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ERP correlates of linear hand movements in a motor reproduction task

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Abstract

Blindfolded participants performed one-dimensional movements towards a mechanical stop and back to the start. After a varying delay, they had to reproduce the encoded target position by a second mechanically unrestricted movement. Average event-related potentials accompanying the "encoding" and the "reproduction" movements revealed a biphasic waveshape over primary sensorimotor areas. The first negative deflection was the gradually increasing motor potential (MP) that precedes movement onset. This was followed by a second negative component (N4) starting about 100 ms after movement onset. Its amplitude and latency increased with increasing movement distance and reached its maximum in unrestricted movements (i.e., during reproduction) shortly before the deceleration peak. These results show that rapid hand movements are accompanied by non-continuous and highly distance specific activity changes measured over the sensorimotor cortex.

Descriptors: ERP, Arm movements, Movement related cortical potentials, Motor control

Kornhuber and Deecke (1965) were the first who systematically studied brain electrical correlates of preparation and execution of limb movements. By asking participants to voluntarily execute a simple motor act, such as to press a button at intervals of their own choice, they observed in the event-related potential (ERP) of the electroencephalogram (EEG) a gradually increasing negative shift with a maximum over the contralateral precentral region that preceded the motor response and that reached its maximum amplitude shortly after movement onset. This negative deflection was labeled "readiness potential" (RP) or "Bereitschaftspotential" (BP). Similar recording situations were extensively studied, and further research revealed descriptions of several components accompanying preparation and execution of single motor responses, which were associated with specific functions and neuronal sources (see, e.g., Brunia, 1987; Brunia & van Boxtel, 2000; Deecke, Beisteiner, & Lang, 1996; Deecke, Grözinger, & Kornhuber, 1976; Tamas & Shibasaki, 1985 for reviews).

Typically the following components are observed (e.g., Brunia, 1987; Brunia & van Boxtel, 2000): An initial slow increase in surface negativity with a maximum over the vertex electrode usually starts between 1 and 2 s prior to the motor act and was referred to as RP I or RP_{sym}. This initial negative potential has been related to activity of the supplementary motor area (SMA) and functionally to motor preparation. From about 500 ms prior to movement, ERP-amplitude is larger over the hemisphere contralateral to the used hand or finger. This part of the readiness potential, labeled RP II, RP_{lat}, or NS, is assumed to have several generators within the primary motor, premotor, and somatosensory areas. Functionally it has been associated with the specification of movement parameters dependent on the external context. The next component is the P1 (also labeled premotion positivity, PMP), a positive deflection with an onset about 50–90 ms prior to movement and a maximum at the midline parietal electrode (PZ). The functional role of this wave is not clear up to now, and it may merely reflect an epiphenomenon of the negativities measured at more anterior sites. The final premovement negative going potential starting about 10–50 ms prior to the onset of EMG (electromyogram) activity with a maximum over precentral electrode positions contralateral to the used finger (motor potential, MP, N2) reflects most likely a discharge of cells in layer V of the precentral gyrus and, thus, the cortico-spinal outflow. After movement onset, a sequence of at least 3 components has been reliably described by several authors and is sometimes termed reafferent potential (RAP) or movement-evoked potential (MEP): P2, N4, and P3. The knowledge about functional aspects and possible sources of these deflections is still sparse. They could be recorded at several sites around the central sulcus and were assumed to be associated with central and peripheral feedback mechanisms. These components appear in the EEG/ERP whenever a voluntary movement is executed by an extremity (finger, arm, foot) whereby the topography varies with

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PSYCHOPHYSIOLOGY

the side and type of the moved limb. These topographic shifts give hints about the localization of the electrical generators of these components.

While much work on movement-related potentials has been done with the aforementioned paradigm of simple ballistic movements, little is known about the electrical correlates of other types of movement preparation and execution, e.g., precision positioning movements. In a series of experiments, Grünewald and colleagues studied precision positioning movements in smooth aiming tasks (e.g., Grünewald & Grünewald-Zuberbier, 1983; Grünewald-Zuberbier & Grünewald, 1978; Grünewald-Zuberbier, Grünewald, Runge, Netz, & Hömberg, 1981). The authors observed that the ERPs during slow movements differed from those accompanying rapid ballistic movements. While the motor potential/readiness potential rapidly declines after initiation of a ballistic movement, a sustained negativity prevails when smooth movements are performed. This persisting negativity, with a larger amplitude contralaterally than ipsilateraly to the moving hand, lasted until the end of the intended action and was labeled "goal-directed movement potential."

A number of previous studies also showed that movement-related cortical potentials (MRP) are sensitive to the variation of external motion parameters, like position and velocity of an effector (i.e., of kinematics) as well as of internal forces (i.e., of kinetics). Slobounov and colleagues (1999), for example, reported an amplitude increase in a late component of MRP (-100 to $+100$ ms) in response to an increase in inertial load applied to finger movements (similar results were previously reported by Kristeva, Cheyne, Lang, Lindinger, & Deecke, 1990). In a further study by the same research group (Slobounov, Rearick, & Chiang, 2000), a gradual increase in amplitude in the same time range was observed as the amplitude of motion increased. Other movement variables, like movement speed (Cooper, McCallum, & Cornthwaite, 1989) or rate of force development (Slobounov, Ray, & Simon, 1998) have also been shown to affect the amplitude of the cortical potentials preceding and accompanying the response.

The aim of the present study was to extend these findings on EEG correlates of goal directed movements. To this end, we analyzed phase-locked (evoked) brain electric activity during rapid linear hand movements in a motor matching task. Blindfolded subjects moved a handle with their right hand until it was stopped and then back to the start position. After this, they tried to reproduce the position of the stop by a second unblocked movement. Eight target positions ranging between 10 and 31 cm were implemented. The main question of interest was to what extent evoked activity measured at scalp during movement execution is related to this manipulation of the range of motion. A characteristic feature of simple rapid movements is that the trajectories tend to be roughly straight and display bell-shaped velocity profiles (Atkeson & Hollerbach, 1985; Flash & Hogan, 1985; Morasso, 1981; Uno, Kawato, & Suzuki, 1989). An increase in target/movement distance is typically accompanied by kinematic changes, such as by an increase in maximum velocity and movement time (e.g., Messier & Kalaska, 1999).[1] Thus, we predicted that a variation of the target distance will affect movement parameters as velocity. Consequently, and based on the results of the previous studies showing a good sensitivity of EEG to kinematic and kinetic changes, we expected a distance specific modulation of the evoked activity especially at electrodes located close to the central sulcus. Moreover, due to the good temporal resolution of EEG, the shape of the averaged signal accompanying movement execution may provide some information about the time course of the involved control processes, e.g., whether they are continuous or phasic. We hypothesized that an increase in target distance and movement time is associated with changes in the ERP from a more phasic time course as observed with simple ballistic movements to a more continuous time course characteristic for smooth motor acts (see above).

[1]This pattern is often observed if subjects are asked to produce movements as rapidly and accurately as possible.

Methods

Participants

Twenty-three right-handed, neurologically normal students of the University of Marburg participated. They gave their written consent and received either course credit or an hourly payment. Data of five participants had to be excluded from the analysis, due to a large number of EEG artifacts. The final sample comprised eight males and ten females with a mean age of 22 years (range 19–28).

Apparatus

Participants were blindfolded and sat in front of a linear tracking device mounted on a horizontal, waist-high table. A pen-like, lightly moveable handle mounted on a sledge allowed linear forward and backward positioning movements at the mid-sagittal axis of the trunk. Participants held the pen between thumb and index finger. Eight lift-magnets could stop the movement at variable distances between 10 and 31 cm from the starting position. The starting position was the nearest possible handle location in relation to the body (approximately 10 cm in front of the body) and successive magnets were separated by approximately 3 cm. To minimize head and gross body movements, the chin and the front of the head were supported by an adjustable headrest. Earphones were used to present acoustic signals and to protect against noise effects of the device. Participants could not see the apparatus, neither before nor during the experiment.

Experimental Procedure and Design

A trial started with an auditory warning stimulus (250 Hz) followed after a fixed interval of 3 s by a first imperative go signal (2000 Hz). The subjects were instructed to move the manipulandum fast towards the stop and then immediately backwards to the start position. After the second go signal (2000 Hz), participants had to reproduce the length of the first movement as accurately and rapidly as possible without corrections. The inter-trial-interval was randomly varied between 3000 and 3350 ms.

The time between the two imperative signals (go 1 and go 2), i.e., the delay between encoding and reproduction movement, was varied systematically such that the reproduction was initiated after less than 500 ms ("delay 0"), after 1000 ms ("delay 1"), and after 5000 ms (delay "5"). Since the duration of the first movement depends on the length of the movement path, we adjusted the time point of the reproduction go signal to the duration of the previous movement. Based on results from a pilot experiment, the duration d_i of the first forward+backward movement towards the target position i amounted to 1038, 1104, 1170,

1236, 1302, 1368, 1434, and 1500 ms. Accordingly, the second go signal was presented either after d_i, d_i+1000, or d_i+5000 ms in respect to the first go signal. The measured intervals between the end of the first backward movement and the second go signal amounted to 226 ms ("delay 0"), 1190 ms ("delay 1"), and 5135 ms ("delay 5") in the present study.

The conditions resulted in a 8 × 3 × 32 (Locations × Delays × Repetitions) within-participants block-design. The experiment had 12 blocks, each of them comprising 64 trials (8 locations × 8 repetitions). The delay between encoding and reproduction was held constant within one block (i.e., subjects were informed about delay duration before each block). Each participant performed three practice blocks including the three delay conditions. The order of blocks and of target positions was randomized with the constraints that two consecutive blocks or targets should correspond to different delay durations or target positions, and the whole sequence of delay or target positions should be completed before another repetition.

Recording and Data Pre-processing

Movement trajectories were recorded with an ultrasound motion device (CMS-20, Zebris Medical GmbH, Isny, Germany). The data were sampled at 100 Hz initially and analyzed with in-house software using LabView codes (National Instruments Corporation, Graphical Programming for Instrumentation, Austin, TX). Tangential velocity and acceleration were computed using standard differentiation techniques. Movement onset was defined as the time where the deviation of the recorded movement trajectory from the baseline (i.e., from the starting position) exceeded 5 mm, while movement termination was related to the point where the velocity curve first crossed the zero-line. Maximal velocity was determined for each trial and both movement phases. Additionally, during the reproduction phase minimal acceleration was also determined on a single trial basis. These values were defined only for forward movements.

The EEG was recorded from 61 AgAgCl electrodes by using a cap with an equidistant positions montage (EASYCAP GmbH, Herrsching-Breitbrunn, Germany, Montage No. 10). All scalp electrodes were referenced to the tip of the nose, grounded to the left mastoid and re-referenced offline to the average reference. Ocular movement artifacts were recorded and monitored with bipolar electrodes, placed vertically above and below the left eye (vEOG) and horizontally at the outer canthi of both eyes (hEOG). Electrode impedances were kept below 5 kΩ. EEG and EOG were amplified with a bandpath from DC to 100 Hz and a gain of 500 using SYNAMPS (Compumedics NeuroScan, Charlotte, NC) equipment. Signals were digitized with a sampling rate of 500 Hz. Acquire software (NeuroScan) was used for the collection and Brainvision Analyzer software (Brain Products, Gilching, Germany) for data analysis. DC drift was corrected according to the method suggested by Hennighausen, Heil, and Rösler (1993). Eye movement artifacts were removed by the application of a regression method (Gratton, Coles, & Donchin, 1983), while trials with other artifacts were rejected based on a threshold criterion, allowing a maximum voltage range of 250 μV within a trial segment. In the final sample of subjects, on average 78% of the trials were classified as free from artifacts (SD = 15%).

Data Analysis

The following movement parameters were defined as dependent measures and analyzed statistically by using repeated measures analyses of variance (ANOVAs) with target distance (8 levels) and delay (3 levels) as within-subjects factors: Variable error (standard deviation of the average movement endpoint), constant error (mean deviation of the moved distance from the target distance), maximal velocity, and movement time (time difference between movement onset and offset).

ERPs were baseline corrected to the defined onset of the encoding and the reproduction movement, respectively. In order to draw conclusions about distance specific differences, which arise during movement execution, we used a short baseline comprising − 10 to 0 ms before movement onset (corresponding to 5 data points). This resulted in a relatively exact adjustment of potentials around zero μV at the time point of each trigger. In general, it has been recommended to use a longer baseline, which reduces possible noise fluctuations (e.g., Picton et al., 2000). However, in the case of ERPs triggered by successive events, new effects due to event i usually "ride" on the activity that was elicited by event i-1. If this prevailing activity differs for different conditions, substantial baseline differences can result that are then captured by a long baseline and which contaminate the new effects expressed as differences relative to the baseline. The main question of interest of the present study was related to the motor control phase. Thus, in order to minimize the influence of the preceding motor planning phase on the results, the implemented baseline correction appeared to be the most appropriate procedure.

After averaging and baseline correction, averaged voltage amplitudes were measured in 6 successive 50 ms long time windows (i.e., in 0–50, 50–100, 100–150, 150–200, 200–250, and 250–300 ms intervals after movement onset). Statistical analysis was performed in a hierarchical sequence. Firstly, time window specific ANOVAs with the within-subjects factors distance (8 levels), delay (3 levels), and electrode (61 levels, see Results) were performed. This procedure aimed to detect time windows where the ERP amplitude responded to the experimental manipulations expressed in significant Electrode × Distance, Electrode × Delay, Electrode × Distance × Delay, or Distance × Delay interactions. Conditional to the results of this superordinate analysis, "electrode specific" ANOVAs were computed with the factor distance (8), providing "sensitive scalp locations" by significant main effects of this variable. The results of the superordinate "time window specific" analyses revealed no significant interactions between the factors distance and delay (see Results). Thus, when analyzing the ERPs at each electrode, one has to consider the main effects of both factors. In the present study, we focused on effects associated with varying motion distance. Accordingly, only differences across the eight target conditions are reported in detail and discussed. Besides reporting individual results of these analyses, we also plotted the *F* values of significant main effects "distance" as topographical maps in order to illustrate the topography of this effect. Moreover, aiming at a more detailed description of pronounced ERP modulations, we performed peak analyses at selected electrodes and analyzed the amplitude and the latency measures with appropriate ANOVAs. Electrode locations and time windows were selected based on the preceding analyses and on a visual data inspection. Whenever necessary, the degrees of freedom in repeated measures ANOVAs were adjusted with the Greenhouse-Geisser epsilon (Geisser & Greenhouse, 1958) in order to correct for any significant violations (Mauchly test) of the sphericity assumption. Unadjusted degrees of freedom but adjusted *p*-values will be reported.

Table 1. *Characteristic Movement Parameters Averaged for All Subjects and Each Experimental Condition*

	Target condition	Variable error (mm)			Constant error (mm)			Maximal velocity during encoding (m/s)			Maximal velocity during reproduction (m/s)			Movement time during encoding (ms)			Movement time during reproduction (ms)		
Delay		*0*	*1000*	*5000*	*0*	*1000*	*5000*	*0*	*1000*	*5000*	*0*	*1000*	*5000*	*0*	*1000*	*5000*	*0*	*1000*	*5000*
condition	*1*	21.6	25.7	29.1	57.9	48.5	47.1	0.96	0.96	0.96	0.98	0.88	0.81	183	191	188	253	265	285
	2	20.8	26.9	30.7	62.6	55.1	53.8	1.08	1.07	1.07	1.08	0.99	0.93	212	219	219	281	297	309
	3	19.6	23.4	28.5	63.1	56.4	54.1	1.16	1.14	1.13	1.15	1.08	1.02	235	242	245	307	319	333
	4	20.1	23.5	24.8	57.5	53.9	49.8	1.20	1.18	1.18	1.21	1.14	1.09	258	268	263	327	340	349
	5	18.2	21.3	25.4	51.8	49.1	42.9	1.23	1.21	1.20	1.26	1.20	1.15	286	295	294	344	355	367
	6	16.4	20.5	23.3	43.6	43.4	37.3	1.23	1.21	1.21	1.31	1.25	1.21	321	330	328	361	376	380
	7	16.6	19.7	23.8	36.6	36.5	30.3	1.23	1.21	1.22	1.36	1.29	1.25	362	369	367	377	393	400
	8	16.0	17.2	21.7	27.5	28.4	22.5	1.23	1.20	1.21	1.40	1.33	1.28	409	418	415	395	412	420

Results

Behavior

An overview of mean values of selected behavioral measures is given in Table 1.

Analysis of the variable error revealed significant main effects for factors delay ($F(2,34) = 35.24$, $p < .001$) and distance ($F(7,119) = 25.24$, $p < .001$). An increase in distance resulted in a decrease of response variability (linear contrast, $F(1,17) = 137.58$, $p < .001$), while the prolongation of the reproduction delay caused an increase of variable error (all $p < .05$).

The constant error was also affected by both factors, delay and distance, as indicated by the corresponding significant main effects ($F(2,34) = 5.45$, $p = .020$, $F(7,119) = 28.82$, $p < .001$). However, the Delay × Distance interaction was significant, too ($F(14,238) = 2.41$, $p = .048$) suggesting delay dependent changes of distance differences, which obviously followed a nonlinear function (see Table 1).

The analysis of maximal velocity during encoding revealed a significant main effect distance ($F(7,119) = 107.96$, $p < .001$) and post hoc comparisons indicated that the target conditions 1, 2, 3, and 4 differed significantly from each other and from the conditions 5, 6, 7, and 8 (all $p < .05$). In contrast to the encoding phase, peak velocity increased significantly from the first to the eighth target position (main effect distance, $F(7,119) = 241.53$, $p < .001$; post hoc comparisons, all $p < .001$). The analysis of the reproduction phase also revealed a significant main effect delay ($F(2,34) = 24.49$, $p < .001$) indicating a decrease in maximal velocity with an increase in delay (all $p < .01$). Compared with these main effects, a Distance × Delay interaction explained much less variance ($F(14,238) = 3.04$, $p = .009$) and was mainly due to somewhat different slopes over the distance in the three delay conditions.

The movement time increased with an increase in distance (main effects distance, $F(7,119) = 289.77$, $p < .001$ and $F(7,119) = 289.87$, $p < .001$ for the encoding and reproduction phases, respectively; linear contrasts, $F(1,17) = 336.33$, $p < .001$ and $F(1,17) = 353.15$, $p < .001$). Additionally, a main effect delay was also significant for both movement types ($F(2,34) = 5.50$, $p = .016$ and $F(2,34) = 10.25$, $p = .002$) indicating a tendency to perform movements slower with an increase in delay (all three delay conditions differed significantly from each other during reproduction, all $p < .05$, while movement times decreased only in the shortest condition as compared with both the others during the encoding phase, both $p < .05$).

ERPs: Encoding Phase

Figure 1 shows the ERP waveforms evoked by the encoding and the reproduction movement between 500 ms before and 1000 ms after movement onset at three midline electrodes (FZ, CZ, PZ). ERPs are grand averages across participants according to the sixth target position.

Visual inspection reveals a sequence of components previously observed as correlates of simple self-initiated ballistic movements (for review, see, e.g., Brunia, 1987; Brunia & van Boxtel, 2000). Although the present study differs from the traditional "Bereitschaftspotential" paradigm, the known components seem to be present nevertheless. After the first imperative stimulus, a negative potential arises which culminates at movement onset and which comprises the lateralized RP_{lat} (RP II), the premotion positivity (P_1), and the final motor potential (MP) traditionally assumed to represent the command to move. After movement onset, three components can be seen: a positive (P2), a negative (N4, and another positive wave (P3), all three of which have been related to sensory feedback mechanisms (e.g., Brunia, 1987).

The potentials accompanying the encoding and the reproduction movement are highly similar, although some differences are evident, e.g., that the P3 component at PZ is less pronounced during the reproduction than during the encoding movement.

In order to delineate time windows in which the ERPs are affected by the experimental manipulations, we computed a superordinate ANOVA with the within-subjects factors target distance (8 levels), delay (3 levels), and electrode (61 levels) and the mean voltage amplitude of each defined time window as the dependent variable.[2] For the encoding movement, this ANOVA revealed significant Electrode × Distance interactions for the three time windows between 150 and 300 ms ($F(420,7140) = 5.09$, 7.18, and 13.09, all $p < .001$). These effects indicate that the distances affected the mean amplitude differently at different scalp sites. All other interactions—Electrode × Delay, Delay × Distance, and Electrode × Delay × Distance—whose significance would justify a more detailed, electrode-specific analysis proved as unreliable for all six time windows. Since the large number of 61 electrodes can inflate alpha-error, we also ran the same analyses with only 17 repre-

[2]Note that the baseline activity defined for statistical analyses encompassed the immediate premovement intervals and was different from that used for aligning the traces in Figure 1.

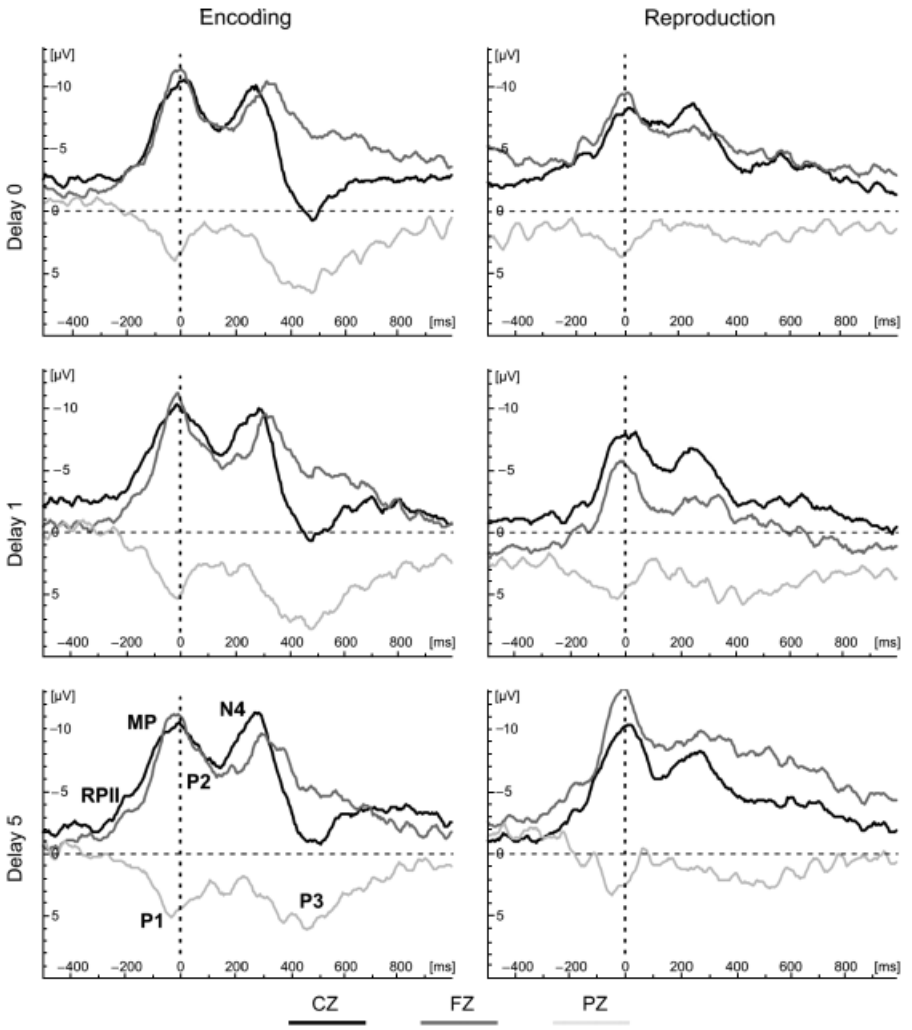

Figure 1. Evoked potentials accompanying the movements to the sixth target location in the three delay conditions "0," "1," and "5" s recorded at Fz, Cz, and Pz. The ERPs of the different delay conditions were time aligned to movement onset (vertical dashed line). The interval between −2000 and −1000 ms before the first imperative tone was used as zero-baseline.

sentatively distributed electrodes. This more conservative analysis provided the same results.

For the three time windows between 150 and 300 ms, which proved to be sensitive to the distance manipulation (see above), electrode specific ANOVAs were run with factor distance as independent and mean amplitudes of the respective window as dependent variable. The results of these electrode-specific ANOVAs are depicted as linearly interpolated F values of the significant main effect distance in Figure 2 (top). These topographic maps and the waveforms shown in Figure 2 (middle) indicate that a negative wave arises between 100 and 300 ms in respect to the defined movement onset that increases in amplitude and latency with increasing distance of the target location. The effect starts to develop at parietal electrodes and extends towards left central and midline central electrodes within the last time window. The maximum effect due to factor distance is observed at electrodes FC1 ($F = 50.46$), CPZ ($F = 50.19$), and CZ ($F = 42.28$). Due to its polarity, latency, and topography, i.e., the maximum is contralateral to the side of the moved limb, we identify this component with the negative deflection previously labeled as N4 (e.g., Brunia, 1987) and functionally related to sensory feedback processes (Shibasaki, Barrett, Halliday, & Halliday, 1980a, 1980b).

For a more thorough analysis, we searched for the most negative peaks at selected electrodes between 150 and 400 ms in the averaged ERPs of each subject and condition. The amplitude and the latency of the negative peak were then analyzed with an ANOVA with distance (8 levels) and delay (3 levels) as within-subject factors. At FC1, the analysis of the peak latency revealed a significant main effect distance ($F(7,119) = 136.01$, $p < .001$) and a significant linear contrast ($F(1,17) = 365.99$, $p < .001$), suggesting a roughly linear latency increase of the negative peak with increasing movement length (187, 202, 232, 249, 269, 292, 318, and 328 ms for distances 1, 2, 3, 4, 5, 6, 7, and 8, respectively). None of the other effects reached the significance threshold. A main effect distance was also significant for the amplitude measure of the negative peak ($F(7, 119) = 30.52$, $p < .001$). The amplitude increased linearly with an increase of movement distance (mean values were 1.86, 1.53, 0.69, 0.42, −0.54, −1.35, −1.95, −2.42 μV for target conditions 1, 2, 3, 4, 5, 6, 7, 8, respectively), expressed

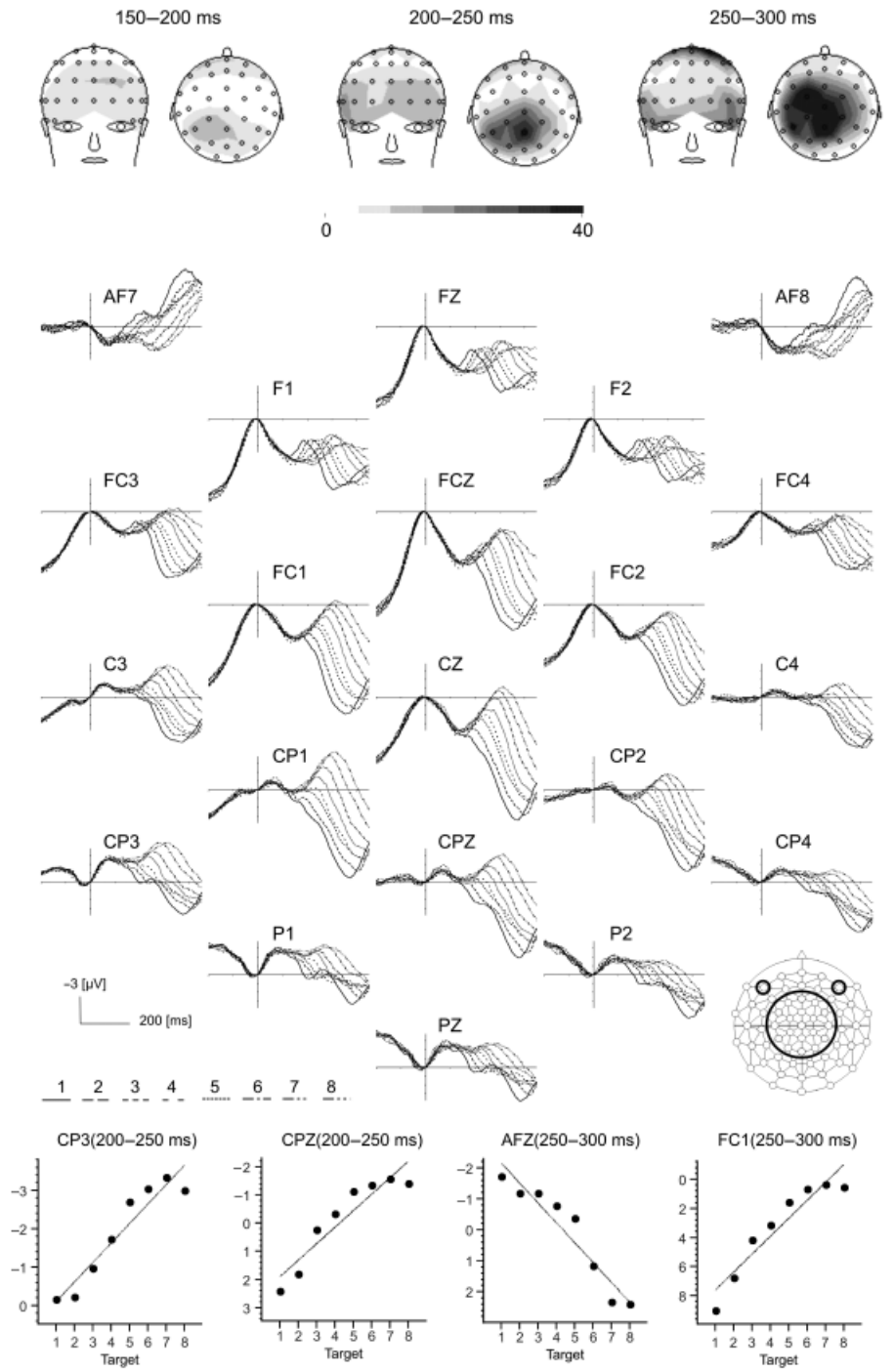

Figure 2. Results of the encoding phase. (Top) Topographical distribution of *F* values of electrode specific ANOVAs. The maps show linearly interpolated *F*-scores relating to the main effect distance in three time windows. (Middle) ERPs of the eight target conditions at selected electrodes (see insert at lower right for recording sites). (Bottom) Mean amplitudes measured for the eight target conditions at selected electrodes and in selected time windows. Note: all time scales are adjusted to movement onset.

also in a significant linear contrast ($F(1,17) = 63.63$, $p < .001$). Thus, an increase of movement distance was associated with an increase in peak latency and peak amplitude of this component.

The most anterior recording sites showed a polarity reversal of this effect, i.e., ERP amplitude decreased with increasing distance (see AF7 and AF8 in Figure 2).

ERPs: Reproduction Phase

Superordinate ANOVAs for successive time windows of the ERPs of the reproduction phase revealed significant interaction effects Electrode × Distance for the four windows between 100 and 300 ms after movement onset ($F(420,7140) = 2.42$, 2.77, 3.50, and 5.54 with $p = .010$, .004, and $< .001$). As during the encoding phase, the Distance × Delay and Electrode × Dis-

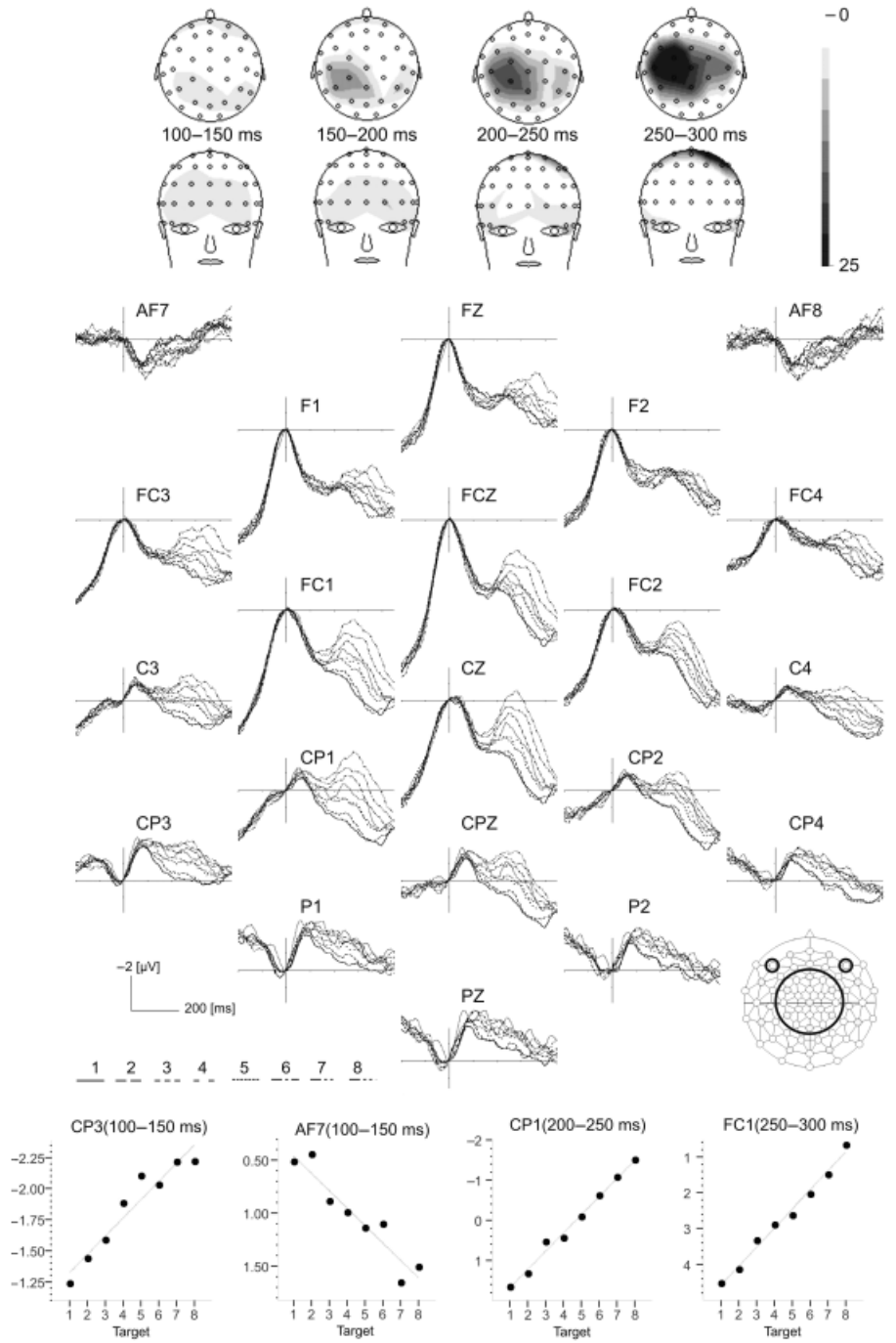

Figure 3. Results of the reproduction phase. (Top) Topographical distribution of F values of electrode specific ANOVAs. The maps show linearly interpolated F-scores relating to the main effect distance in three time windows. (Middle) ERPs of the eight target conditions at selected scalp electrodes (see insert at lower right for recording sites). (Bottom) Mean amplitudes of evoked activity measured at selected locations and in selected time windows. All times are given with respect to the onset of the reproduction movement.

tance × Delay interactions were unreliable for all time windows.[3]

The results of the detailed analysis of the interactions Electrode × Distance with electrode specific ANOVAs are summarized in Figure 3. By and large the pattern of effects is equivalent to that seen during the encoding movement. Significant differences between the movements of different length appeared at first at left centroparietal sites (from 100–150 ms) and drifted then towards left central and frontocentral sites. Again, the amplitude at parietal, central, and frontal sites increased systematically with increasing distance of the target position, while a polarity reversal occurred at an-

[3]We also found a series of significant Electrode × Delay interactions within the three windows between 0 and 150 ms ($F(120,2040) = 2.95$, 2.37, 2.83 with $p = .014$, .037, and .017). However, due to the focus of the present study on the range of motion, we did not consider them further. Moreover, the fact that neither Delay × Distance nor Delay × Distance × Electrode interactions were observed suggests that the distance manipulation affected the ERPs independently from the delay manipulation.

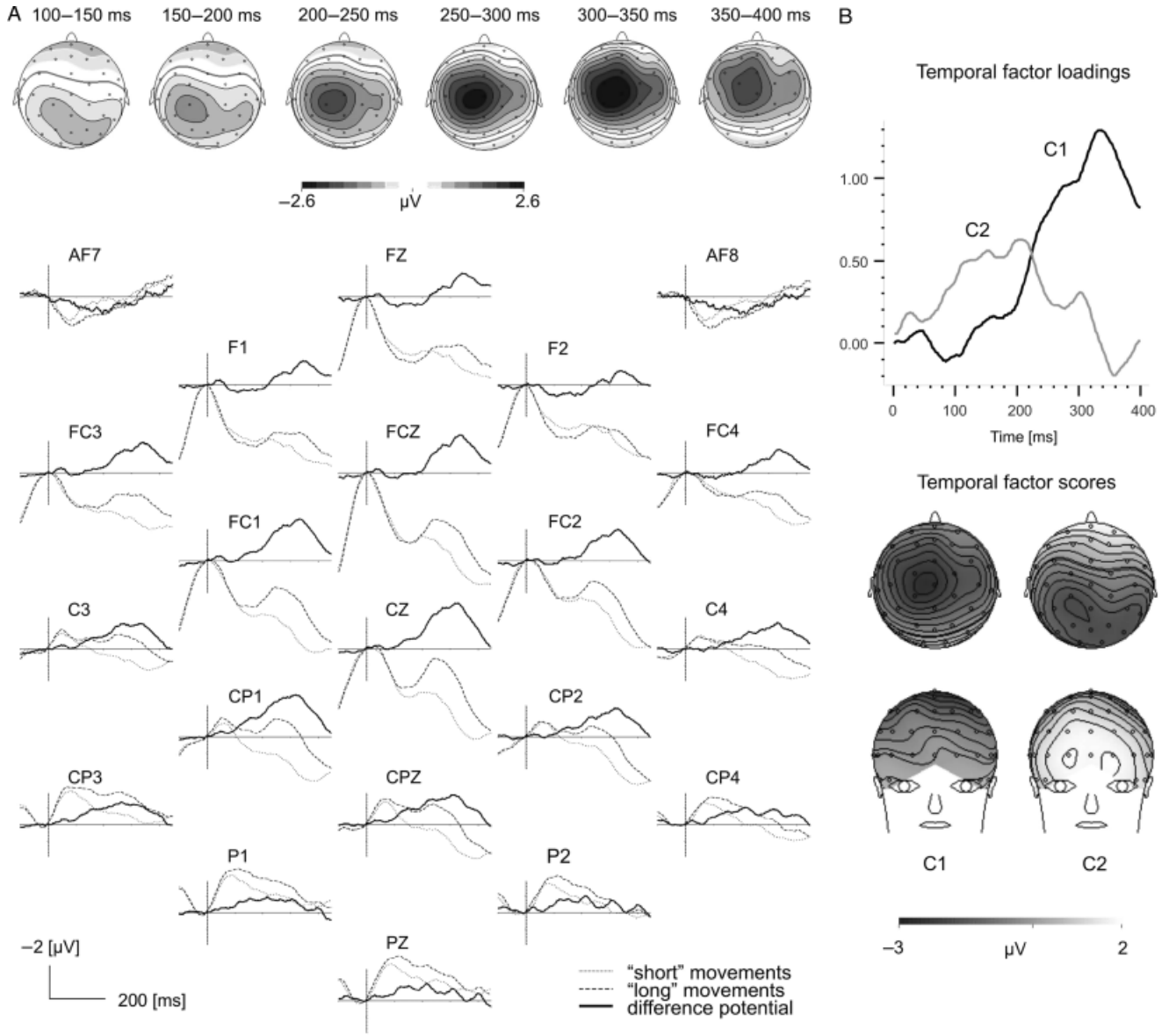

Figure 4. (A) Scalp topography and time course of difference potentials at selected locations (see also Figures 2 and 3). The difference waveforms were computed between the average ERPs of the four near and the four far target conditions. (B) Factor loadings (top) and factor scores (bottom) of the first two Varimax-rotated factors of a PCA of the difference waves.

terior frontal electrodes (see middle and bottom parts in Figure 3).

We examined the latency and the amplitude modulation of N4 accompanying reproduction further by searching for the most negative peaks at selected electrode locations between 150 and 400 ms in the individual ERPs. As during the encoding phase, an increase in target distance was associated with an increase in peak amplitude and in peak latency of the negative peak at FC1 (mean values: 2.06, 1.90, 1.33, 1.05, 0.88, 0.45, -0.34, -0.95 μV and 201, 206, 228, 239, 244, 257, 275, 290 ms for the distance conditions 1, 2, 3, 4, 5, 6, 7, 8 of the latency and amplitude, respectively). The corresponding ANOVAs yielded significant main effects distance for both the latency ($F(7,119) = 18.75$, $p < .001$) and the amplitude measures ($F(7,119) = 30.29$, $p < .001$).

The time-dependent topographic shift of the maximum effect from more posterior to more central-frontal sites suggests that different generators might be involved. We tested this by computing difference potentials between the four shorter and the four longer movement distances. Figure 4(A) shows the corresponding waveforms and topographies. The topographical maps are highly similar to the F value distributions computed for all target conditions (Figure 3, top). A temporal PCA (Principal Component Analysis) with Varimax rotation was applied to the grand average difference waves between movement onset and 400 ms. According to the eigenvalue criterion ($\lambda > 1$), three orthogonal components were extracted accounting for 79.5%, 18.6%, and 0.8% of the total variance. The loadings and the factor scores of the first two Varimax-rotated components, which explain most of the variance, are shown in Figure 4(B). The first component

Table 2. *sLORETA Current Density Estimates of Local Maxima of the N4 Component During the Reproduction Phase Whose Activity Surpassed 3.1 Microampere (μA)*

Anatomical area	Brodmann area	Talairach coordinates X	Y	Z	Current density (μA)
Medial Frontal Gyrus	6	−5	−26	66	3.47
Medial Frontal Gyrus	6	−5	−21	66	3.39
Medial Frontal Gyrus	6	−5	−26	61	3.38
Postcentral Gyrus	4	−10	−31	66	3.38
Paracentral Lobule	6	−5	−31	66	3.35
Precentral Gyrus	4	−15	−26	66	3.35
Precentral Gyrus	6	−10	−16	65	3.33
Precentral Gyrus	6	−15	−16	65	3.31
Medial Frontal Gyrus	6	−5	−16	65	3.22
Medial Frontal Gyrus	6	−10	−26	57	3.20
Superior Frontal Gyrus	6	−15	−11	65	3.19
Medial Frontal Gyrus	6	−5	−26	57	3.19
Superior Frontal Gyrus	6	−20	−11	65	3.17
Precentral Gyrus	4	−15	−26	61	3.17
Medial Frontal Gyrus	6	−5	−17	56	3.13
Precentral Gyrus	6	−20	−16	65	3.12
Medial Frontal Gyrus	6	0	−26	61	3.11

captures the N4 effect, and the resulting pattern suggests that N4 modulation is mainly restricted to electrodes located closely to the primary sensorimotor and medial frontal areas. The second, much weaker component covers the latency between 100 and 200 ms and has a more posterior and anterior frontal topography.

In order to delineate possible generators of N4, a source localization analysis was performed. Using the sLORETA algorithm (Standardized Low Resolution Brain Electromagnetic Tomography, Pascual-Marqui, 2002) we computed a current source density distribution for the difference ERPs mentioned above (i.e., reflecting the difference between the four short and the four long distance conditions) at the mean time of maximum activity of N4 (i.e., at 340 ms in respect to movement onset, see Figure 4). The results of this analysis are summarized in Table 2. As shown, the main current density cluster predominantly comprises medial frontal areas as well as regions close to the central sulcus located almost exclusively in the left hemisphere, i.e., contralateral to the moving hand.

Joint Analysis of Behavior and ERPs

Figure 5 illustrates the close relationship between movement kinematics and the N4 effects. The top part shows the displacement, velocity, and acceleration of the movement; the lower part shows the ERPs from electrode FC1. The peak of the movement path indicates the target location, positive velocities indicate the forward, negative velocities the backward movement, i.e., the zero crossings of the velocity curve indicate the point of return. In the acceleration curves of the encoding movements, the first upward peak indicates the forward movement acceleration and the following negative peak the maximum deceleration. These two peaks are followed by the acceleration and the deceleration peaks of the backward movement (due to clipping the time course at 500 ms, the backward trajectories are not completely shown).

For the encoding phase, the distance dependent changes of the measured motion characteristics proved to be somewhat unusual. In case of near target conditions, the velocity trajectory is not bell-shaped, and the corresponding acceleration course has an atypical form characterized by an excessive magnitude of peak deceleration. The fact that both profiles became more "typical" with an increase in distance and that peak acceleration did not scale with distance seems to indicate that subjects aimed at a far

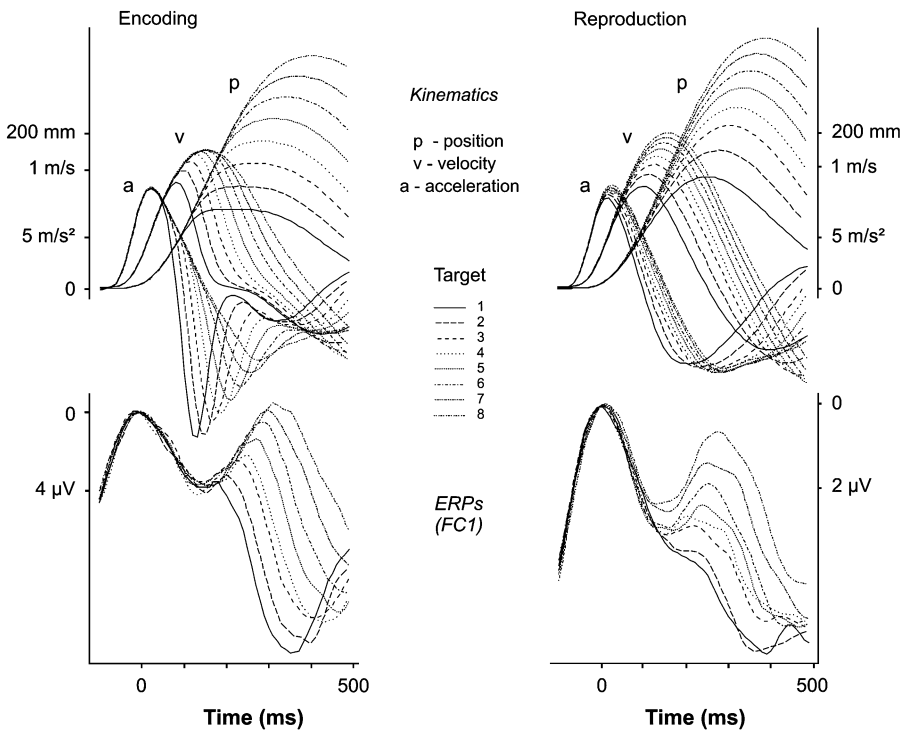

Figure 5. Time course of the kinematic descriptors of the movement trajectory (p = position, v = velocity, a = acceleration) and the ERPs measured at FC1. Note: the ERPs of the reproduction phase are low-pass filtered (10 Hz).

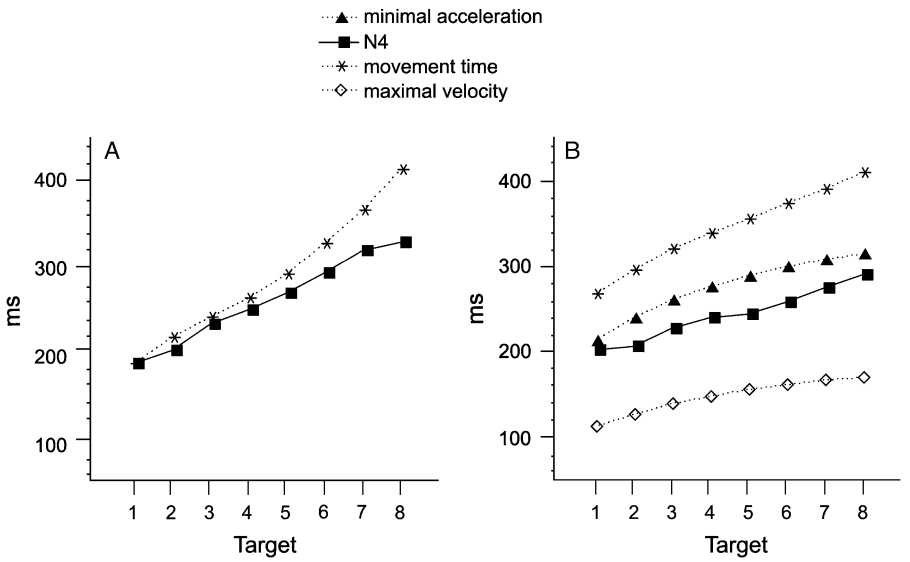

Figure 6. Distance dependent changes of the latency of the maximum amplitude of N4 and the movement time during encoding (A) and of the latency of the maximum amplitude of N4, the movement time, the latency of maximum velocity, and the latency of maximum deceleration during reproduction (B). Note: kinematic descriptors are based on single trial data, and ERP descriptors are based on single subject averages.

position initially and were abruptly stopped when the actual distance was shorter (i.e., initial force pulse was similar for all distance conditions und was terminated in case of short distances resulting in an unusual course of deceleration). The latency of the maximum negativity (N4) for shorter distances coincides with the stop position (i.e., the zero crossing of the velocity curves). For longer distances, the peak latency precedes the end of the movement, and this difference seems to increase gradually with an increase in distance (see Figure 6(A)).

In contrast to the encoding phase, the motion parameters during the reproduction tended to have normal features of unrestricted movements, like bell-shaped velocity courses, whose maximums increased from the first to the eighth target position (see Figure 5). During this phase, N4 modulation seems to occur approximately parallel to the kinematic changes (see Figure 6(B) for means). The N4 latency was reached 95 ms after peak velocity, 32 ms before peak deceleration, and about 100 ms before movement termination on average, and this interval varied to some extent dependent on distance (see Figure 6(B)). This suggests that the maximum amplitude of N4 measured at FC1 during unrestricted movements has been reached approximately in the middle range of the decelerative phase shortly before maximal deceleration.

In order to evaluate the observed relationship between the evoked activity and the kinematic data further, a multiple linear regression analysis was carried out. Over all subjects and the three delay conditions, averaged data of the reproduction phase was used to develop a model for predicting ERP time course from position, velocity, and acceleration trajectories. The sampling rate of the ERPs was adjusted to that of the kinematic parameters (i.e., to 100 Hz). Each distance condition was considered separately, and the analysis was run in a time window between 50 ms before the defined movement onset[4] and the mean movement offset (see also the last column in Table 1). Moreover, acceleration traces during the deceleration phase (i.e., after the zero crossing) were multiplied by -1. This was done to avoid artificial correlations due to the polarity reversal.[5]

The three-predictor model was able to account for 98.8% (target 1), 98.1% (target 2), 97.2% (target 3), 92.7% (target 4), 86.5% (target 5), 75.1% (target 6), 65.6% (target 7), 52.8% (target 8) of the variance in the ERPs ($F(3,29) = 857.2$, $F(3,32) = 605.9$, $F(3,34) = 435.0$, $F(3,36) = 165.7$, $F(3,38) = 88.8$, $F(3,39) = 43.2$, $F(3,41) = 29.0$, $F(3,43) = 18.1$, all $p < .001$). The standardized regression coefficients (β) for position were 1.002, .997, .967, .945, .889, .806, .692, .401 (all $p < .001$) for the eight distance conditions, respectively. The effect of the velocity on the ERPs, in contrast, was rather weak and less systematic: $\beta = -.066$ (target 1, $p = .004$), $-.012$ (target 2, $p = .647$), .063 (target 3, $p = .047$), .048 (target 4, $p = .323$), .057 (target 5, $p = .383$), .092 (target 6, $p = .292$), $-.028$ (target 7, $p = .781$), $-.070$ (target 8, $p = .537$). The acceleration predictor had again systematic and significant partial effects in the full model: $\beta = -.154$, $-.216$, $-.327$, $-.332$, $-.403$, $-.381$, $-.509$, $-.654$ (all $p < .001$) for the distance conditions from 1 until 8.

This result pattern indicates a strong relationship between the ERPs and the measured kinematics[6]). Moreover, it suggests that

[4]Due to the used onset criterion of 5 mm in respect to the position trajectory (see Methods), changes in kinematic profiles were also present before the defined movement onset. In order to include the whole profiles in this analysis, we extended the time segments appropriately.

[5]A neuronal activation pattern similar to that of the biphasic acceleration course with polarity reversal is physiologically quite implausible. Rather, muscle activity as well as neuronal responses accompanying acceleration and deceleration of an effector can be expected to increase (see, e.g., Sergio, Hamel-Paquet, & Kalaska, 2005).

[6]The high correlation between movement parameters and the ERP waveform raises the suspicion that the observed ERP effects are possibly caused by noncerebral sources, i.e., muscle artifacts or body movements. However, such an influence is more than unlikely. Muscle artifacts, which may contaminate the EEG, typically occur in a high frequency range and, therefore, cannot account for the found ERP components and their scaling with movement length or acceleration. Body and head movements that could affect the contact between scalp and electrodes can also be excluded. First, participants were partially immobilized by using a chin and forehead support. By this, gross head movements were precluded. Second, remaining movement artifacts were removed by means of stan-

brain electric activity accompanying the motion of the hand is related to the displacement and the acceleration of the used effector, rather than to the velocity. The observed increase of β with distance for position and the simultaneous decrease of β for acceleration appear to indicate further that the N4 component reflects with increasing strength the time course of the deceleration phase of motion.

Discussion

In the present study, we examined EEG-ERP correlates of linear movements in a motor matching task. In each trial, participants first performed a rapid hand movement towards a mechanical stop and back to the start position and then they had to reproduce the encoded stop position (the movement length) by a second, reproduction movement. Here we examined the evoked activity related to varying movement distances during the encoding and the reproduction movement.

Behavior

As in our previous study using a similar experimental setup, in which the reproduction of kinesthetically defined spatial locations was required (Kirsch, Hennighausen, & Rösler, 2009), we observed results deviating from previous findings for selected movement parameters. In contrast to an increase in endpoint variability with movement distance that typically occurs in unrestricted movements, we here obtained an opposite pattern: The variable error decreased with distance. Moreover, the subjects generally overestimated the target distance (see also Hollingworth, 1909, cf. Granit, 1972 for related results in a similar setup), and this bias showed the tendency to increase from the first to the third target position and to decrease thereafter. We assume that these results are related to the specific experimental situation and may reflect the fact that movements were preplanned to aim at a ''default'' distance during encoding, which may be located somewhere at the farthest stop position. The atypical change of the kinematics with increasing distance during the encoding phase seems to confirm this conclusion: The velocity and acceleration profiles became successively more bell-shaped and symmetrically biphasic with an increase in distance (see Figure 5). If so, then the external movement interruption should cause a ''conflict'' between motor outflow and sensory inflow signals, which should decrease with an increase in distance. As a consequence, distance dependent changes in the quality of final position estimation (or in encoding efficiency, cf., e.g., Wolpert, Ghahramani, & Jordan, 1995) may account for the obtained decrease in variability with target distance. Moreover, the strong positive bias decreasing with movement distance may reflect a distance dependent effect of movement of higher amplitude (i.e., of a far default position) on the sensorimotor integration. We addressed this question in more detail in another manuscript, in which the current data set was analyzed in respect to the movement interruption caused by the mechanical stop (in preparation).

The analyses of behavioral data also revealed a series of significant differences across the three delay conditions. Most of them were related to the tendency to execute movements slower with an increase in delay. In the present report, we aimed to examine the ERP indicators during movement execution, which are associated with a varying movement distance. During this motor control phase, we did not detect substantial delay dependent and distance specific changes as revealed by the statistical results. Accordingly, distance differences found during both movement phases were similarly pronounced in all delay conditions and were independent from the delay manipulation. This fact does not necessarily speak against distinct sensorimotor mechanisms involved in short and long delay conditions (see, e.g., Kirsch et al., 2009) and may possibly indicate distinct motor planning rather than control processes (see, e.g., Figure 1 for different DC drifts prior to the reproduction movement). Because of space reasons, we discuss in the following only the distance effects.

ERPs

ERPs measured during this rapid positioning and reproduction task showed a series of deflections, which were reported previously as accompanying simple, ballistic movements. The statistical analyses substantiated significant differences between the eight target conditions for several time windows and electrode sites.

During encoding, the most pronounced distance specific ERP effects were observed at electrodes close to Cz. These effects had maximum strength between 250 and 300 ms after movement onset and became manifest as both a latency and an amplitude modulation of a negative going wave starting at about 120 ms after movement onset. An increase in movement distance was associated with a gradual increase in peak latency and peak amplitude of this component. According to the terminology of Brunia (1987), this negative wave was labeled N4. Maximal amplitudes of N4 were reached at Cz, FC1, and CP1, while maximal F values were observed at FC1. This suggests the role of regions located close to the primary motor cortex of the left hemisphere as well as to the medial frontal areas as probable sources of activity. The topography of maximal significant effects and amplitudes of N4, as well as the PCA and a source localization analysis of ERPs of the reproduction phase, confirm this conclusion.

The time at which this negativity reached its maximum amplitude seemed to be differently related to the movement time in the encoding and the reproduction phase. During encoding, movement time and peak latency coincided for the near target locations but diverged progressively for longer distances, i.e., with longer distances, peak latency preceded the time where the movement endpoint was reached. In contrast, the latency modulation of the negative component during reproduction preceded movement termination for all distances. Moreover, the highly distance specific amplitude and latency modulation and their relation to the kinematic parameters indicate that the process underlying N4 seems to take place during the decelerative phase.

dard artifact detection and rejection procedures (see Methods). Third, and this seems to be the strongest counter argument, the observed ERP effects had a specific topography (e.g., a maximum over the sensorimotor cortex contralateral to the moved arm). Since electrodes had been fixed by means of a cap, it is most unlikely that only a selected set of electrodes (located on one hemisphere) were affected by movements. If movement artifacts had had a significant influence on the recordings, such an effect should had become manifest at all electrodes sites. Last but not least, it has to be added that the observed wave shape, topography, and timing of the ERP deflections (especially of N4) are highly comparable to those reported in several previous studies in which movements with other effectors and smaller amplitudes (e.g., finger movements) were used and in which a contamination by movement artifacts can be safely excluded. This high similarity also strengthens the claim that the ERPs recorded in the present study had genuine cortical generators. In conclusion, there is no valid basis for the assumption that the ERP results observed in the present study are contaminated by noncerebral sources such as movement artifacts.

In unrestricted movements, as during reproduction, N4 reached its maximum shortly before the point of maximum deceleration. These differences between encoding and reproduction may also be related to the differences in the planning of the encoding and reproduction movements (see above). If movements are preplanned to a distant default position during encoding, it is reasonable to expect that the same process is initiated irrespective of the distance manipulation and would be disrupted, especially when movements are stopped shortly after their onset. In contrast, in case of longer distances the control mechanisms accompanying the deceleration phase should be more congruent with those occurring in unrestricted movements. As can be seen in Figures 5 and 6, the results are compatible with this idea.

With simple ballistic movements (e.g., finger flexions or extensions) the motor control processes are typically accompanied by a ramp-like negativity increasing before and decreasing after movement onset and by a series of phasic positive and negative waves following movement onset (see, e.g., Cui & Deecke, 1999; Cui et al., 2000; Kristeva et al., 1990; Kristeva, Keller, Deecke, & Kornhuber, 1979; see also Brunia, 1987; Brunia & van Boxtel, 2000; Deecke et al., 1976; Tamas & Shibasaki, 1985 for reviews). The premovement shifts were shown to be affected by various kinematic and kinetic variables (e.g., Kristeva et al., 1990; Slobounov et al., 1998, 1999, 2000) and are assumed to reflect specific functions such as preparation and response selection mechanisms (RP I, RP II) or motor command (MP). In contrast, knowledge about the functional significance of post-onset ERP deflections is limited. Most of them were related to sensory feedback (e.g., Brunia, 1987). The N4 like activity has been consistently observed at postcentral and precentral sites with only moderate amplitudes in simple motor tasks (see, e.g., Brunia, 1987; Cui et al., 2000; Deecke et al., 1976; Shibasaki et al., 1980a, 1980b; Tamas & Shibasaki, 1985). Our data suggest that the generator of N4 in the present task is not restricted to postcentral regions but may also comprise more anterior cortical motor areas. Cui and Deecke (1999) came to a similar conclusion as they observed a congruent topography for RP II, MP, and a negative going potential equivalent to our N4. The authors proposed that the role of this activation may involve online modifications of the movement trajectory dependent on feedback signals from peripheral sensory receptors and lower motor centers. On the other hand, there is evidence that N4 like negativity resembles evoked responses of passive movements with a postcentral origin contralateral to the stimulated effector (Shibasaki et al., 1980a, 1980b; Tamas & Shibasaki, 1985). As noted by Cui and Deecke (1999), the source may originate in the primary sensory as well as in primary motor areas, possibly leading to reciprocal activation since precentral and postcentral areas are functionally closely connected forming the ''sensorimotor cortex,'' Our results, especially those of the reproduction phase, agree with this notion. The maximum of the distance specific effects (see Figures 3 and 4) seems to move with progressive time from more postcentral to more precentral locations, possibly indicating a distance specific activation shift from sensory to motor areas.

As mentioned in the introduction, the ERPs during slow movements usually differ significantly from those accompanying rapid ballistic movements. Instead of phasic bursts, a sustained negativity appears when smooth movements are performed (see, e.g., Grünewald & Grünewald-Zuberbier, 1983; Grünewald-Zuberbier & Grünewald, 1978; Grünewald-Zuberbier et al., 1981). Initially, we had expected that an increase in movement distance may change the ERP waveshape from a more phasic towards a more sustained negativity. The data, however, show that the maximum negativity appeared at movement onset at central and frontocentral sites and disappeared during the first 100 ms in all distance conditions and during both encoding and reproduction. Thus, a sustained negativity that was reported by Grünewald and colleagues during slow goal-directed hand movements was not observed in the present task. Instead, after an interval of approximately 100 ms a second phasic negative going activity was observed, whose peak latency and peak amplitude proved to be highly distance specific. This suggests that electrophysiological processes accompanying rapid joint displacements differ from those which occur during slow adjusting motor acts. These differences may be related to a specific pattern of muscle activity associated with rapid hand movements (see, e.g., Berardelli et al., 1996). The first activation of the agonist muscle (AG1) provides the force to accelerate the joint, which is then decelerated by the following antagonist activity (ANT). The second phasic agonist activation (AG2) is assumed to terminate the decelerative force pulse and, thus, stabilizes the limb at the end of the movement. There is some evidence that the primary motor cortex plays a key role in generating such phasic signals that trigger agonistic and antagonistic muscles (Sergio, Hamel-Paquet, & Kalaska, 2005; Sergio & Kalaska, 1998). By measuring responses of neurons in caudal primary motor cortex of monkeys, these studies showed that motor signals during reaching do not have a simple, ramp-like characteristic. Rather, the response characteristic of many cells corresponded to the muscle activity, as expressed in force profiles and the EMG signal. Therefore, the authors suggested that all components of the triphasic EMG signal (AG1, ANT, AG2) are generated in M1. These results also agree with findings reported by Mills and Kimiskidis (1996). By using transcranial magnetic and electrical stimuli during ballistic forearm and finger movements, the authors identified two phases of cortical excitability, one at the beginning of movement and a second starting about 100 ms after movement onset (see also MacKinnon & Rothwell, 2000 for similar results). Moreover, based on their results, the authors attributed the second phase to a similar mechanism, as suggested by Cui and Deecke (1999) for an N4 like negativity (i.e., a corrective command based on error signals).

Implications for Motor Control Theories

Our results are compatible with these observations, and they suggest that the control of rapid hand movements is accompanied by discrete bursts of activity in sensorimotor areas. Moreover, they extend previous findings by indicating that the second phase of activation of sensorimotor areas is highly distance specific. Furthermore, by analyzing ERPs during movement reproduction, we observed that the activation time course at electrodes located closely to primary sensorimotor areas coincided with the acceleration rather than with the velocity changes. The first and the second negative maximum were reached at the time of maximum acceleration and maximum deceleration, respectively (see Figure 5). Since according to Newton's Laws of Motion, acceleration changes are closely related to force changes (F (force) = m (mass) * a (acceleration), see also, e.g., Scott, 2004) and a strong association exists between acceleration and muscle activity as expressed in the EMG for single joint movements (Brown & Cooke, 1990; Cooke & Brown, 1994; Ghez & Gordon, 1987; Gordon & Ghez, 1984; Gottlieb, Corcos, & Agarwal, 1989), this result may agree with direct muscle control models.[7] The discharge of corticospinal neurons in the primary motor

cortex, which is assumed to be associated with the last negative shift visible in EEG (MP, see, e.g., Arezzo & Vaughan, 1980; Brunia, 1987; Brunia & van Boxtel, 2000; Deecke, Scheid, & Kornhuber, 1969; Gilden, Vaughan, & Costa, 1966) may reflect a descending volley initiating AG1 activity, while the second phase of motor cortex activity may control the "breaking pulse" (i.e., ANT activity).

The most striking aspect of the results of the present study is the fact that the ERP effects changed in a non-monotonic manner with increasing movement distance. While the N4 amplitude was negligible with short distances, it reached a considerable magnitude with longer movements. This seems to be a result of a fixed onset time of this negative deflection with respect to movement onset ($\sim$ 100 ms) and a distance and/or movement time-specific amplitude increase. Thus, the question whether movement control is monotonic or nonmonotonic (e.g., Ghafouri & Feldman, 2001; Sergio et al., 2005) or continuous vs. phasic (e.g., Desmurget & Grafton, 2000) may be answered differently depending on the length of the movement path and/or the duration of the movement. At this point, the results would fit rather well into the "classic" dual-component theory of motor control, initially proposed by Woodworth (see, e.g., Elliott, Helsen, & Chua, 2001 for review). According to his basic assumption, simple target-aiming movements comprise *two phases*, a central preprogrammed initial ballistic phase and a second feedback-based control phase. One may speculate that the first activation phase of the ERP (MP) is associated with a preprogrammed "excitation pulse"[8] controlling the initial part of a trajectory. In contrast, the later component (N4) may reflect trajectory adjustments depending on internal and/or sensory feedback signals (e.g., Cui & Deecke, 1999; Gordon & Ghez, 1987; Messier & Kalaska, 1999; Mills & Kimiskidis, 1996; Novak, Miller, & Houk, 2002), for example, via modulation of spinal reflex circuits affecting timing and magnitude of the antagonist.[9]

More generally, the results relating to the brain activity measured over sensorimotor areas in the present experiment suggest that the action execution comprised two discrete processes. This appears to be the result of the given setup, in which rather phasic muscle activity of the arm is involved. On the other hand, the data do not seem to indicate a strong one-to-one relationship between the central and the peripheral processes during a late phase of control in which the target is reached. Assuming that the observed ERP pattern corresponds to two distinct commands generated by the CNS (e.g., a go-command and a stop-command), which trigger the muscle activity, one may argue that the latency of the stop-signal needs to be timed appropriately for hitting the target. However, the strong modulation of the N4 amplitude, its similar onset across the target range, as well as the regression analyses of movement parameters on the ERP suggest that the influence of the signal reflected by the N4 component on action execution increases with distance and/or with time. This may be due to a difficulty of simultaneously programming two opposite commands within a short time window as in the short distance conditions (e.g., as a result of physiological conduction delays). Consequently, the control mechanisms relating to the termination of action may rely more on other than central processes within the system in these cases, such as by the stretch reflex (e.g., Ghez & Martin, 1982). In contrast, an increase in duration and/or intensity of an intended act may allow (or require) a higher level of online control, in which the central nervous system (CNS) is involved. At this point, the data appear to point to a high flexibility of action control mechanisms.

Systematic amplitude differences across the eight target conditions were also found at more posterior and anterior frontal electrodes. The topography of the distance effects and the initial ERP dynamics at posterior electrodes (see, e.g., CP3) is similar to that of the P1 wave described in previous studies,[10] i.e., a positive deflection preceding movement onset, whose functional role is still not determined. The waveforms give the impression that the distance effects result from the modulation of a negative wave overlapping with the decline of P1, especially visible in the computed difference potentials (see Figure 4). Its topography seems to involve centroparietal and parietal locations with a maximum over the left hemisphere (see, e.g., Figures 3 and 4). The performed PCA of the difference potentials suggest that the time course of activation precedes the N4, thus indicating an earlier processing stage.

The ERPs measured at anterior frontal sites were characterized by a polarity reversal as compared with those recorded at parietal and centroparietal locations. This fact as well as the mean amplitude decrease with increasing movement distance at the most anterior electrodes may suggest that the effects may have a common origin. The results of the PCA analysis performed for the reproduction phase support this notion: The variance of the difference activity measured at anterior frontal and posterior electrodes was explained by one single component. Although conclusions relating to this result pattern must be tentative, we assume that areas other than primary sensorimotor may also participate in the control of movement execution and mediate some aspects of monitoring and sensory/internal feedback.

Conclusion

The primary goal of the present study was to investigate ERP correlates of rapid hand movements. We observed several components, which were previously reported in similar recording situations. By manipulating the movement distance, we could identify time epochs and electrode locations, which showed distance specific changes of ERP components. Our results suggest that areas close to the central sulcus are activated during motor control in a discontinuous manner with temporal dynamics similar to changes of accelerating and decelerating forces. This nonmonotonic control pattern that becomes manifest in the ERP

[7]This statement is related to the controversially discussed question, whether motor cortical areas, like M1, primarily code high-level parameters, like direction or velocity of an effector or rather low-level variables, like joint angles or muscle tension.

[8]Such a "pulse" or "impulse" is considered as forces produced over time (force-time integral, see, e.g., Schmidt, 1982) resulting, for instance, from descending presynaptic input converging and summating in the alpha motor neuron pool (Gottlieb et al., 1989).

[9]This assumption would be in line with the work of Schmidt and colleagues (1978, 1979). These authors showed that for rapid movements (less than 200 ms) the well-known speed-accuracy relations between movement amplitude, movement time, and error can be exclusively explained by motor output variability (i.e., by the variability of initial force pulse) without referring to feedback-based correction processes.

[10]In relation to a "resting" baseline, e.g., a window extending from -2000 to -1000 ms before the imperative go signal (see Figure 1), the activity at parietal electrodes can be described as an initial positivity starting with the acoustic go signal, lasting until shortly before movement onset, and subsequently disappearing.

seems to agree with findings obtained with single neuron recordings as well as with transcranial magnetic stimulation effects. It may indicate a ''direct'' coding of low-level kinetic parameters (forces and muscle activity) rather than of high-level kinematic variables in sensorimotor areas. Moreover, the results appear to delineate a rather flexible central control mechanism of action execution, as they suggest that discrete processes, such as stop or trajectory adjustment commands, may differently be involved depending on task context (here: distance) and thus, may have varying influence on action outcome. These conclusions are, of course, tentative and have to be considered with caution, due to a number of factors that may limit functional interpretations.

For instance, N4 may be related to the programming of the backward movement, rather than to the deceleration phase of the forward movement. Although possible, this appears to be rather unlikely. The negative going potential, preceding forward movements (MP), coincided with the defined movement onset (see, e.g., Figure 1). Accordingly, a similar deflection related to the backward movement should peak around the onset of the backward movement, which is clearly not the case during both analyzed movement phases (see Figure 5). Moreover, the time difference between the N4 maximum and the onset of the backward movement was about 100 ms during reproduction. This time lag is considerably higher than some recent estimates of cortico-muscular delays (cf. MacKinnon & Rothwell, 2000; Petersen, Christensen, Morita, Sinkjaer, & Nielsen, 1998). However, due to a close temporal relationship between forward and backward movements, some aspects of cyclic response programming may have altered the observed ERP waveforms. To rule out this possibility, we inserted a temporal delay between forward and backward movements in a follow-up study using a similar apparatus, in which targets were defined visually and delayed responses were required (manuscript in preparation). Despite differences in the set-up, we obtained very similar results.

Another possible caveat may be related to the unusual experimental setup used in the present study, which may have biased the processing towards the control of intrinsic variables. Moreover, some aspects of memory and/or memory-related sensorimotor transformations may have contributed to the formation of the ERPs. Further experiments using other modalities and/or tasks may clarify this question.

Finally, it should also be noted that the implemented distance manipulation was accompanied by a variation of all measured movement variables, as velocity, movement time, and acceleration. Thus, the observed ERP effects may be related to the control of all of them and accordingly are in line with several findings demonstrating the influence of kinematic and kinetic variables on the movement-related potentials (see introduction). Varying one movement variable, while controlling the other, appears to be a promising approach in order to provide more detailed information about the nature of motor control processes mediated by the CNS.

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