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ERP correlates of linear hand movements: Distance dependent changes

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ABSTRACT

Objective: This study examined the sensitivity of event-related cortical potentials (ERPs) preceding and accompanying goal-directed hand movements to the variation of movement distance.
Methods: Participants performed linear hand movements to memorized target locations, which were arranged in distances between 10 and 31 cm from the starting position of the hand. EPRs were analyzed time-locked to the imperative go signal as well as to the movement onset.
Results: An increase in target distance was associated with an increase in amplitude of a negative component measured over sensorimotor areas that preceded movement onset (MP). Another negative deflection arising at similar scalp locations (N4) and following the MP decline was also highly distance dependent.
Conclusions: The data demonstrate distance specific brain activity accompanying accelerative and decelerative phases of motion during goal-directed hand movements.
Significance: The modulation of MP may to be related to the modulation of the initial force pulse, while N4 effects may reflect distance dependent changes in the magnitude of decelerative control.

1. Introduction

Rapid goal-directed movements of a joint are typically characterized by approximately linear position-, single-peaked velocity- and biphasic acceleration-time courses (Atkeson and Hollerbach, 1985; Flash and Hogan, 1985; Morasso, 1981). They are produced by two phasic contractions of the agonist muscle at the beginning and at the end of the movement, and an intermediate burst in the antagonist muscle (e.g., Berardelli et al., 1996). Despite much attempt to identify the nature of motor control processes underlying these properties, no consensus about their origin exists. One controversially discussed question is whether motor-related areas of the cortex, like primary motor area, primarily code high-level parameters, like direction or velocity of an effector (Georgopoulos et al., 1986; Caminiti et al., 1990; Reina et al., 2001) or rather low-level variables, like joint angles or muscle tension (Evarts, 1968; Scott and Kalaska, 1997; Kakei et al., 1999; Todorov, 2000).

EEG research in this area showed that the manipulation of external motion parameters, like position and velocity (i.e., of kinematics) as well as of internal forces (i.e., kinetics) affects the amplitude of the movement-related cortical potentials preceding and accompanying the response (e.g., Cooper et al., 1989; Hink et al., 1983; Kristeva et al., 1990; Kutas and Donchin, 1974, 1980; Siemionow et al., 2000; Slobounov et al., 1998, 1999, 2000, 2002). For instance, Slobounov and colleagues (2000) reported that the movement amplitude of index finger flexion consistently affected ERPs before and during movement execution at several recording sites. Cooper et al. (1989) found a high correlation between velocity of a pursued target and ERPs in a tracking task. Other results emphasis the role of kinetic variables showing ERP modulations in response to changes in inertial load applied to finger movements (Kristeva et al., 1990; Slobounov et al., 1999) and in rate of force development (Slobounov et al., 1998). There are also findings, which indicate differential effects of kinematic and kinetic variables on components of movement-related potentials (Slobounov et al., 1999).

We recently examined the influence of the varying range of motion on ERPs during a motor matching task (Kirsch et al., in press). The blindfolded subjects performed rapid one-dimensional hand movements towards a mechanical stop and back to the start. After a varying delay, they had to reproduce the given stop position with another movement. We observed that in contrast to slow and smooth motor acts, which are usually accompanied by continuous EMG activity and a rather sustained negativity over motor areas (Grünewald and Grünewald-Zuberbier, 1983; Grünewald-Zuberbier and Grünewald, 1978; Grünewald-Zuberbier et al., 1981), rapid

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joint displacements were associated with a rather phasic ERP course. The last premovement negative shift declined rapidly and was not substantially affected by the implemented manipulation of movement distance. After an interval of approximately 100 ms, another negative component occurred over primary sensorimotor areas and was modulated by the range of motion to a high degree. An increase in distance caused an increase in amplitude and peak latency of this deflection, which we referred to as N4 according to Brunia (1987). The temporal characteristics of ERPs recorded around the central sites during unrestricted movements proved to be closely related to the measured acceleration-time courses rather than to velocity changes. The maximal negative amplitudes of a negative component preceding movement onset and of the second negative deflection (N4) were achieved around the times of maximal and minimal acceleration. This result appeared to confirm some prior observations (Cui and Deecke, 1999; MacKinnon and Rothwell, 2000; Mills and Kimiskidis, 1996; Sergio et al., 2005; Sergio and Kalaska, 1998) and to suggest that rapid goal-directed movements are accompanied by at least two phases of cortical excitability. Moreover, the second activity phase seemed to be time dependent due to similar onsets of N4 across a wide target range and very distance specific due to latency and amplitude modulation dependent on the range of motion.

The present analyses aimed to replicate and to extend these findings. In particular, we were interested in whether the N4 also occurs in another task situation, where targets are defined visually and will be similarly modulated by movement distance. Moreover, the Newton's laws of motion (F (force) = m (mass) $*$ a (acceleration)) predict that the acceleration patterns directly reflect the time course of the resultant forces generated by the neuromuscular system, if the moving limb is assumed to be of a constant mass (see also e.g., Plamondon, 1998; Scott, 2004). Since this strong relation between acceleration and muscle activity is well supported for single joint movements (Brown and Cooke, 1990; Cooke and Brown, 1994; Ghez and Gordon, 1987; Gordon and Ghez, 1984; Gottlieb et al., 1989) and due to the observed relationship between N4 and deceleration, we assumed that N4 modulation may be associated with the control of activity of the antagonistic muscles. Since distance specific scaling of deceleration is usually preceded by proportional scaling of acceleration one would expect that changes in accelerative forces are also accompanied by distance specific cortical potentials before and during the acceleration phase of motion (see also e.g., Siemionow et al., 2000 for a high correlation between ERPs, force and muscle EMG signals shortly before and after the onset of isometric elbow-flexion contractions). Accordingly, a results pattern including distance specific ERP effects accompanying accelerative and decelerative phases would speak for direct control of low-level variables, like of forces or muscle tension.

We asked the subjects to perform movements to visual targets arranged similarly to the stop positions of the previous study (i.e., along the line of sight on a horizontal plane). We were also interested in the effects of different stimulus–response intervals on electrophysiological and behavioral indicators of memory, motor planning and control processes. Hence, we adjusted the times of imperative go signals to 200, 1000 and 5000 ms in respect to target offset. In the present report we mainly focused on the markers of mechanisms accompanying later programming stages and motor control during movement execution associated with a varying range of motion.

2. Method

2.1. Participants

Twenty-two right-handed, neurologically normal subjects participated in the present study. They gave their informed consent for the procedures and received an honorarium or course credit at the end of the experiment. One subject was excluded from the analyses due to insufficient quality of kinematic and EEG data. The final sample included 11 males and 10 females between 21 and 35 years of age (mean 25 years). None of the participants had any visual deficit except those corrected by lenses.

2.2. Apparatus

The subjects sat in front of a linear track device, allowing one-dimensional movements of a pen-like, lightly moveable handle on the horizontal plane slightly above the waist. Eight green LEDs with visible surface of 6 mm^2 were integrated at distances between 10 and 31 cm from the starting position (3 cm between successive LEDs) along the mid-sagittal axis of the trunk. The starting position was defined as the nearest possible handle location in respect to the body (approximately 10 cm). A fixation light (red LED with visible surface of 1 mm^2) was mounted 70 cm in front of the subjects and its height was adjusted to the individual's eye level. The experiment was performed in total darkness, apart from rest periods, in which the room was illuminated and the vision of the whole device was occluded. Thus, the subjects were prevented from seeing the apparatus.

2.3. Experimental procedure and design

At the beginning of a trial, subjects positioned their head on an individually adjusted headrest and an auditory warning stimulus (2000 Hz) was presented for 100 ms at a moderate volume. Two seconds later a red fixation LED was illuminated. After a fixed interval of two seconds, one of eight target LEDs was lighted for a period of 50 ms. After a memory delay of 200, 1000, or 5000 ms in respect to the target offset, the fixation light was extinguished, indicating that subjects should initiate the movement towards the remembered target position. The movements had to be performed as accurate and fast as possible without corrections. After an interval of 2 s a second auditory stimulus (250 Hz) was presented for 100 ms and subjects could return the arm to the starting position. The inter-trial interval was randomly varied between 3000 and 3350 ms.

A $8 \times 3 \times 32$ (Target $\times$ Delay $\times$ Repetition) within-participants block-design was used. The experiment was divided into 12 blocks; each of them consisted of 64 trials (8 locations $\times$ 8 movements). The delay duration within each block was constant. Eight targets were randomly presented with the constraint that the whole sequence of positions should be completed before another repetition. The order of blocks was also randomized for each participant. Each subject performed three practice blocks including all delay conditions. After each block a rest was made, the duration of which was adjusted to the individual's demand.

2.4. Recording and data preprocessing

An ultrasound motion devise (ZEBRIS, CMS 20) was used to record the movement trajectories of the manipulandum. The data were sampled at 100 Hz initially and analyzed with in-house software using Lab View codes (National Instruments, Graphical Programming for Instrumentation). The recorded spatial coordinates of the movement hand path were filtered using two zero-phase lag filters, a median filter (based on three data points) and a moving average filter (five data points) in order to reduce noise and recording artifacts. Velocity and acceleration changes were computed through numerical differentiation. Movement onset was defined as the first time when position trajectory exceeded 5 mm, while movement termination was related to the point where the velocity curve first crossed the zero-line. Additionally, maximal

velocity and maximal acceleration values were also determined for each trial. Trials with artifacts and with a movement onset, which exceeded 1.5 s in respect to the go signal, were excluded from further analyses.

EEG data were recorded continuously from 61 scalp locations during task performance. A cap with an equidistant position montage was used (Easy cap, System Falk Minow, Montage Nr. 10). All scalp electrodes were initially referenced to the tip of nose and re-referenced offline to the average reference. Electrooculographic activity (EOG) was recorded from electrodes, placed vertically from above and below the left eye (vEOG) and horizontally from the outer canthi of both eyes (hEOG). Electrode impedances were kept below 5 kΩ. EEG and EOG were amplified between DC and 100 Hz by using two 32 channel amplifiers (Synamps, Neuroscan) and digitized with a sampling rate of 500 Hz. DC drift was corrected according to Hennighausen et al. (1993). Eye movement artifacts were removed by application of the regression method suggested by Gratton et al. (1983), while trials with other artifacts were rejected based on a threshold criterion, allowing a maximum voltage range of 200 μV within a trial segment. Acquire software (Neuroscan) was used for collection and BrainVision Analyzer software (Brainproducts) for analysis of data. Triggers indicating the offset of the fixation light (go signal) were recorded online, while markers associated with movement onset times were imported offline after the preprocessing of movement data described above.[1]

2.5. Data analysis

The following 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: movement distance, movement time, constant error (mean deviation of the moved distance from the target distance), maximal acceleration and maximal velocity.

Single trial EEG and EOG data time-locked with the offset of the fixation LED (motor preparation phase hereafter) and with the defined movement onset (motor control phase hereafter) were extracted from continuous EEG and were used for averaging. The baselines were determined as the averaged activity in the −100 to 0 ms interval preceding each trigger. The goal of the statistical analyses was to identify time periods and locations, where the distance manipulation was associated with differences in the mean amplitude of the recorded evoked potentials shortly before movement onset and during movement execution. For this purpose we defined the intervals 300–400 and 400–500 ms in respect to the imperative go signal, and 0–50, 50–100, 100–150, 150–200, 200–250, 250–300, 300–350, 350–400 ms in respect to the onset of movement as time-windows of interest.

While ERPs of all delay conditions in the motor control phase appeared to be comparable, visual inspection of the motor preparation phase revealed quite different courses of the evoked activity dependent on the delay condition.[2] On this account, we included all delay conditions in the initial statistical analyses in the motor control phase and performed time-window specific ANOVAs with the within-subjects factors distance (8 levels), delay (3 levels) and electrode (61 levels). In contrast, in order to ensure comparability of used measures (mean amplitude) in the motor preparation epoch, we computed ANOVAs for each delay condition separately (within-subjects factors: distance (8 levels) and electrode (61 levels)).

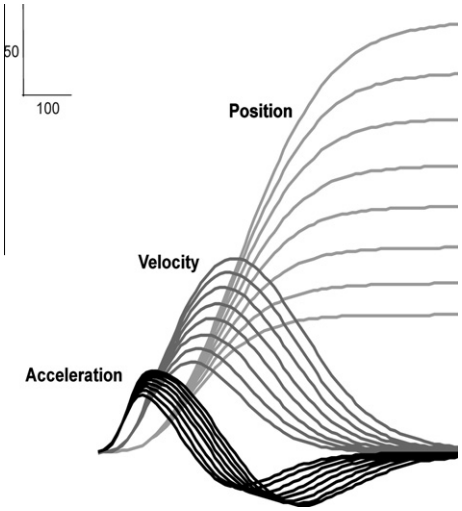

Fig. 1. Averaged acceleration, velocity and position profiles of movements under eight distance conditions. Scale units of the *Y*-axis are mm (position), 150 × m/s (velocity) and 10 × m/s^2 (acceleration). The *X*-axis reflects time in ms. The shown traces are time-locked to the defined movement onset. Note, the high smoothness of the time courses is not a result of filtering, but is due to a large number of trials entering averaging.

These analyses provide information about time segments, in which significant differences between experimental conditions may occur, which could be expressed in significant Electrode × Distance, Electrode × Delay, Electrode × Delay × Distance, or Delay × Distance interactions. Since we were mainly interested in effects caused by the distance manipulation, we performed electrode specific ANOVAs only for time-windows, where distance effects became significant.[3] In the case of the motor preparation phase, we treated each delay condition separately again and computed one-way ANOVAs with the within-subjects factor distance (8 levels) for each delay condition and each electrode. The motor control phase was analyzed by using two-way ANOVAs (distance and delay as factors) for each electrode. In order to give a complete picture of the effects, we plotted the significant *F* values of the main effects distance derived from electrode specific ANOVAs as topographic maps.

Univariate repeated measures analyses of variance (ANOVAs) were conducted by using algorithms generated by the General Linear Models procedure of SPSS (12.0). For all analyses, significance was tested on an alpha level of 0.05 and degrees of freedom were adjusted according to Huynh and Feldt (1976).

3. Results

Fig. 1 shows averaged acceleration-, velocity- and position-time functions according to the eight distance conditions.

The recorded kinematic parameters had usual characteristics as obtained in comparable task situations, like single-peaked approximately bell-shaped velocity profiles, biphasic acceleration and linear position courses. Table 1 gives an overview of mean values of selected measures (see also Supplementary Table S1 for mean values of each delay condition).

[1] Event markers indicating the offset of the fixation LED were also registered by the recording software of the ZEBRIS equipment. During analysis of the movement data, single trial segments were extracted in respect to these triggers. After artifact rejection and setting of selected markers, the latency differences between the offset of fixation LEDs and movement onset times were used for the import of corresponding triggers to the EEG analysis software. That is, movement onset latency was imported offline trial by trial by adding a corresponding time interval to the latency of the go signal.

[2] Especially the shortest delay condition showed a quite different dynamic, where a pronounced phasic activity over posterior recording sites was observed. The effects of varying delay on motor planning are discussed in a next paper.

[3] If it appeared to be useful, some other results were also presented.

Table 1
Characteristic movement parameters averaged for all subjects and all delay conditions according to target distances.

Target condition	Movement distance (mm)	Movement time (ms)	Constant error (mm)	Maximal velocity (m/s)	Maximal acceleration (m/s^2)
1	77	354	−24	.38	3.77
2	94	385	−34	.43	4.10
3	114	416	−46	.49	4.37
4	136	442	−53	.55	4.57
5	158	472	−61	.60	4.84
6	184	502	−65	.66	5.04
7	209	534	−69	.72	5.25
8	237	575	−70	.77	5.46

An increase in target distance was associated with a significant increase in movement time ($F(7, 140) = 178.7$, $p < .001$), movement distance ($F(7, 140) = 121.4$, $p < .001$), constant error ($F(7, 140) = 11.1$, $p = .002$), maximal acceleration ($F(7, 140) = 44.4$, $p < .001$) and maximal velocity ($F(7, 140) = 94.7$, $p < .001$). We also observed a series of delay effects. However, apart from the movement times, which showed a significant Delay × Distance interaction ($F(14, 280) = 2.7$, $p = .018$) the factor distance proved to be independent from the factor delay.[4]

The evoked activity during a late period of motor preparation was strongly affected by the stimulus distance and consequently by the subsequent movement amplitude. The Electrode × Distance interactions of the time-window specific analyses were significant in both selected time-windows and in all three delay conditions: $F(420, 8400) = 2.1$, 3.0, 1.5, 1.9, 1.9 and 2.6 with $p = .003$, <.001, .045, .012, .006 and <.001. The results of ANOVAs performed for each electrode are shown in Fig. 2A as linearly interpolated significant F values of main effect distance. The most pronounced distance effects were observed around the central regions and were in all delay conditions comparable. They consisted of the amplitude modulation of a negative deflection preceding movement onset (the mean times between the imperative go signal and movement onset ranged between 480 and 520 ms). The longer the stimulus distance was, which had to be covered by the hand, the higher the amplitude of the mentioned potential was (see Fig. 2B and C).

The main results derived from windowed ANOVAs in the time range between movement onset and 400 ms after are depicted in Table 2.

The distance manipulation affected the ERP amplitude in four of the six time segments as expressed in significant Electrode × Distance interactions. Moreover, the last mentioned effects missed the significance threshold in the two residual time-windows only marginally (see Table 2, time-windows 0–50 and 350–400 ms). Neither significant Delay × Distance nor Delay × Distance × Electrode interactions were found, suggesting that the observed delay differences were independent from the distance effects (see Supplementary Table S2 for the corresponding results). In the present report we focused on the effects of distance manipulation and thus, do not consider the delay effects further.

The results of the electrode specific ANOVAs are depicted in Fig. 3A. Significant differences between movements of different length occurred at first at left centroparietal and frontopolar sites (50–150 ms) and drifted then towards the frontocentral sites, showing again higher F values over the left hemisphere (200–400 ms). Centroparietal differences were characterized as an increase in negative activity, when movement distance increased (see Fig. 3B and C for a representative electrode). Near distances caused more negative activity at anterior frontal electrodes in contrast to far locations (see FPZ in Fig. 3B and C). Maximal F values of the current processing phase were found between 250 and 300 ms over left frontocentral areas. These effects were caused by a distance specific modulation of a negative deflection, which occurred from about 120 ms after movement onset and showed an amplitude increase with an increase in movement distance (see FC1 in Fig. 3B and C). Additionally, significant distance differences were found over occipital and occipitoparietal areas in the range between 250 and 300 ms. Apart from the shortest target condition, an approximately linear decrease in negative activity was present when movement distance increased (see PO4 in Fig. 3B and C).

For descriptive purposes we also computed difference potentials between the four near and four far target conditions. The corresponding waveforms at selected scalp locations and the topographies are also shown in Fig. 3D. These seem to fit rather well into the statistical results described previously. The difference waves of maximal amplitude were mainly present close to the central sites with a precentral dominance. Moreover, an obvious drift of differences from left centroparietal to frontocentral locations as well as anterior frontal and posterior effects also seem to be visible in comparable time ranges.

The most pronounced distance effects, which occurred shortly before movement onset and during movement execution, mainly comprised electrodes locating close to the central sulcus. Fig. 4 shows the temporal relation of the measured kinematic parameters to these distance specific brain responses.

The maximal amplitude of a highly distance specific negativity preceding and accompanying movement onset seems to be achieved shortly before maximal acceleration (~20–50 ms). As in our previous study, the second phase of negative going potentials appears to start about 120 ms after the defined movement onset. The course of the signal, i.e., its amplitude and latency modulation, seems to be directly related to the modulation of deceleration, rather than to velocity or position changes (e.g., negative going activity lasts until shortly before maximal deceleration is reached and became sharply positive going after that). These results confirm our prior observations (Kirsch et al., in press) and suggest that the second phase of cortical excitability over sensorimotor areas during movement execution is time dependent due to an obviously equal onset and distance specific to a high degree due to the distance dependent modulation of amplitude and duration.

4. Discussion

The purpose of the present analyses was to examine the sensitivity of evoked brain activity to the range of motion in a delayed visuomotor task. We asked the subjects to perform rapid hand movements to visually presented targets and analyzed ERPs preceding and accompanying the motion of the hand.

During movement execution, the most pronounced distance differences occurred at the central and frontocentral electrode locations and were the result of a distance specific modulation of an ERP component that we referred to as N4, according to the literature (Brunia, 1987). As in our previous study, the decline of negativity preceding movement onset lasted approximately 100 ms in all distance conditions. The following N4 deflection was almost absent, when short movements were performed and seemed successively to develop, when movement distance increased. Its offset seems to coincide with maximal deceleration, while no direct relation to velocity changes is evident. Moreover, in contrast to a few

[4] The delay manipulation was partially expressed in a tendency to perform movements slower, as indicated by a decrease in movement times, maximal acceleration and velocity with an increase in stimulus–response interval. The mentioned Delay × Distance interaction was related to a somewhat different distribution of movement times of the longest delay condition across the eight targets as compared with the shorter delays (see Supplementary Table S1).

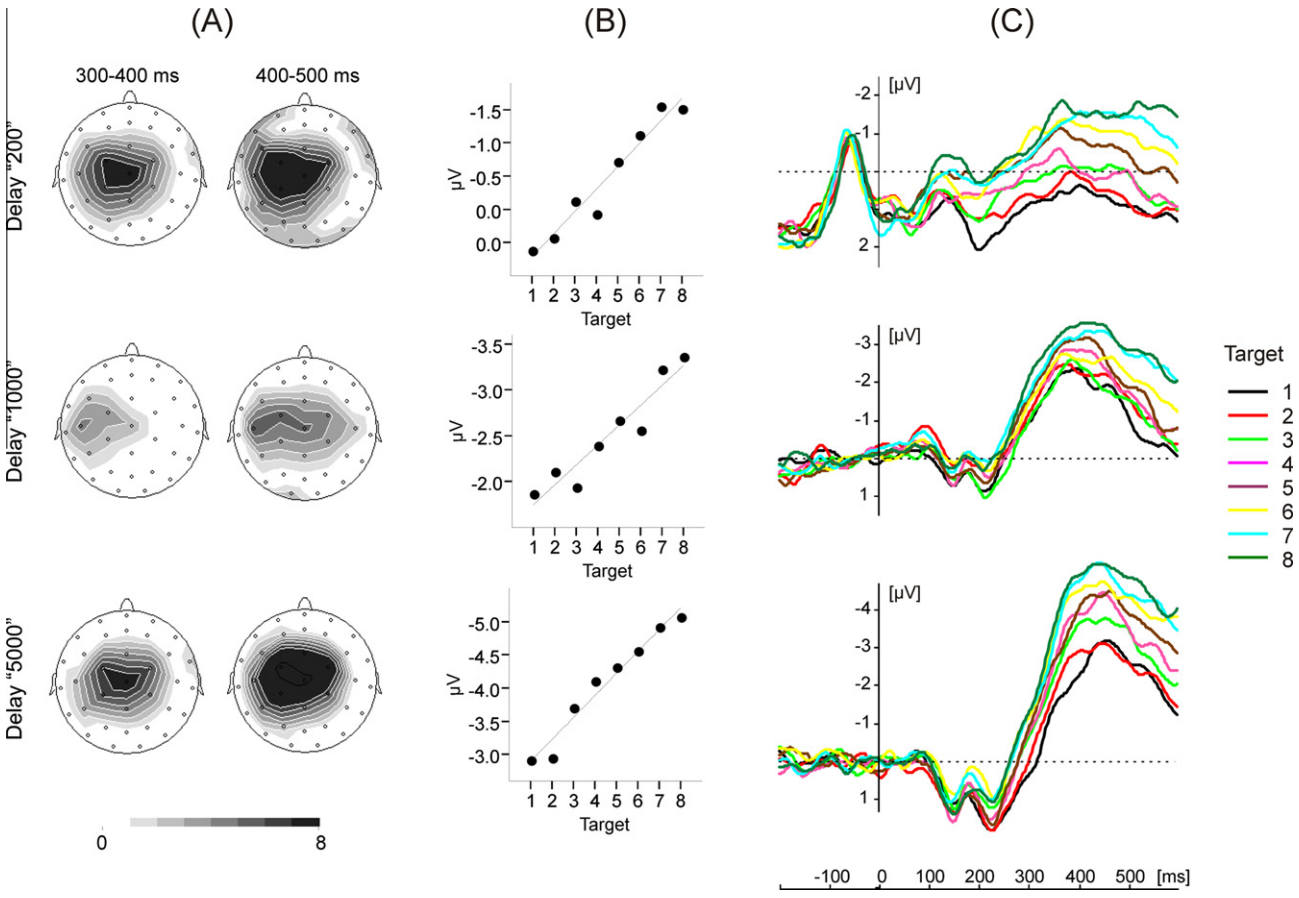

Fig. 2. (A) Topographical distributions of *F* values of significant main effect distance, derived from electrode specific ANOVAs computed for each delay condition separately. (B) Mean amplitudes of eight target conditions at CZ electrode in the time-window 400–500 ms after the imperative go signal. (C) Low-pass filtered ERPs (15 Hz) measured at CZ. The time scale is adjusted to the go signal (i.e., 0 ms represents the offset of the fixation LED). The rows reflect the three delay conditions.

Table 2
Electrode × Distance interactions of time-window specific ANOVAs performed on mean amplitude during movement execution.

	0–50	50–100	100–150	150–200	200–250	250–300	300–350	350–400
F(420, 8400)	1.60	**2.00****	**2.82****	**1.57***	**2.18****	**2.73****	**1.96***	1.78
p	.052	**.002**	**<.001**	**.047**	**.004**	**<.001**	**.018**	.050

Note: All tests were adjusted according to Huynh and Feldt (1976). The shown degrees of freedom are not corrected, while probabilities represent corrected values.
* $p < .05$.
** $p < .01$.

previously reported results suggesting primarily sensory feedback functions (Brunia, 1987; Deecke et al., 1976; Shibasaki et al., 1980) we assumed based on the topographical distributions of distance effects and amplitudes as well as on results of a source analysis that the N4 may also be associated with a rather executive control mechanism (Kirsch et al., in press). The results of the present study seem to support this notion. Maximal distance differences during movement execution were found over left frontocentral areas, suggesting primarily involvement of motor cortices in generating this deflection. These temporal and spatial characteristics are in line with our previous results and may indicate a role of this component in the control of deceleration.

We also analyzed ERPs preceding movement onset in the current study in order to examine programming processes taking place shortly before movement initiation. After the imperative go signal, we obtained similar deflections and distance differences around the central electrodes for all delay conditions. A negative going potential with an onset latency of about 200 ms and a maximum of about movement onset was present in all conditions and was strongly modulated by the target distance showing an increase in amplitude with an increase in distance. Such components belong, like N4, to a group of movement-related potentials, which are usually accompany motor acts (see e.g., Brunia, 1987; Brunia and Van Boxtel, 2000; Deecke et al., 1976; Tamas and Shibasaki, 1985, for reviews). The last premovement negative shift is the "motor potential" (MP), which was attributed to the discharge of pyramidal tract neurons in the primary motor cortex and thus, is assumed to represent the command to move (Arezzo and Vaughan, 1980; Brunia, 1987; Brunia and Van Boxtel, 2000; Deecke et al., 1969; Gilden et al., 1966). Our results are in accordance with several previously reported observations showing a high sensitivity of this deflection to various kinematic and kinetic variables (e.g., Slobounov et al., 1999, 2000; Kristeva et al., 1990; Siemionow et al., 2000).

Additionally, the observed distance effects and the shape of ERPs around movement onset seem to be directly related to the modulation of acceleration rather than to velocity changes (see Fig. 4). Maximal amplitudes of MP are achieved shortly before

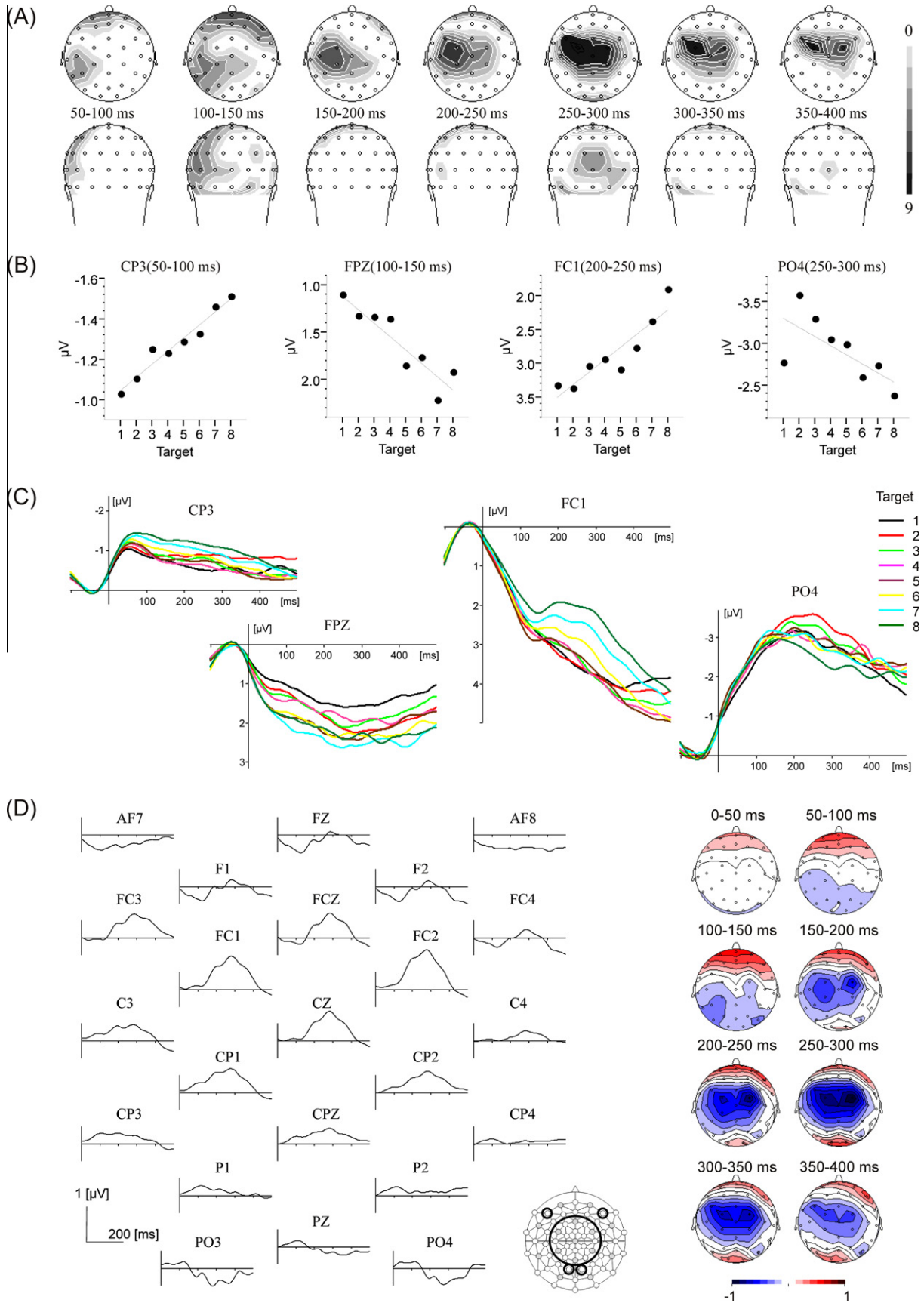

Fig. 3. (A) Significant *F* values of main effects distance, computed for each electrode including all delay conditions. (B) Mean amplitude values of eight target conditions at selected electrode locations and in selected time-windows. (C) ERPs at corresponding electrodes (low-pass filtered (5 Hz) potentials are shown). (D) Difference waves between the averaged ERPs of the four near and of the four far target conditions at selected locations (left) and their time dependent topographical distribution (right). All time scales are adjusted to the defined movement onset (0 ms).

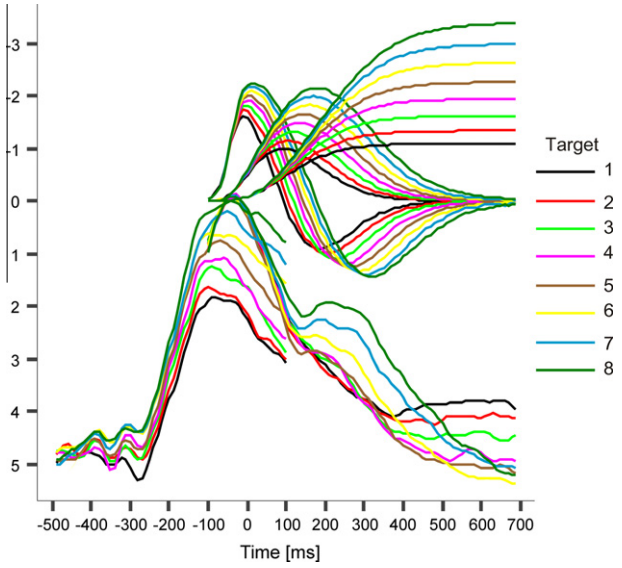

Fig. 4. Kinematic parameters of the handle and ERPs at FC1 before and during movement execution. Apart from the ERPs of the motor control phase, which are illustrated according to the original μV-scale, the *Y*-axis for all other potentials and kinematics reflects for descriptive purpose converted μV, mm, m/s, m/s^2 values (μV + 4.7, mm $*(-1)/70$, m/s $*(-1)*3$, m/s^2 $*(-1)/2$). The time scale shows the time in respect to movement onset (0 ms). *Note:* The relation of the movement onset to the ERPs of the motor preparation phase based on average reaction time values (i.e., the imperative go signal occurred at approximately −490 ms in respect to the defined begin of the movement).

maximal acceleration (about 20–50 ms on average) and this lag seems to fit well into the recent estimations of cortico-muscular delays (MacKinnon and Rothwell, 2000; Petersen et al., 1998). In contrast, the peaks of velocity curves are temporally further away and do not seem to show any relation to the ERP course. As mentioned in Section 1, acceleration is strongly related to force and muscle activity visible in EMG. For instance, activation of agonistic muscle groups (AG1) providing the driving force for setting the limb in motion, as well as the following antagonistic burst (ANT) associated with decelerative forces are accompanied by the second derivative of the position trajectory temporally as well as in respect to the magnitude (Brown and Cooke, 1990; Cooke and Brown, 1994; Ghez and Gordon, 1987; Ghez and Martin, 1982; Gordon and Ghez, 1984; Gottlieb et al., 1989). The modulation of the initial acceleration (and/or of the AG1 burst) is supposed to result from the variation of a control signal, labeled force pulse, excitation pulse or impulse, whose "height" (intensity) and "width" (duration) can be adjusted to various task situations (i.e., the CNS is supposed to determine a type of varying force–time integral, see e.g., Schmidt, 1982; Gottlieb et al., 1989). Such a pulse has been defined as descending presynaptic input, which converges and summates in the alpha motor neuron pool (Gottlieb, 1993; Gottlieb et al., 1989). The spatial and temporal summation of all converging action potentials was assumed to be related to the pulse height, while duration of that firing burst was attributed to the pulse width. If the MP is indeed associated with the corticospinal outflow initiating the movement as suggested (see above), the modulation of its intensity and duration may possibly be related to a modulation of the pulse height and pulse width of the initial force pulse. Accordingly, the found increase of negative amplitude over sensorimotor areas around movement onset may reflect distance specific scaling of motor command (i.e., scaling of neural input to the alpha motor neuron pool, for similar suggestions see e.g., Siemionow et al., 2000; Slobounov et al., 1999).

In conclusion, the current results demonstrate that the control of rapid movements is accompanied by distance dependent evoked activity measured at several scalp locations. Such a highly task specific activity seems to comprise several brain regions, with a special prominence of areas locating close to the central sulcus, which appear to be involved in a non-continuous fashion showing two phases of negative going potential changes. The first phase takes course parallel to the acceleration of the hand and seems to be related to the well-known motor potential preceding movement onset. After an obviously fixed interval of approximately 120 ms a second negative potential occurs, which is highly distance specific and also appears to follow the acceleration-time courses rather than the other kinematics. These results confirm our previously reported findings as well as results observed with single neuron recordings (Sergio et al., 2005; Sergio and Kalaska, 1998) and are in agreement with several force control schemata suggesting a direct low-level muscle control rather than the coding of higher-order motion parameters.

The conclusions are of course tentative and should be considered with caution due to the limitations of the methods used. For instance, although the observed relation between ERPs and kinematic parameters is very obvious, it is of course descriptive and needs to be substantiated by quantitative analyzes in future studies. Moreover, the data does not seem to indicate a one-to-one relation between the central and peripheral processes due to the time-dependence of onset of N4. Thus, the control mechanisms relating to the termination of action may also rely on other than central processes within the system, such as by stretch reflex (e.g., Ghez and Martin, 1982). This may hold true for short distance condition, where the N4 component is nearly absent. On the other hand the modulation of N4 may also be due to distance differences in the involvement of antagonistic muscle activity (e.g., if short movements were mainly controlled by agonists). Finally, it is possible that the ERP effects are related to movement time rather than to the movement amplitude and its derivatives. Future studies can address this question by employing similar target eccentricities with invariant movement times. Our force-related explanation would predict an increase in amplitude of MP and N4, whereas their peak latencies may be expected to be comparable.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.clinph.2010.02.151.

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