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Supplementary motor area activation while tapping bimanually different rhythms in musicians

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Summary. In 15 musicians, cortical DC-potentials were recorded from the scalp before and during the execution of bimanual motor sequences. Subjects (Ss) either tapped with their two index fingers in synchrony (quavers against quavers; "2 against 2") or they tapped quavers against triplets ("2 against 3"). Either the right or the left finger started tapping the quavers (onset time t_1), after about 4 s the other finger joined in (t_2) either with quavers as well (easy rhythm) or with triplets (difficult rhythm). Ss were free to start the sequences, i.e. to determine the onset times t_1 and t_2. Shifts of cortical DC potentials were averaged twice; (1) time-locked to t_1 and (2) time-locked to t_2. When moving in synchrony (easy rhythm) DC-potential shifts and maps of radial current densities across the scalp indicated activations of the two primary motor cortices (MI). When bimanually tapping different rhythms, there was not only an activation of MI cortices, but in addition a very large activation of the mesial, central cortex was observed. It is suggested that this cortical area which mainly contains the supplementary motor area (SMA) has the function of controlling the initiations of movements in the difficult sequence which have to fit into a very precise timing plan. Interestingly, activation of the mesial, central cortex preceded the actual performance of the difficult rhythm by about 4 s. This finding indicates that the preparatory set differs between the two tasks.

Key words: Cortical DC potential shift – Movement-related potentials – Bereitschaftspotential – Bimanual coordination – Supplementary motor area – Human

Introduction

Von Holst (1939) described the tendency of the nervous system to generate only one temporal pattern when moving different parts of the body. He observed fin movements in fish and discovered that rhythmic movements of different body parts have either identical (absolute coordination) or harmonically related (relative coordination) temporal patterns. Rhythmic movements in fish or in earth worms were not altered when cutting sensory afferents. Consequently, von Holst postulated a central representation of temporal patterns not depending on sensory feedback.

Interestingly, the model of a "central timing system" has proven not only to be valid in automatic rhythmic activities of animals but also in human voluntary movement. Evidence came from behavioral analysis of bimanual motor sequences: There is a strong tendency for the two hands to start and stop movements in synchrony even when performing different movements (Kelso et al. 1983) or movements with different loads (Gantchev et al. 1988; Kristeva et al. 1989). Bimanual motor sequences did not interfere with each other if temporally compatible, i.e. harmonically related. However, interference occurred when the two hands moved at different rhythms (Klapp 1979). An interference between speech production and limb movements can even be taken as evidence that the "central timing system" coordinates the initiations of all kinds of movements (Kinsbourne 1981). In bimanual motor tasks, mainly two patterns of interference were noticed (Peters 1981): Ss either tended to switch in a "time sharing" mode between sides (right or left) and rhythms, resp., or tended to move in synchrony ("concurrent move-

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Offprint requests to: W. Lang (address see above) ments") with one of the two rhythms serving as time base to start movements. Musicians who have acquired the skill to move bimanually at different rhythms (e.g. quavers against triplets) may avoid interference by integrating the two rhythms into a "common time base" for starting movements of either side (Lashley 1951; Deutsch 1978; Klapp 1979).

Constraints of the "central timing system" to use only one time base for starting movements in bimanual sequences may have structural reasons: Shifts of the cortical DC-potential preceding a voluntary movement indicated that the starting function of voluntary actions is centralized in one brain structure, the mesial fronto-central cortex (including the supplementary motor area, SMA; for review see Kornhuber 1984a, b; Deecke et al. 1985; Kornhuber et al. 1989).

In a recent study, shifts of cortical DC potentials have been investigated in four different bimanual motor sequences (Lang et al. 1988b). In these tasks Ss moved their index fingers successively to three positions, a flexed, an intermediate or an extended one. In two situation, Ss alternated the initiation of movements between the two hands (moving the right finger, then the left, then the right and so on). In these situations, which were called sequential tasks, execution was associated with a large and sustained negative DC-shift in recordings over the fronto-central midline. This activation was not present in situations in which the two hands acted in synchrony or in a task in which bimanual sequences were performed without any constraint for temporal or spatial coordination.

In the present study, trained musicians performed bimanual motor sequences which were not harmonically related (quavers against triplets). This task required Ss not only to switch between the two hands for the initiation of movements (as in Lang et al. 1988b) but also to do so according to a very precise timing plan. The hypothesis was that the fronto-mesial cortex has the function of controlling initiations of movement elements during the motor sequence. Consequently, an activation of this area (which mainly includes the SMA) was expected. In the present study, Ss started with one rhythm and chimed in with the second rhythm. This experimental design enables the investigator to test task-specificity of neurophysiological correlates of the preparatory set which is likely to differ depending on whether the 2:2 ratio or the 2:3 ratio has to be performed.

Benecke et al. (1985) have investigated the Bereitschaftspotential (BP) preceding several simultaneous and sequential movements. Changes of the BP have been considered to reflect changes of task-specific planning. The present situation is even more complex: the initiation of the second sequence has to be integrated into an already ongoing performance.

Methods

Subjects

15 musicians (7 males; 8 females) aged 19 to 30 years (mean: 23 years) participated in the study. They each played more than one instrument; 8 of them mainly piano, 4 violin, 2 drums and 1 cello. All of them scored 100% dextrality (Oldfield 1971).

Tasks

Four tasks were performed in one experiment (Fig. 1a, b): (1) RH-S (right hand – simple): Subjects started at t_1 to tap with their right index finger at a frequency of about 2/s (quavers). After a self-selected time, at t_2, the left index finger started to move in synchrony. (2) RH-C (right hand – complicated): The right index finger started to tap 2/s, the left finger was brought in later (t_2) but now with a differing rhythm of 3/s (triplets). (3) LH-S (left hand – simple): Corresponding to RH-S, but with the left finger starting and the right one joining in with 2/s at t_2. (4) LH-C (left hand – complicated): Corresponding to RH-C, but now with the left finger starting at t_1 and the right finger chiming in at t_2. Ss started the sequences at their own volition, i.e. they were free to determine onset

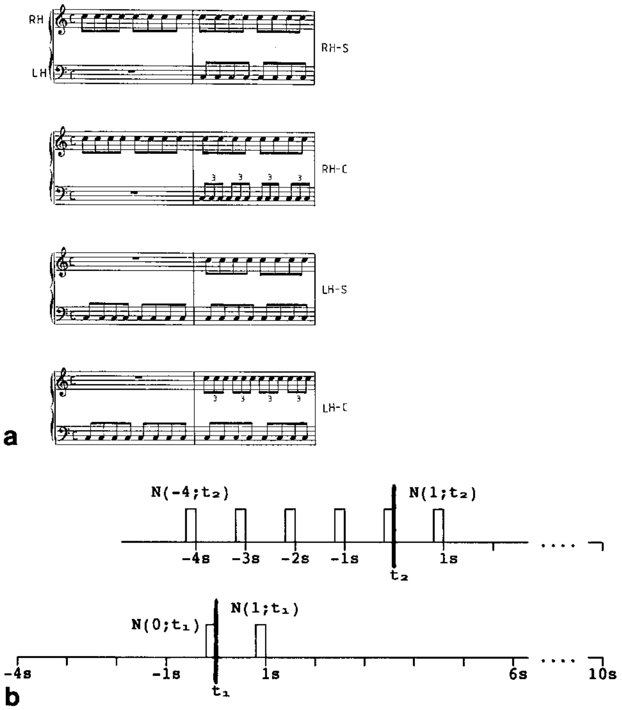

Fig. 1. **a** The four rhythmic tasks in note script. RH-S and LH-S: quavers against quavers; RH-C and LH-C: quavers against triplets. **b** Sketch of periods of measurement of the epoch for statistical analysis. White columns indicate time intervals from which mean amplitudes of DC-potentials were calculated. Intervals were either time locked to t_1 (bottom) or t_2 (top)

times t_1 and t_2. The only instruction was to chime in with the other forefinger some seconds after the first one. Ss were advised to perform the movements for about 12 to 18 s after t_1. Again, they were free to stop performance at their own volition. However, trials in which duration of performance was less than 10 s were excluded from the analysis. Ss had to tap in accordance with a precise relative timing. An absolute time scale, e.g. to tap quavers against triplets within a fixed time epoch was not emphasized.

Experimental procedure

In a training session of about 10 trials of each task, Ss became acquainted with the experimental requirements. During the subsequent experiment, the order of the four tasks was randomized. After a trial had been finished, a slide was projected on a screen in front of the S with a delay varying between 4 to 8 s. After the slide, Ss were free to decide when to initiate the next trial. Before starting the task and during its execution, Ss had to fixate on a point straight ahead in order to prevent eye movements. To ensure a sufficient resting period trials starting earlier than 8 s after the slide were not used for averages. Ss were instructed to perform the task as accurately as possible. They had no visual control of the movements (hands were hidden under wooden boxes) and no auditory control either (hearing was masked with white noise of 60 dB).

Ss were comfortably seated in an EEG chair, the arms being abducted to about 50 deg at the shoulder. S's forearms lay pronated on an arm rest mounted on sides of the chair. Forearm, hand and forefinger of either side were fixed in a manipulandum which allowed Ss to freely flex and extend their forefingers. Angular positions were measured by potentiometers at the proximal finger joints. In the resting period the two index fingers lay relaxed on the plates. Sequences were initiated by extending the index finger. A signal of the potentiometer served as trigger for movement onsets at t_1 and t_2.

Data acquisition

Details of DC recording methods have been described elsewhere (Lang et al. 1988a, 1989). EEG was recorded from F3, Fz, F4, C3*, (1 cm anterior to C3 to overlie the hand area of the primary motor cortex; Shibasaki et al. 1980), Cz* (1 cm anterior to Cz), C4* (1 cm anterior to C4), C1* (10% left of Cz*) C2* (10% right of Cz*), P3, Pz, and P4. Linked ears served as reference. The frequency band of amplification ranged from DC to 30 Hz (upper cutt-off frequency). Interelectrode impedance at 10 Hz was reduced to less than 1 kΩ. In addition, EOG (medial upper versus lateral lower orbital rim; frequency band 0.0015 to 35 Hz) and EMG (right and left M. extensor indicis, frequency band 0.3 to 700 Hz) were recorded. Data were acquired in digital form at a rate of 100 samples/s using a 12 bit analog-to-digital converter (MicroVAX II). In an off-line procedure, each trial was controlled for artifacts caused by eye, head or orofacial movements. Due to the free selection of t_2, the delay between t_1 and t_2 (dt) varied within and between subjects. Only those trials were included for averaging in which dt ranged between 3 and 7 s and in which performance was longer than the analysis time of 10 s after t_1. In each condition, at least 50 artifact-free trials were averaged.

The analysis epoch started 4 s prior to t_1 and lasted 14 s. Baseline was taken from the first 1 s of the epoch. Data were averaged twice, with triggers set either at t_1 or at t_2. All averages were referred to the same baseline mentioned above.

Data analysis

Two approachs were used to analyse the data: DC potential amplitudes were used for statistics. In addition, radial current densities across the scalp were mapped in order to examine the topography of cortical activity.

DC potential amplitudes. In order to describe event-related DC potential shifts, mean amplitudes across periods lasting 200 ms (20 consequtive data points) were calculated (referred to the baseline taken from the first second of the analysis period) as shown in Fig. 1b. Periods were selected time-locked to predominant events within the task:

- $N(0; t_1)$: Bereitschaftspotential (BP) preceding the initiation of the first finger.
- $N(1; t_1)$: Negative DC shift associated with movements of the first finger.
- $N(-4; t_2)$, $N(-3; t_2)$, $N(-2; t_2)$, $N(-1; t_2)$, $N(0; t_2)$: Negative DC shifts preceding the onset of the second finger.
- $N(1; t_2)$: Negative DC shifts during bimanual performance.

For statistics, dependent variables were tested selectively for each electrode by the repeated MANOVA procedure (SPSSX software) using the within-subject factors "H" (side of the performing hand; right or left) and "C" (task-complexity; simple versus complicated rhythm).

Radial current density analysis. Topographic mapping offers the possibility to assimilate spatial dependencies of scalp potential data into a series of images. Maps of isopotential fields have the disadvantage of being a function of reference and to be rather widespread due to volume conduction. Therefore, radial current densities in the scalp are calculated and mapped. This procedure, as suggested by Hjorth (1975) and Nunez (1981) has the advantage to be reference-free and to decrease the effect of volume conduction. To estimate radial current density, the scalp distribution of DC-potentials was interpolated between electrode positions by use of polynomial cubic splines (Perrin et al. 1987). Based on such a "potential-surface continuum" the radial current density across the scalp was estimated by applying the 2-dimensional laplacian operator. The method is described in detail by Lindinger et al. 1990. For calculations and display of images, a simple head model is used: The scalp is assumed to be a square with left/right boundaries at T3/T4 and inferior/posterior boundaries at Fp1, Fp2/01, 02. For boundary estimation it is assumed that potentials decrease continuously to zero outside of the square as a function of distance.

Activations of cortical areas cause local shifts of the cortical DC-potential as demonstrated by surface-to-depth recordings in animals (e.g. Sasaki and Gemba 1982) or by subdural electrodes in humans (Neshige et al. 1988). Both techniques demonstrated increased surface-negativity of cortical areas when activated prior or during movements (Sasaki and Gemba 1982; Neshige et al. 1988). Therefore, an area of the map having a maximum of current density with the current flow directed into the scalp (due to surface-negativity of the cortex) was taken as being indicative of activated cortical areas.

Motor performance. In an off-line procedure, the start of finger extensions and the completion of finger flexions were marked by triggers for each tapping movement. This was done to find out the ways by which Ss coordinated bimanual tappings of different rhythms (quavers against triplets). For this purpose, temporal relations of starts and completions of tappings between the two hands were measured. Furthermore, Ss were interviewed about the stratagies they had used.

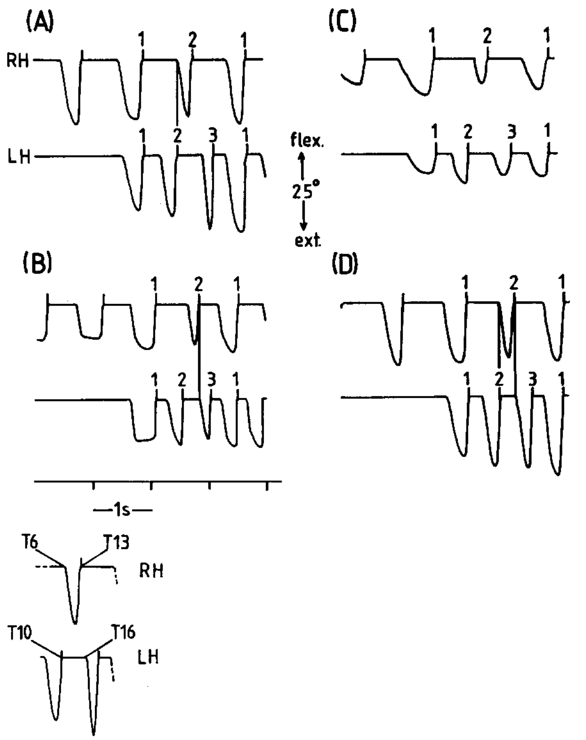

Fig. 2 A–D. Angular positions of index fingers of the right hand (RH) and of the left hand (LH) are displayed as a function of time (goniometer readings), finger flexion (flex.) is upward, finger extension (ext.) downward. Ss were classified into four groups (**A–D**). For each group, the characteristic pattern of bimanual coordination is demonstrated in the respective part of the figure. Always the same condition, RH-C, is performed: the right hand starts with 2/s rhythm (quavers), the left hand joins in with the 3/s rhythm (triplets). During bimanual tapping, the first tapping of either side is completed at the same time (cf. the temporal coincidence of time point "1"). In **A**, **B** the 2nd tapping of the right hand is temporally related either to the 2nd (cf. part **A**) or the 3rd (cf. part **B**) tapping of the left hand. In **D**, temporal relations exist for both events. Each event (start of extension and completion of flexion) has been marked by triggers. Important events are: T6 for starting and T13 for completing the 2nd tapping of the 2/s rhythm; T10 for completing the 2nd and T16 for starting the 3rd tapping of the 3/s rhythm. Table 1 gives mean latencies between temporally related events of the two sides

Results

Motor performance

The mean latency between t_1 and t_2 was 5.0 s across all subjects and conditions. Latencies were only slightly larger for the complicated rhythms than they were for the easy ones: 4.8 s (SE 0.5) in RH-S, 4.7 s (SE 0.5) in LH-S, 5.1 s (SE 0.7) in RH-C, and 5.0 s (SE 0.6) in LH-C.

Figure 2 shows the temporal relations between movements of the two hands when tapping quavers against triplets. The whole sequence was composed of periods containing 2 tappings against 3. Within these periods, always the 1st tapping of the 3/s sequence coincided with the 1st tapping of the 2/s rhythm. A classification of Ss into four groups was possible based on the temporal relations between the 2nd and/or the 3rd movement of the 3/s sequence on one side and the 2nd movement of the 2/s sequence on the other side (Fig. 2; Table 1): Group A (3 Ss) finished the 2nd tapping of the 3/s rhythm at about the same time when starting the 2nd tapping of the 2/s rhythm. Group B (6 Ss) started the 3rd tapping of the 3/s rhythm when finishing the 2nd tapping of the 2/s rhythm. Group D (5 Ss) had both features that of Group A and that of B, whereas Group C (including only 1 subject) had none of these temporal relations. Here, the subject interposed the second tapping of the 2/s task between the second and third tapping of the 3/s rhythm.

All Ss had learned to perform quavers against triplets by acoustic feedback. The internal use of rhythmic music or sounds was judged to be helpful during the performance.

General course of DC potential shifts

Figure 3 gives the example of a single subject. Figure 4 shows the grand average of negative DC

Table 1. T10-T6: Latency between the completion of the 2nd tapping of the 3/s rhythm (T10) and the start of the 2nd tapping of the 2/s rhythm (T6). T16-T13: Latency between the start of the 3rd tapping of the 3/s rhythm (T16) and the completion of the 2nd tapping of the 2/s rhythm (T13). For illustration see Fig. 2

	Mean latencies of each subject (ms)			
Typ (A): (3 Ss)	T10–T6 in RH-CO:	10, 30, 20 ms	in LH-CO:	60, 10, 20 ms
Typ (B): (6 S)	T16–T13 in RH-CO:	−70, −30, −20, −60, −10, −10 ms	in LH-CO:	−60, −00, −00, −40, −30, −20 ms
Typ (C): (1 S)	T16–T13 in RH-CO:	110 ms	in RH-CO	280 ms
	T10–T6 in RH-CO:	−120 ms	in LH-CO:	−120 ms
Typ (D): (5 Ss)	T10–T6 in RH-CO:	80, −40, −50, 80, 20 ms	in LH-CO:	20, −10, −80, 40, 20 ms
	T16–T13 in RH-CO:	20, 60, −60, 60, 00 ms		40, 60, −60, 80, 00 ms

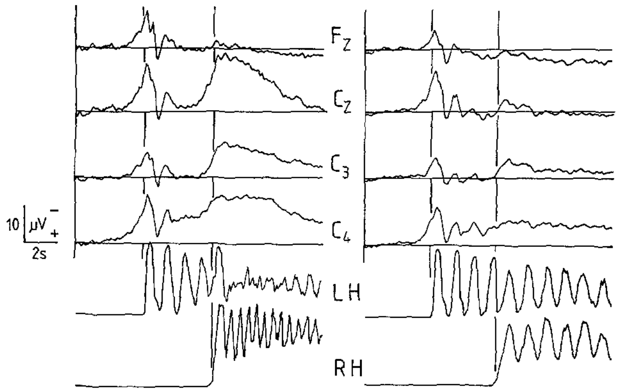

Fig. 3. Movement-related DC shifts of a single S, time-locked to t_1 (vertical line when the S starts to move the left hand (LH)). LH-C: left side, LH-S: right side. Bottom: Goniometer readings for the left hand (LH) and the right hand (RH); averages across all trials. Starts of LH and RH are marked by vertical lines. Note, there is a large negative DC shift before RH starts to tap the triplets (LH-C)

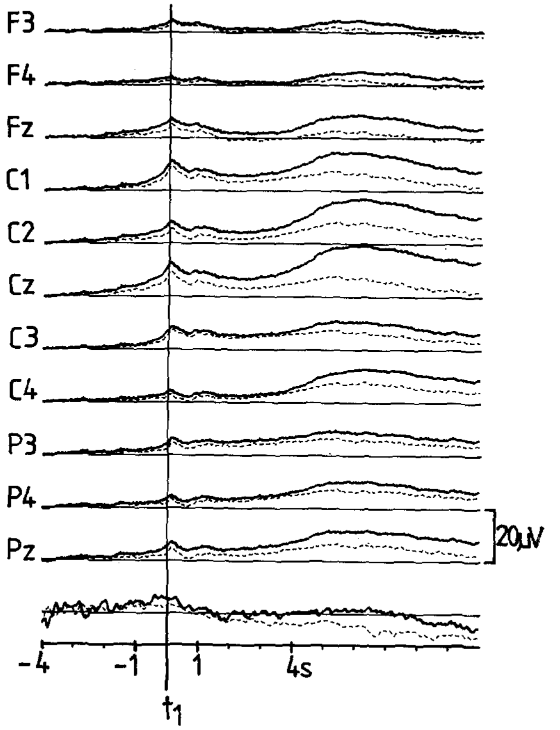

Fig. 4. Grand average across all 15 Ss, time-locked to t_1. RH-S is displayed by the thin, hatched line; RH-C by the thick line. Negative up

shifts (across all Ss) for RH-S and RH-C as averaged time-locked to t_1. A slow negative DC shift, the Bereitschaftspotential (BP) precedes this event having its maxima in recordings of the central midline (Cz*, C1*, C2*; $N(0; t_1)$ in Cz*: -5.4 µV, SE 1.2 for RH-S; -6.8 µV, SE 1.5 for LH-S; -8.7 µV, SE 1.5 for RH-C; -7.9 µV, SE 1.4 for

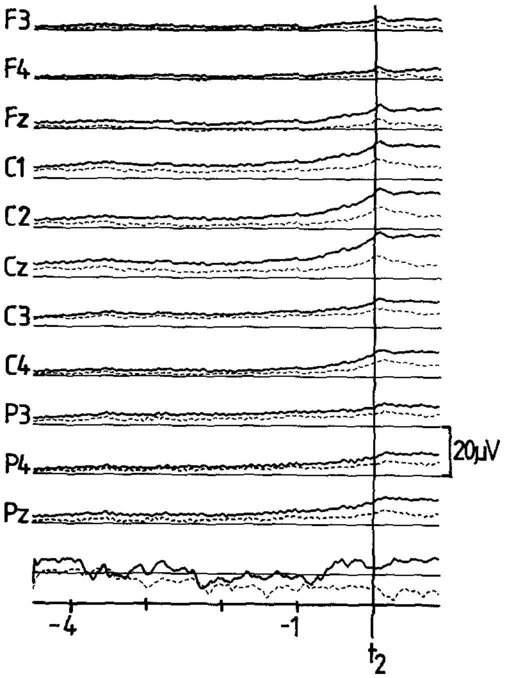

Fig. 5. Grand average across all 15 Ss, time-locked to t_2. RH-S is displayed by the thin, hatched line; RH-C by the thick line. Negative up

LH-C). When moving at 2/s with the right hand a sustained negative DC shifts remains in central and, to a smaller extent, in parietal recordings. In centro-lateral recordings (C3* and C4*), this negativity is larger over the left hemisphere which is contralateral to the movement: For instance, in RH-S, amplitudes of $N(1; t_1)$ were 5.0 µV, (SE 1.1) in C3* but 1.2 µV (SE 1.0) in C4*. The initiation of the second rhythm by the left hand at t_2 is preceded by a slow negative DC shift. Because of variable delays between t_1 and t_2, this shift can best be studied in averages time-locked to t_2 (Fig. 5): It is considerably larger in RH-C than than it is in RH-S. Bimanual performance after t_2 is associated with a sustained negative DC shift.

Topographical distributions of radial current densities

are displayed and described in Fig. 6. In general, maxima of radial current densities with current flow entering the scalp were found in three different areas of the maps: Left centro-lateral (area of C3*), right centro-lateral (area of C4*), and centro-mesial (area of Cz*). In the simple tasks (RH-S, LH-S), current flow into the scalp was found in centro-lateral areas: When tapping with the right finger, radial current density was high in the left centro-lateral area; when tapping with both

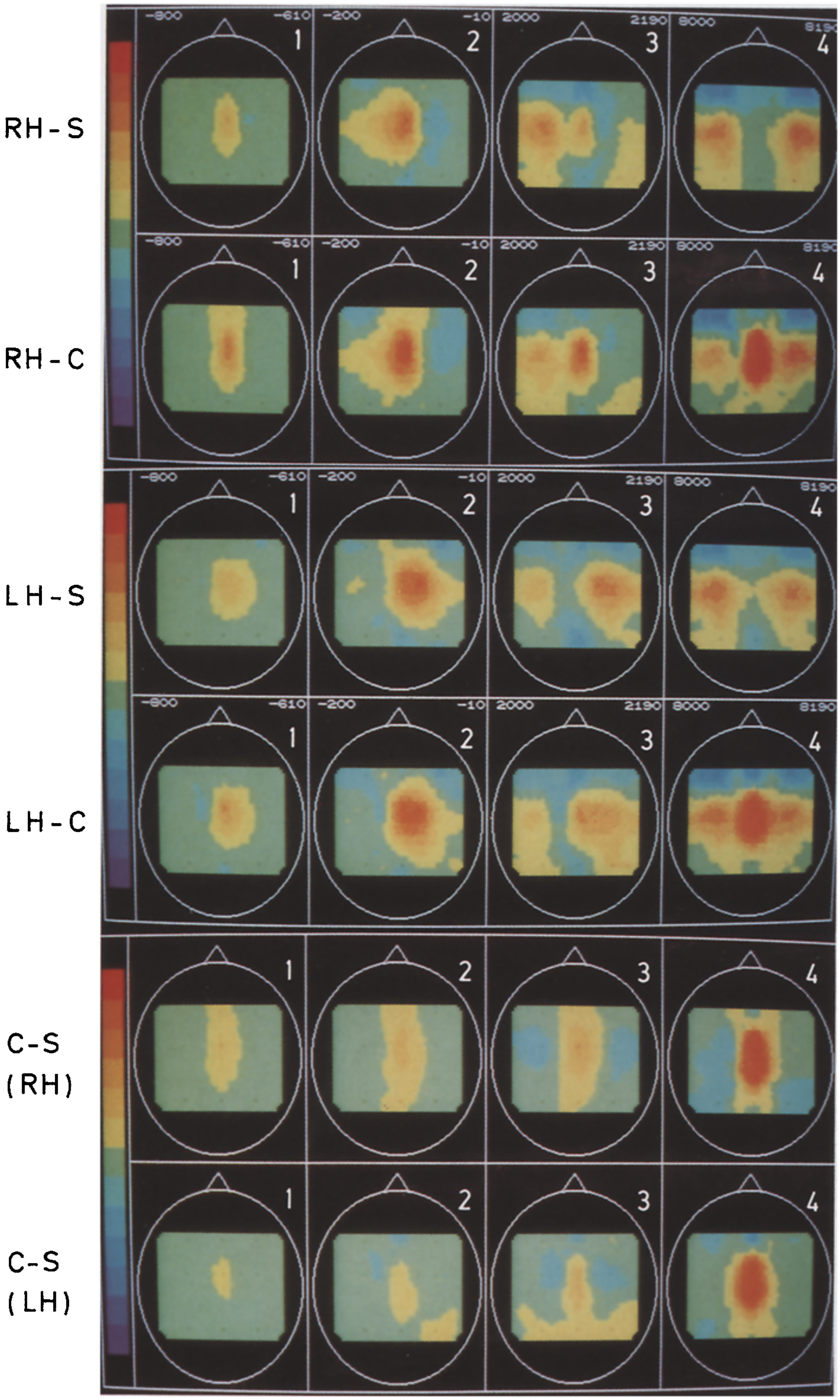

Fig. 6. Maps of radial current density across the scalp. Maps are based on DC-potential amplitudes as measured time-locked to t_1. Maps no. 1 and 2 are taken from the BP period preceding the initiation of the first sequence (600 to 800 ms, or 200 to 0 ms, respectively, before t_1). Map no. 3 displays current densities when tapping 2/s (quavers) with one finger (2 s to 2.2 s after t_1), whereas map no. 4 displays bimanual performance (8 to 8.2 s after t_1, a time at which bimanual movements were executed in all trials). The upper four rows present maps for conditions RH-S, RH-C, LH-S, and LH-C. In the lower two rows, corresponding complex and simple rhythmic tasks have been subtracted. Colour "green" indicates that current density is zero, current flow entering the scalp (due to cortical surface-negativity) is indicated by red, exiting the scalp by blue colours. For both directions, scaling of colours is proportional to radial current densities. All maps are equal scaled

fingers, high radial current densities were found in centro-lateral areas of both sides. Current flow entering the centro-mesial area of the scalp (area of Cz*) was almost absent in the simple rhythm. In contrast, when moving quavers against triplets very high current flow densities were present in the centro-mesial area of the scalp with a maximum in Cz*. When subtracting maps of corresponding complicated and simple tasks (RH-C minus RH-S; LH-C minus LH-S) it is obvious that

Table 2. Results of repeated analysis of variance (MANOVA procedure; SPSSX): Effects of within-subject factors "C" (task-complexity; complex versus simple rhythm) and "H" (performing *h*and; right or left) on DC-potentials

		F3	F4	Fz	C1*	C2*	Cz*	C3*	C4*	P3	P4	Pz
N(=; t_1)	C	F=0.6	0.1	3.0	4.5	7.1	_25.2_ #	0.7	1.3	5.1	2.4	7.0
	H	F=1.5	0.6	1.8	1.4	4.7	4.0	1.0	5.7	0.0	0.2	0.3
	HxC	F=0.6	0.1	0.7	1.1	0.6	1.3	0.7	0.1	0.0	0.1	0.3
N(1; t_1)	C	F=0.0	0.0	1.2	6.9	4.3	_10.3_*	0.3	0.7	5.8	7.1	_9.8_*
	H	F=2.0	0.0	1.0	_14.1_*	_25.9_ #	1.4	_13.0_*	_30.7_ #	7.3	1.7	0.3
	HxC	F=0.3	0.0	1.1	0.9	0.8	1.2	0.2	0.2	0.4	1.6	0.0
N(−4; t_2)	C	F=0.0	0.0	2.0	_10.2_*	6.2	_11.8_*	1.5	1.4	7.7	_9.6_*	_13.7_*
	H	F=0.9	0.0	0.1	_14.4_*	_19.7_**	2.4	_17.3_*	_34.3_ #	8.9	1.6	1.3
	HxC	F=0.7	1.0	1.6	1.7	1.7	1.6	1.1	1.1	0.1	0.6	0.1
N(0; t_2)	C	F=0.0	0.0	2.9	_25.0_ #	_14.0_*	_24.9_ #	2.6	4.9	4.9	6.1	_14.7_*
	H	F=0.7	0.1	0.6	1.2	2.9	0.3	3.8	5.5	4.2	0.2	1.4
	HxC	F=0.6	0.2	1.1	0.1	0.1	0.0	0.3	0.2	0.9	3.5	0.9
N(1; t_2)	C	F=3.1	1.9	_10.8_*	_68.8_ # #	_42.8_ # #	_63.1_ # #	_15.4_*	_16.4_*	_15.8_*	_13.3_*	_31.7_ #
	H	F=0.1	0.1	0.2	4.0	0.0	0.0	3.6	0.2	0.2	0.1	0.2
	HxC	F=0.6	0.7	1.1	0.3	0.3	0.0	0.2	0.0	1.6	2.3	1.9
dF=1.14		$p<0.01$ *	$p<0.0001$ #			$p<0.001$ **	$p<0.00001$ # #					

the additional activation of the centro-mesial cortex in the complex situation constitutes the main physiologic difference between these tasks (Fig. 6).

Effect of "task complexity" on negative DC-shifts

ANOVAs showed that in general, negative DC-shifts were larger for the complicated rhythm than they were for the simple ones. Differences had their maxima in Cz*, C1*, C2*, and were significant here (see Table 2). The effect of task complexity was even true for DC potentials at time intervals in which the ongoing performance did not differ between conditions (cf. N(0; t_1) and N(1; t_1) in Table 2). Conditions differed by "task-complexity" already 4 s before starting the second sequence at t_2 (cf. N(−4; t_2 in Table 2; for Cz*: F=11.8, $p<0.01$). This difference increased on approaching t_2: For N(0; t_2), high and significant differences were found for Cz*, C1*, C2*, Cz*, and Pz (for Cz*: F=24.9, $p<0.0001$). When moving with the two fingers, differences between complex and simple tasks was even larger (for Cz*: F=63.1; $p<0.00001$) than they were before t_2. E.g. the mean amplitude of N(1; t_2) was 4.8 µV (SE 1.1) in RH-S but as much as 18.7 µV (SE 1.2) in RH-C.

Effect of "side of performing hand" on negative DC-shifts

When performing the first sequence, DC potentials (N(1; t_1)) were lateralized in centro-lateral recordings (C3*, C4*, but also in C1* and C2*) with larger amplitudes contralateral to the moving hand. This led to significant effects on amplitudes in C3*, C4*, C1*, C2* (cf. Table 2). On approaching t_2, this effect disappeared because the other finger prepared to move: The "side of the performing hand" affected N(−4; t_2) but not N(0; t_2).

Discussion

Negative DC potential shifts during bimanual tapping

When tapping bimanually in the same rhythm, primary motor cortices (MI) of both hemispheres became surface-negative causing current flow entering the scalp around C3* and C4*. When tapping quavers against triplets, in addition to MI cortices the centro-mesial cortex was activated. The activation of the centro-mesial cortex for the complicated task was displayed by radial current density maps and tested by analyses of DC-potentials.

In a previous study, we compared simultaneous with sequential movements of the two index fingers (Lang et al. 1988b). In Cz*, C1*, and C2*, performance-related, negative DC shifts differed significantly between these two tasks with the higher amplitudes occurring during the sequential movements. The difference between these two tasks averaged 4.2 µV in Cz* across all Ss within the first second of performance. The reason for this additional negativity in the centro-mesial area in the sequential task might be that now starting signals for movement initiations are dissociated between the two sides: Movement-initiation on one side is associated with inhibition on the other and vice versa. Switching for movement-initiation between the two sides is more demanding than to move in synchrony. In fact, patients having lesions of the mesial, fronto-central cortex are frequently falling back to simultanity when asked to perform sequential movements (Lang et al. 1988c).

In the present study, Ss had to meet two demands, (1) to switch for movement initiation from one side to the other. But (2) they had to act according to a precisely defined timing pattern with different intervals between the successive tappings. These demands caused negative DC potentials in Cz* of a magnitude never observed before: 18.7 μV in RH-C. Compared to DC potentials in synchronous tapping, there was an increase in amplitude in Cz* of 14 μV which is three times larger than the difference between the sequential and simultaneous movements of in the previous study (4.2 μV).

As already shown by Deutsch (1978) and Klapp (1979) we seem to have a common time base (or timing structure) for movement initiations on both sides when performing different rhythms. Starts and, in particular, completions of tappings are precisely performed according to this timing structure. It seems likely to assume that demands on timing of volitional actions as well as the motivational and intentional involvement to act are the main cause for the pronounced activation of the centro-mesial cortex in the complicated rhythm. These physiological findings fit quite well with clinical observations in patients having unilateral lesions of the SMA. Foerster (1936) made the following observations in 40 patients in whom he had removed area 6aß (SMA) because of epilepsy: "Composed movements exhibit a loosening of their structure. There is a disruption of the fluent continuity by which single motor elements are spatially and temporally linked together. Single motor elements are performed separately, there are delays between them, one element can be omitted for a while and sometimes, an additional, "extra" impulse of will must be given for its initiation" (translation of the original text, p. 279). Jonas (1981) made similar observations for speech production when describing symptoms such as: hesitations during speech, explosive speech, running of phonemes together, variability in the rate of speech emission and speech arrest. In the paper of Jonas, it is of particular interest that phonemes and the sequence of phonemes remained correct (a function for which the area of Wernicke and, perhaps, basal ganglia are responsible). There were only impairments of the timing structure. Cortical lesions in the patients as observed by Foerster and Jonas can not exclusively be attributed to the SMA. Rather, lesions extended into lateral parts of the premotor cortex and into other areas or the frontal cortex. We have examined 15 right-handed patients having chronic lesions of the dorso-mesial frontal cortex including the SMA in a simple sequential task which required alternations between finger movements of the two sides (Lang et al. 1988c). These patients showed frequent omissions of movement initiations on one side while continuing to move at the other side.

DC potential shifts before the second hand joins in

A slow negative DC shift of increasing amplitude preceded t_2. Before t_2, the ongoing 2/s performance was the same in corresponding complex and simple tasks (right-handed tapping in RH-C and RH-S; left-handed tapping in LH-C and LH-S). Furthermore, corresponding simple and complex tasks had the same initial movement which started the second sequence at t_2. Despite of these congruencies, DC potentials started to differ between complex and corresponding simple tasks as early as 4 s before t_2 with higher amplitudes occurring with the complex tasks. In the beginning (4 s before t_2) this difference was significant in mesial, central and parietal (Cz*, C1*, and Pz at $p<0.01$) but also in lateral parietal recordings (P4 at $p<0.01$ and P3 at $p<0.05$). On approaching t_2, a clear maximum of this difference was found in centro-mesial recordings indicating an activation of this cortical area in the complex tasks. The centro-mesial cortex mainly contains the SMA. Two conclusions can be drawn: (1) DC-potentials indicate that task-specific preparation precedes performance as early as about 4 s. (2) Cortical activation due to task-specific preparation may be more widespread (centro-mesial and parietal) in the beginning of this period, but in later stages, the activation of the centro-mesial cortex (including the SMA) clearly prevails. A more detailed description of the processes that constitute task-specific preparation could give a closer insight into the role of the centro-mesial cortex, say SMA:

Concepts that the SMA subserves anticipatory postural adjustments (Massion et al. 1989) or instruction-induced pre-adjustements of sensori-motor reactions (Tanji 1984) cannot explain present findings. Rather, this finding could be explained by two models of SMA function which are currently discussed in the literature:

The SMA and task-specific anticipatory "programming". Many observations indicate that not just the execution of the initial movement is programmed in motor sequences but rather a number of movements: Complex sequences of learned movements can be executed at a rate too fast to be guided by continuous sensory feedback or for the individual components to be each under conscious control (Keele 1968; Sternberg et al. 1978). In speech production, one realizes that whole sentences are prepared in advance when observing anticipatory phonematic paraphasias in the speech of healthy subjects (e.g. "I *sope so*" instead of "I hope so"). It is, therefore, reasonable to assume that not only the first tapping is programmed in advance when the second hand is brought in but rather the whole sequence (or a longer period of it). Furthermore, the intended action – to join in with the second hand – has consequences for the ongoing performance. These consequences are conflicting when moving quavers against triplets. Therefore, not only the 3/s rhythm has to be programmed but also its integration into the 2/s performance underway. Bernstein (1984) proposed that Ss use memory-based "models of the future" to prospectively control behaviour and its integration into actions being underway. According to Goldberg (1985), the SMA has the function of anticipatory programming by using internal-based models.

The SMA tranduces motives and intentions into action. Kornhuber (1984a, b), Kornhuber et al. (1989) and Deecke et al. (1985) distinguish three stages of volitional actions, (1) selection between motives, (2) selections of plans, and (3) the selection of the right moment to initiate. Concepts such as of that of Goldberg (1985) still assume that cognitive representations of goals and plans initiate actions and, therefore, do not consider the existence of a system that is responsible to transduce motives and intentions to act into effective actions. According to the hypothesis of Kornhuber et al. and Deecke et al., the initiation of any kind of volitional action is centralized in the SMA. In order to select the right moment for giving the starting signal, the SMA should have access to or control over anticipatory motor planning and its integration into actions underway, which themselves may be organized in various parts of the brain such as parietal cortex, basal ganglia or cerebellum.

Constraints of the central timing system to use only one time base for movement initiations in volitional acts (see Introduction and the analysis of movements in the present study) point to the centralization of this system in the brain. Such a rigid control of movement initiation may be necessary because of the consequences for posture and motor behaviour underway.

Activation of both primary motor cortices during left-handed tapping

Figure 6 (maps no. 3 in LH-S and LH-C) shows the phenomenon that unilateral, left-handed tapping is associated with current flow entering the scalp in the area of C4* (centro-lateral) but also that of C3* (ipsilateral to the movement). Unilateral, right-handed tapping (Fig. 6, map no. 3 in RH-S and RH-C) is associated with current flow contralateral to the performance. In a previous study on right-handed Ss it has been found that movements of the right hand cause a larger hemispheric asymmetry of performance-related DC shifts (comparing C3* with C4*) than movements of the left hand (see Fig. 2 in Lang et al. 1989). This was due to the fact that the ipsilateral side (C3*) had a large negative DC shift in left-sided movements. Recent epicortical recordings in humans (Neshige et al. 1988) and recordings of magnetic fields (Cheyne and Weinberg 1989; Cheyne et al. 1989) have provided evidence for an ipsilateral activation of the MI cortex in unilateral movements.

A possible hypothesis explaining the present data could be that the "dominant" left MI cortex is activated during movements of the left hand in right-handed Ss to a larger extent than is the "minor" right MI cortex during movements of the right hand. In fact, behavioural analyses of bimanual, sequential movements indicate that the right hand interferes to a larger degree than the left one (Lang et al. 1988c; Peters 1981).

The bilateral activation of the MI cortex may reflect the tendency of the nervous system to act in bilateral synchrony when moving the finger. In patients having unilateral lesions of the SMA, a tendency to switch from a sequential into a simultaneous movement pattern has been found (Lang et al. 1988c). Furthermore, the clinical symptom of mirror movements has also been observed after lesions of the mesial fronto-central cortex (Chan and Ross 1988; authors' observations, unpublished). This corroborates the physiological finding that the mesial fronto-central cortex is activated in sequential movements in which initiation of movement on one side is associated with inhibition on the other side and vice versa.

Temporal pattern of the Bereitschaftspotential

The Bereitschaftspotential preceding a movement has been suggested to have mainly two sources, the SMA and the primary motor cortex (MI). Furthermore, a temporal sequence of activation has been proposed: SMA may be activated first, then MI (for review see Deecke 1987). Figure 6 (maps no. 1 and 2) would substantiate this view. First, there is a localized maximum of radial current density (current flow into the scalp) in the centro-mesial area (map no. 1), then the centro-lateral area has increased current densities as well (map no. 2). This finding may demonstrate the importance of spatial transformations before studying changes in time (cf. Lehmann 1984; Gevins 1987). Certainly, this procedure will become more powerful when more electrodes are used.

Does the centro-mesial activation habituate during performance?

Figure 3 shows a clear decline of DC-potentials in the last 4 s of the analysis period. A similar decline of performance-related negativity has been found in the sequential and simultaneous bimanual movements of the previous study. This effect has not systematically been tested so far. It may reflect habituation due to an increasing automatization, an effect which may become useful for testing the ability of Ss to transfer a voluntarily controlled process into automaticity.

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