Hz desynchronization and 40 Hz synchronization during finger movements. *Neuroreport*, *3*, 1057-1060.
- Pfurtscheller, G., Stancak A., & Edlinger, G. (1997). On the existence of different types of central beta rhythms below 30 Hz. *Electroencephalography and Clinical Neurophysiology*, *102*, 316-325.
- Rappelsberger, P., Pfurtscheller, G., & Filz, O.(1994). Calculation of even-related coherence – a new method to study short-lasting coupling between areas. *Brain and Topography*, *7*, 121-127.
- Rescher, B., & Rappelsberger, P. (1999). Gender dependent EEG-changes during a mental rotation task. *International Journal of Psychophysiology*, *33*, 209-222.
- Rizzolatti, G., Luppino, G., & Matell, I. M. (1998). The organisation of the cortical motor system: new concepts. *Electroencephalography and Clinical Neurophysiology*, *106*, 283-296.
- Rodriguez, R., Aguilar, M., & Gonzalez, G. (1989). Left Non-dominant Hand Mirror Writing. *Brain and Language*, *37*, 122-144.
- Rodriguez, R. (1991). Hand Motor Patterns after the Correction of Left-Nondominant Hand Mirror Writing. *Neuropsychologia*, *29*, 1191-1203.
- Rossetti, Y., Desmurget, M., & Prablanc, C. (1995). Vectorial coding of movement: vision, perception, or both? *Journal of Neurophysiology*, *74*, 446-457.
- Sainburg, R. L., & Wang, J. (2002). Interlimb transfer of visuomotor rotations: independence of direction and final position information. *Experimental Brain Research*, *145*, 437-447.
- Sakai, K., Hikosaka, G., Miyauchi, S., Takino, R., Sasaki, Y., & Putz, B. (1998). Transition of brain activations from frontal to parietal areas in visuomotor sequencing learning. *Journal of Neuroscience*, *18*, 1827-1840.

Scott, S. E., Sergio, L. H., & Kalaska, J. F. (1997). Reaching movements with similar hand paths but different arm orientation. II. Activity of individual cells in dorsal premotor and parietal area 5. *Journal of Neurophysiology*, 78, 2413-2426.

Seitz, R. J., Canvan, A. G. M., Yaguez, L., Herzog, H., Tellmann, L., Knorr, U., Huang, Y., & Homberg, V. (1997). Representation of graphomotor trajectories in the human parietal cortex: evidence for controlled and automatic performance. *European Journal of Neuroscience*, 9, 378-389.

Servos, P., & Goodale, M. A. (1994). Binocular vision and the on-line control of human prehension. *Experimental Brain Research*, 98, 119-127.

Shadmehr, R., & Holcomb, H. H. (1997). Neural Correlates of Motor Memory Consolidation. *Science*, 277, 821-825.

Shibasaki, H., Barrett, G., Halliday, E., & Halliday, A. M. (1980). Components of the movement-related cortical potential and their scalp topography. *Electroencephalography and Clinical Neurophysiology*, 49, 213-226.

Silberstein, R. B., Danieli, F., & Nunez, P. L. (1999). Fronto-Parietal Evoked Potential Synchronization is Increased During Mental Rotation. *Neuroreport*, 14, 67-71.

Singer, W. (1995). Development and plasticity of cortical processing architectures. *Science*, 270, 758-763.

Slobounov, S., & Ray, W. (1998). Movement-related potentials with reference to isometric force output in discrete and repetitive tasks. *Experimental Brain Research*, 123, 461-473.

Slobounov, S., Rearick, M., & Chiang, H. (2000). EEG correlates of finger movements as a function of range of motion and pre-loading conditions. *Clinical Neurophysiology*, 111, 1997-2007.

Soechting, J. F., & Flanders, M. (1989). Errors in pointing are due to approximations in sensorimotor transformations. *Journal of Neurophysiology*, 62, 595-608.

Stoddard, J., & Vaid, J. (1989). Asymmetries in intermanual transfer of maze learning in right- and left-handed adults. *Neuropsychologia*, 34, 605-608.

- Taylor, M. J. (1978). Bereitschaftspotential during the acquisition of a skilled motor task. *Electroencephalography and Clinical Neurophysiology*, *45*, 568-576.
- Taylor, H. G., & Heilman, M. (1980) Left-hemisphere motor dominance in right handers. *Cortex*, *16*, 587-603.
- Thut, G., Cook, N. D., Regard, M., Leenders, K. L., Halsband, U., & Landis, T. (1996). Intermanual transfer of proximal and distal motor engrams in humans. *Experimental Brain Research*, *108*, 321-327.
- Thut, G., Halsband, U., Regard, M., Mayer, E., Leenders, K. L., & Landis, T. (1997). What is the role of the corpus callosum in intermanual transfer of motor skill? A study of three cases with callosal pathology. *Experimental Brain Research*, *113*, 365-370.
- Toro, C., Deutschl, G., Thatcher, R., Sato, S., Kufta, C., & Hallett, M. (1994). Event-related desynchronization and movement-related cortical potentials on the ECoG and EEG. *Electroencephalography and Clinical Neurophysiology*, *93*, 280-389.
- Vaid, J., & Stiles-Davis, J. (1989). Mirror writing: An Advantage for the Left-Handed? *Brain and Language*, *37*, 616-627.
- Velay, J. L., & Benoit-Dubrocard, S. (1999). Hemispheric asymmetry and interhemispheric transfer in reaching programming. *Neuropsychologia*, *37*, 895-903.
- Voyer, D. (1995). Effect of practice on laterality in a mental rotation task. *Brain and Cognition*, *29*, 326-335.
- Ward, J., Alvis, G., Sanford, G., Dodson, D., & Puaskulich, R. (1984). Qualitative differences in tactuo-spatial motor learning by left-handers. *Neuropsychologia*, *27*, 1091-1099.
- Wolpert, D., Ghahramani, Z., & Jordan, M. I. (1995). Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study. *Experimental Brain Research*, *103*, 460-470.
- Yang, M. (1997). Mirror writing in right-handers and in left-handers: A study using Chinese Characters. *Neuropsychologia*, *35*, 1491-1498

8 Acknowledgements

I gratefully thank Prof. Dr. Preilowski and PD Dr. Christoph Braun for helpful comments and Jürgen Dax for assisting in the analysis of the behavioural data. This research was supported by a grant from the Volkswagen-Stiftung (junior research group ‘Cortical reorganization and learning’, AZ I/73035) and by the Deutsche Forschungsgemeinschaft (SFB 550/C6).

9 Curriculum Vitae

Name: Lange

Vorname: Regine Kerstin

Geb.: 1.10.1972

Geburtsort: Hamburg

Staatsangehörigkeit: Deutsch

Bildungsweg:

Abitur: 1993

Studium der Humanmedizin

Frühjahr 1994 - Frühjahr 1996: Universität Hamburg

Frühjahr 1996: Physikum

Frühjahr 1996- Herbst 1999: Medizinische Universität zu Lübeck

Frühjahr 1999: 2. Staatsexamen

Frühjahr - Herbst 1999: Praktisches Jahr, Chirurgie und Innere Medizin

Herbst 1999- Frühjahr 2000: Eberhard-Karls-Universität Tübingen: Praktisches Jahr,
Wahlfach Neurologie

Herbst 2000: Wissenschaftliche Angestellte im Institut für Medizinische Psychologie und
Verhaltensneurobiologie

Juli 2001: Promotion in der medizinischen Fakultät: Kortikale Aktivierungsmuster bei
Normal- und Spiegelschrift, gemessen mit der funktionellen Magnetresonanztomographie

Seit Anfang 2004: Mitarbeit an einem Projekt eines Stipendiums am Kantonsspital Basel