

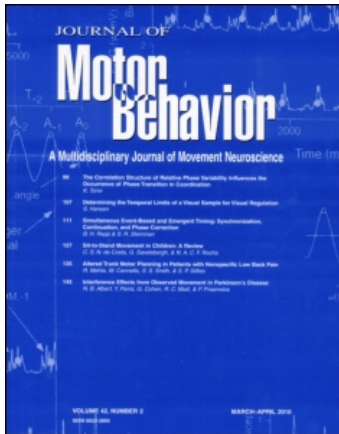
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RAPID COMMUNICATION

Kinematic Markers of Distance-Specific Control in Linear Hand Movements

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ABSTRACT. In this article, the authors analyze kinematic characteristics of reaching movements to memorized visual target locations. An increase in target distance was associated with a decrease in correlation between peak acceleration and movement distance and with a simultaneous increase in correlation between peak acceleration and movement time. According to the previous work on motor control in isometric force responses and in reaching movements these results seem to indicate a continuous transition from a rather preplanned to a more corrective mode of movement control, which may be associated with an adaptive mechanism serving to counteract an increase in signal-dependent noise of the motor system.

Keywords: arm movements, motor control, trajectory control

A common view of motor control is that some characteristics of movement trajectory are preplanned before movement onset, while others may be modified online (e.g., Desmurget & Grafton, 2000). For instance, analyzing trajectory control in targeted isometric force responses, Gordon and Ghez (1987a, 1987b) observed that initial peaks of the second time derivative of force (d^2F/dt^2) were highly predictive of the final force achieved. Based on this result, they suggested that the peak d^2F/dt^2 can be used as an operational measure of the preprogrammed scaling of responses (i.e., of the contribution of preplanned motor program to trajectory formation). A strong association between early kinematic parameters such as peak acceleration or peak velocity and movement distance has also been reported in reaching movements to memorized visual targets (e.g., Messier & Kalaska, 1999). Additionally, the authors of these studies reported evidence of a systematic reciprocal coupling between acceleration and movement or force rise time, when individual target distances were considered separately: An increase in peak acceleration was often associated with a decrease in movement or force rise time, and conversely longer lasting movements or force responses tended to have lower acceleration peaks (cf. Gordon, Ghilardi, Cooper, & Ghez, 1994; Martin, Cooper, & Ghez, 1995). This finding has been used as an argument for an error-correction mechanism, which is applied to compensate for trajectory variability by adjusting duration (Gordon & Ghez, 1987b) and has also been integrated within a general model of motor control as one of the automatic properties relating to trajectory control (Bullock & Grossberg, 1988). The rationale behind the proposed mechanism is the following: If the acceleration for a given target distance is too high early in a movement, the trajectory is corrected by shortening the movement time, and, conversely, if acceleration is too low, the movement time

is prolonged. If this compensation not occur, the faulty initial acceleration produces movement distances, which are inappropriate for a given target (i.e., target is undershot or overshoot).

Thus, compensatory adjustments have been assumed to counteract errors in initial specification of trajectory and, thus, to improve accuracy by reducing movement or force variability at a given target amplitude. This notion raises the possibility that the relation between preplanning and on-line adjustment processes in joint movements may depend on the range and duration of motion. Harris and Wolpert (1998) suggested that neural motor control signals are accompanied by noise (i.e., by noise in the firing of motor neurons), the variance of which increases with the absolute size of the control signal. Moreover, the CNS has been assumed to aim at minimization of consequences of noise in the sensorimotor system, that is, at minimization of the variance of the final effector position (Van Beers, Baraduc, & Wolpert, 2002; Harris & Wolpert). Thus, the contribution of compensatory adjustments of trajectory to final accuracy may depend on movement magnitude and may serve to counteract variations in signal-dependent noise. Accordingly, movements of small amplitude may mainly be controlled by the initial motor command because the deviations of trajectory from the desired path may rather be small due to the low level of noise. An increase in movement distance and time may require successively stronger involvement of corrective mechanisms to compensate for an increase in noise during the specification of motor commands.¹

In support of this notion, Desmurget et al. (2005) observed a decrease in correlation between peak acceleration and movement amplitude as a consequence of an increasing target eccentricity in visually directed point-to-point movements. They presumed that this result would reflect stronger involvement of feedback loops in movements of longer durations and amplitudes. Thus, Desmurget et al.'s study seems to point to an adaptive mechanism that may be applied to deal with noise variability associated with variability in movement magnitude. However, one possible caveat in respect to the observed change of the relationship between peak acceleration and movement distance is that it may be related to noise in the implementation of the motor program but

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unrelated to corrective adjustments of movement trajectory (cf., Gordon & Ghez, 1987b). Accordingly, the assumption of an increasing influence of feedback loops with movement magnitude would be strengthened, if it is possible to show that a decreasing relation between an early kinematic marker, such as peak acceleration and endpoint distance indicating a decreasing influence of a preplanned control mode is accompanied by a simultaneous increase in relation between this kinematic marker and movement time, which can be associated with an increasing role of online adjustments of trajectory. With the present analyses we aimed to test this hypothesis.

Method

Participants

Participants were 22 right-handed individuals.² They gave their written consent and received either course credit or an hourly payment. Two participants were excluded from the analyses due to insufficient quality of data (as a result of violation of the instructions). The final sample included 10 men and 10 women between 21 and 35 years of age (M age = 25 years, $SD = 4$).

Apparatus

Kinematic data were acquired using an instrumented manipulandum. The manipulandum was a plastic penlike handle mounted on a linear track device that allowed one-dimensional movements on the horizontal plane slightly above the waist. Eight green light-emitting diodes (LEDs; visible surface 6 mm²) were placed at distances between 10 and 31 cm from the starting position (3 cm between successive LEDs) in front of the participants. The starting position was the nearest possible handle location in respect to the body (approximately 10 cm). An additional red LED with visible surface of 1 mm² was used as a fixation light. It was mounted 70 cm in front of the participants at the eye level. The experiment was performed in darkness, apart from rest periods, in which the room was illuminated. During the experiment participants positioned their head on an individually adjusted headrest.

Experimental Procedure and Design

At the beginning of a trial, a red fixation LED was illuminated 2 s after an auditory warning stimulus (2000 Hz). Two seconds later, one of eight target LEDs was lighted for 50 ms. After 200, 1,000, or 5,000 ms in respect to the target offset, the fixation light was turned off.³ This served as a go signal, indicating that participants should initiate the movement toward the remembered target position. After an interval of 2 s a second auditory stimulus was presented (250 Hz) in response to which the handle could be returned to the starting position.

The experiment consisted of 12 blocks with 64 trials each (8 locations \times 8 movements). The delay within each block was constant, while eight targets were randomly presented with the constraint that the whole sequence should be completed before another repetition. The order of blocks was also randomized across participants. At the beginning of the experiment, participants performed three short practice blocks including all delay conditions, which did not enter the analysis.

Recording and Data Preprocessing

The movement trajectories of the manipulandum were recorded by means of an ultrasound motion device (ZEBRIS, CMS 20) with a sampling rate of 100 Hz. The recorded movement trajectories were filtered with two zero-phase lag filters, a median filter (based on 3 data points) and a moving average filter (5 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 3% of the maximal velocity, and movement termination was related to the point in time when velocity fell below the same threshold. Additionally, maximal acceleration and movement distance were determined for each trial. These markers were set using automatic routines based on Lab View codes (National Instruments, Graphical Programming for Instrumentation) and were approved by the visual data inspection.

Participants were instructed to perform movements as accurately and fast as possible without corrections. Accordingly, the motion parameters associated with the displacement of the handle proved to have usual characteristics such as single-peaked velocity and biphasic acceleration trajectories. However, in some cases corrections of the trajectory were obvious. We first excluded trials with overt discontinuities or interruptions in the temporal pattern of the recorded position signal from analysis. After this, velocity profiles were screened. Trials with more than one velocity peak were kept if velocity did not return to the defined offset threshold. Beyond that point, any obvious corrections were not considered as a part of the movement.

Moreover, we rejected trials with reaction times, which were longer than 1.5 s and shorter than 100 ms. Furthermore, trials with outlier values (3 standard deviations above or below the mean peak acceleration, movement time and movement distance as determined separately for every participant, every delay and every distance condition) were also discarded. After this preprocessing procedure, the number of trials entering the analyses was 14,045 (91.4%).

Data Analysis

The original method leading to the mentioned conclusions about preplanning and trajectory adjustments comprised a

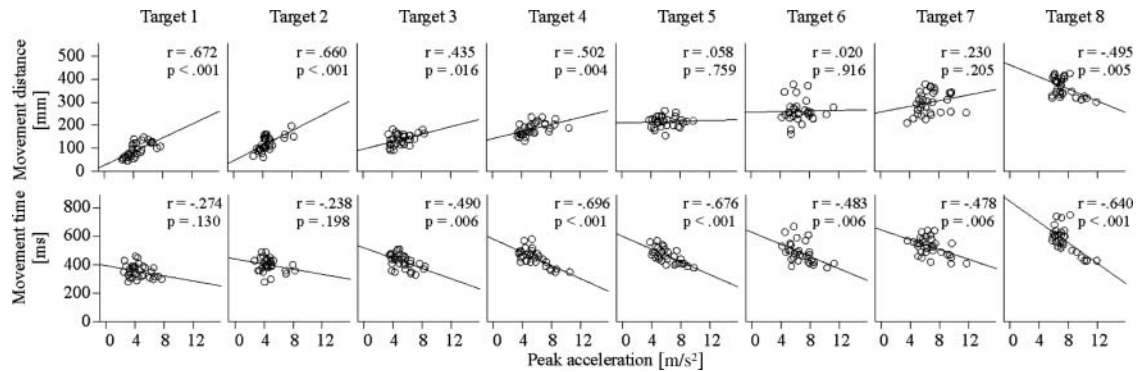


FIGURE 1. Relations between peak acceleration and movement amplitude (top) and between peak acceleration and movement time (bottom). The data of a single participant according to one delay condition and eight targets is shown. Lines are regression lines fitted to the data of each target condition. Pearson correlation coefficients (r) and corresponding p values are also inserted into each plot.

causal statistical model and multiple regression analyses including peak force, d^2F/dt^2 , target amplitude, force rise time and EMG patterns as variables (for details, see Gordon & Ghez, 1987b). Because the main results were well supported we used a simplified approach in the present study. To examine the magnitude of central planning and corrective processes, we analyzed the relation between maximal acceleration and movement distance as well as between maximal acceleration and movement time (time difference between movement onset and offset) by computing Pearson's correlation coefficients on a trial basis for each participant, target, and delay condition separately (cf. Gordon et al., 1994; Martin et al., 1995). We expected that an increase in target distance would be associated with a decrease in positive correlation between peak acceleration and movement distance due to an increase in noise at the stage of motor command specification. Simultaneously, an increase in negative correlation between peak acceleration and movement time would be obtained if trajectory adjustments were indeed increasingly used to reduce the variability of the hand path. Changes in the magnitude of mean correlation coefficients, caused by target or delay manipulations, were tested with two-way analyses of variance (ANOVAs) with delay (3 levels) and distance (8 levels) as within-participants factors. We also performed additional analyses, the details of which are reported in the *Results* section.

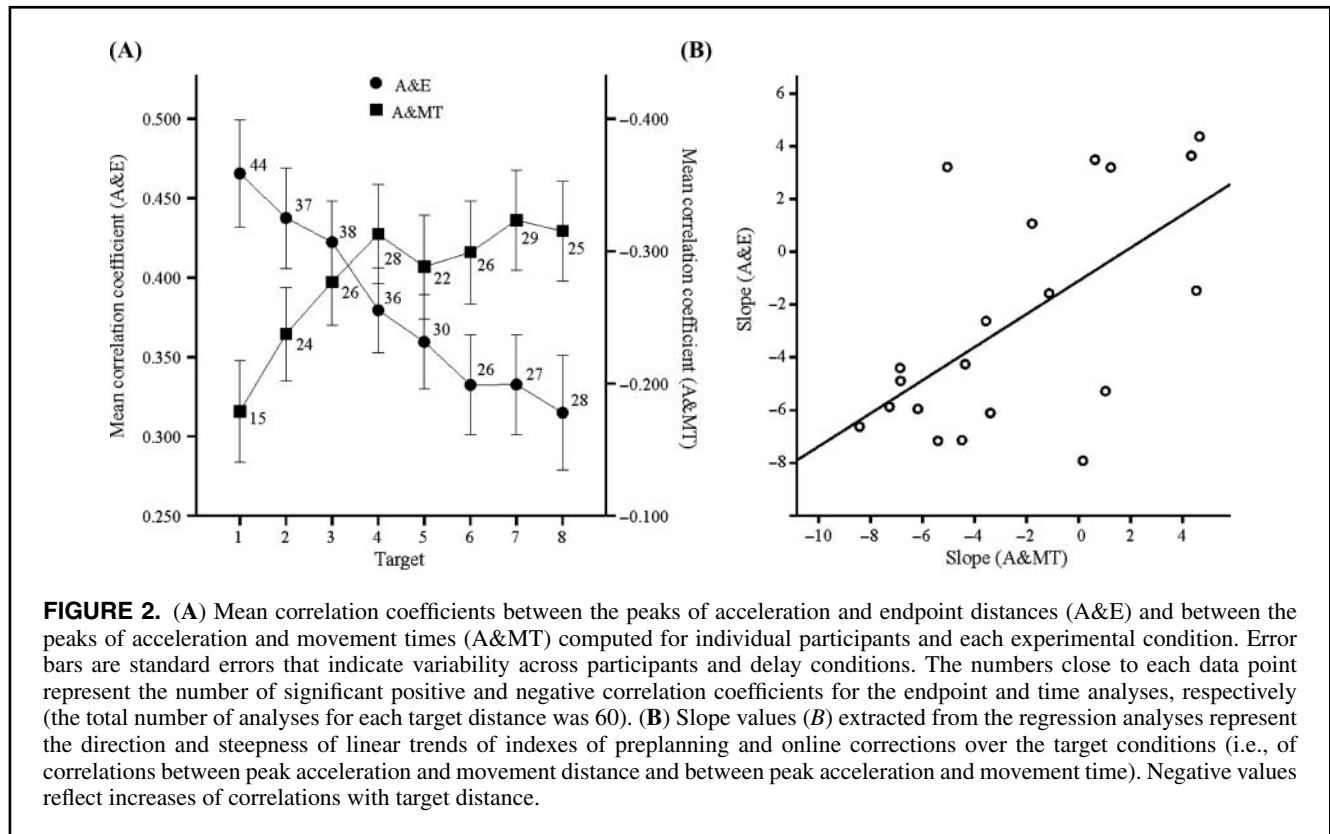
For all reported analyses the factor delay proved to be independent from the factor distance (i.e., all interactions including distance and delay as factors were not significant). Hence, all reported changes in kinematic markers across the implemented range of distances were similarly pronounced for all delay conditions. Because of this and due to a lack of a priori hypotheses in respect to possible delay effects, we restricted the presentation of results to distance effects only.

Results

The implemented manipulation of target distance (100, 130, 160, 190, 220, 250, 280, 310 mm) was accompanied by usually observed variations of movement time (339 [$SD = 64$], 363 [$SD = 65$], 390 [$SD = 66$], 418 [$SD = 71$], 447 [$SD = 73$], 473 [$SD = 75$], 500 [$SD = 76$], 538 ms [$SD = 84$]), movement distance (77 [$SD = 27$], 94 [$SD = 30$], 114 [$SD = 32$], 137 [$SD = 37$], 159 [$SD = 41$], 186 [$SD = 44$], 211 [$SD = 45$], 239 mm [$SD = 48$]), maximal acceleration (3.85 [$SD = 1.28$], 4.15 [$SD = 1.32$], 4.47 [$SD = 1.37$], 4.67 [$SD = 1.40$], 4.92 [$SD = 1.40$], 5.17 [$SD = 1.43$], 5.35 [$SD = 1.48$], 5.53 m/s² [$SD = 1.52$]), time to maximal acceleration (61 [$SD = 30$], 63 [$SD = 30$], 64 [$SD = 31$], 67 [$SD = 33$], 68 [$SD = 33$], 72 [$SD = 35$], 74 [$SD = 39$], 76 ms [$SD = 38$]), and maximal velocity (.38 [$SD = .12$], .44 [$SD = .13$], .50 [$SD = .13$], .56 [$SD = .14$], .62 [$SD = .14$], .68 [$SD = .15$], .74 [$SD = .15$], .79 m/s [$SD = .16$]).

The focus of our main analysis was the relation between maximal acceleration and movement distance, and between maximal acceleration and movement time. Figure 1 shows the data from a single participant.

If each target condition was considered separately, the peak acceleration was typically positively related to movement distance and negatively to movement time. However, additionally to these, also previously reported results (e.g., Gordon & Ghez, 1987a, 1987b; Messier & Kalaska, 1999), we observed that the magnitude of these relations was dependent on target distance. The maximal acceleration often predicted the final distance better when movements were performed toward near targets as compared with movements performed toward far targets (cf. Desmurget et al., 2005). In contrast, negative correlations between acceleration and movement time were more pronounced when movements of higher amplitude were executed. We quantified these relations by means of two ANOVAs with within-participants



factors distance and delay performed with correlation coefficients computed for each participant and each experimental condition separately. The results indicated a significant main effect for factor distance in both analyses, $F(7, 133) = 2.5, p = .02$, for correlations with movement time, and $F(7, 133) = 3.4, p = .002$, for correlations with movement distance, suggesting significant distance specific changes of the mentioned relationships. Figure 2A illustrates the mean values from these analyses according to the eight distance conditions. As shown, an increase in target distance was associated with a decrease in correlation between maximal acceleration and final distance and, simultaneously, with an increase in correlation between maximal acceleration and movement time.

We explored the consistency of the results across participants using linear regression analyses with correlations coefficients as independent variables and target (1–8) as the dependent variable. The critical measure was the slope value extracted from the regression equations (unstandardized regression coefficient *B*), which represents how steep the regression line was for each participant. The slopes were negative⁴ for both correlation types on average, $B = -2.4$ ($SD = 4.1$) for correlations between peak acceleration and movement time and $B = -2.6$ ($SD = 4.3$) for correlations between peak acceleration and movement distance, and were both significantly different from zero, $t(19) = -2.6, p = .018$; $t(19) = -2.7, p = .013$, respectively. Thus, the trends shown in Figure 2A are consistently present in the

examined sample of participants. However, there were also marked differences in the deviation of the individual values from the averaged pattern. For instance, some participants did not express an increasing trend in negative correlations with distance (7 of 20) or a decreasing trend in positive correlation (6 of 20) as indicated by positive *B* values. A part of this variance might arise because some participants did not apply more trajectory adjustments with distance in spite of a decrease of preplanning or some participants might have applied progressively greater corrections although the impact of preplanning did not change with distance. Alternatively, preplanning of the trajectory and the amount of online corrections might be related to each other, as we hypothesized, but might not follow the predicted distance specific pattern in some participants. If so, then participants who did not show an increase in corrections with distance should also show no decrease in preplanning. To evaluate this issue we correlated the mentioned slopes (*B*, see previous) with each other. The corresponding correlation reached a value of .609 ($p = .004$), suggesting a considerable interdependence of distance specific changes of the correlations between peak acceleration and movement time and between peak acceleration and movement distance (see Figure 2B). Thus, in addition to the predicted distance specific changes of preplanning and adjustments markers, there was a rather consistent trend toward an inverse relation between them (e.g., participants, who unexpectedly showed an increase in correlation between

peak acceleration and movement distance with an increase in target distance tended to show a decrease in negative correlation between peak acceleration and movement time and vice versa). Accordingly, the deviating results patterns observed in some participants do not contradict the general idea of a varying relation between preplanning and online control, but rather seem to suggest that an increase in movement magnitude does not necessarily lead to a decreasing role of preplanning and to an increasing role of compensatory adjustments of trajectory (see also Additional Analysis Point 3).

If the observed tradeoff is indeed due to a varying reliance on planning and corrections as a consequence of variability in neural noise within the sensorimotor system, then some additional predictions can be inferred and tested.

1. The relation between the variable error in movement distance and the variability in peak acceleration should vary as a function of target distance. An increase in target distance may be assumed to be associated with a decrease of endpoint error in comparison to the error in initial acceleration. This should hold true if online corrections indeed serve to reduce endpoint variability as suggested (cf. Gordon & Ghez, 1987b), and, if they are indeed more frequently used for movements to far targets than for movement to closer targets. In this case final error should be more profoundly reduced relative to acceleration error for long movements than for short movements because initial movement variability (or noise) would be stronger reduced by more adjustments applied in movements to far targets. Otherwise (i.e., if trajectories would be corrected or not corrected to a similar degree across the target range), the endpoint error should either change proportionally with the initial variability in acceleration if the amount of noise remains constant in the course of the movement or increase with distance relative to variability in peak acceleration if motor noise is accumulated in the course of the movement.

A consequence of neural noise is the imprecision of the movement (i.e., the variable error; e.g., Van Beers et al., 2002; Harris & Wolpert, 1998). However, the variability in movement distances may not only reflect imprecision in motor planning (e.g., Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979), it may also be a result of processes going on during movement execution (e.g., Gordon & Ghez, 1987b). In the present study the endpoint variability values (i.e., standard deviations in movement distance) were 27, 30, 32, 37, 41, 44, 45, and 48 mm for the target conditions 1, 2, 3, 4, 5, 6, 7, and 8, respectively. The factor target proved to be significant in the corresponding statistical analysis (ANOVA), $F(7, 133) = 18.16, p < .001$. Thus, the overall movement variance increased with distance. We then estimated the precision of the initial motor command by examining the variability of the peak acceleration (or of the initial force pulse height). The corresponding standard deviation also increased significantly with target distance (1.28, 1.32, 1.37, 1.40, 1.40, 1.43, 1.48, 1.52 m/s²), $F(7, 133) = 5.53, p < .001$. More importantly, the relation between the relative errors in acceleration and in

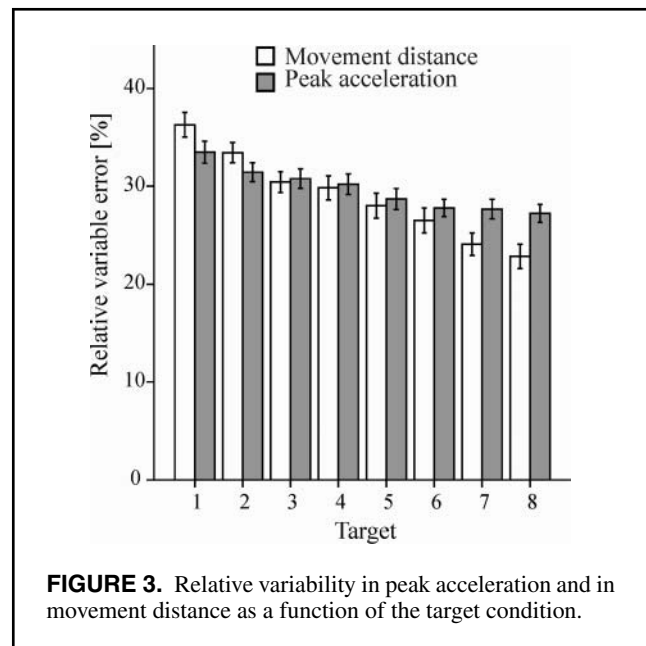


FIGURE 3. Relative variability in peak acceleration and in movement distance as a function of the target condition.

movement endpoints was dependent on target distance (see Figure 3).

An analysis of variance performed on the relative variable errors in peak acceleration and movement distance yielded a significant interaction between the factors type of error and target distance, $F(7, 133) = 5.06, p < .001$.⁵ Thus, endpoint variability decreased with distance at a higher rate than variability in peak acceleration suggesting a successively increasing impact of mechanisms reducing endpoint variability online during movement execution.

2. If online corrections of trajectory are used to counteract noise in the initial motor program and, thus, to reduce endpoint variability, then participants showing a higher degree of online control can be assumed to exhibit lower endpoint variability as compared with participants using trajectory adjustments to a lesser degree. Moreover, it may be presumed that individual differences in application of trajectory corrections are also related to the precision of the initial motor command (e.g., participants programming movements precisely may not have to rely on online control mechanisms). The data confirmed these predictions.

We computed mean correlation between peak acceleration and movement time for all participants individually and correlated these values with the respective relative variable errors in movement distance and in peak acceleration. As shown in Figure 4, the index of trajectory correction (i.e., the correlation coefficient between peak acceleration and movement time) positively correlated with the endpoint variability ($r = .578, p = .008$) and negatively with variability in peak acceleration ($r = -.474, p = .035$). That is, participants using online adjustments rather rarely (i.e., those with more positive correlations between peak acceleration and movement time) exhibited more variability in movement distance than participants correcting the trajectory more

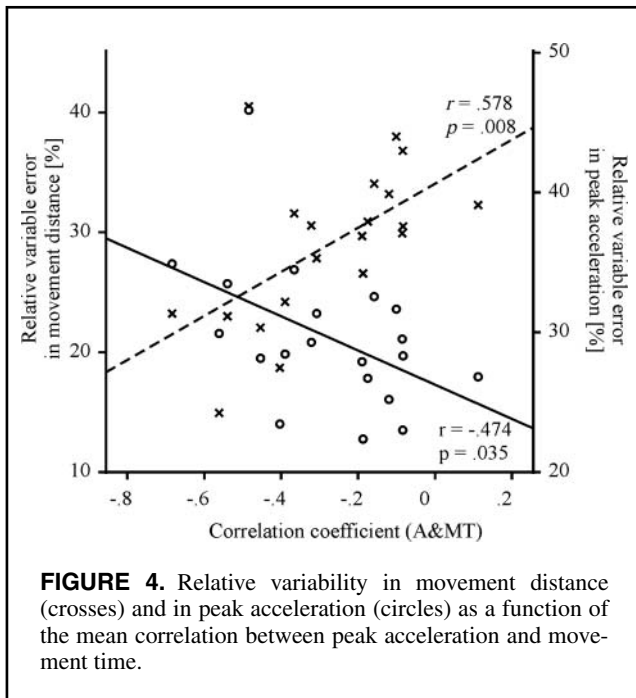


FIGURE 4. Relative variability in movement distance (crosses) and in peak acceleration (circles) as a function of the mean correlation between peak acceleration and movement time.

frequently (cf. dashed line in Figure 4). For the variability of the peak acceleration this relationship was reversed. Those participants who seldom corrected the trajectory tended to have less variability in peak acceleration (cf. solid line in Figure 4).

3. The assumed relations between the magnitude of noise and trajectory corrections on the one hand and between trajectory corrections and final accuracy on the other hand should also be expressed in correlations between changes of these markers over target distance. In particular, the individual slopes of correlations between peak acceleration and movement time across the eight target conditions should vary as a function of individual slopes associated with the changes of variability in peak acceleration and movement distances. In other words, a distance specific increase in online adjustments of trajectory should correspond to a distance specific increase in the imprecision of the initial motor command (i.e., the stronger the difference in noise of the initial motor command across the eight distances, the greater the difference in adjustments needed). Moreover, the rate of changes in adjustments should be inversely related to the rate of changes in the endpoint variability. That is, an increasing tendency to apply more adjustments with distance should result in a relative decrease of endpoint variability with distance (because more corrections may be assumed to stronger reduce inaccuracy as mentioned).

Individual slopes of distance specific changes in variability of peak acceleration and of movement distances were computed using linear regression analyses with target as independent variable. These values are shown in Figure 5 as functions of the slope, indicating linear trends in changes

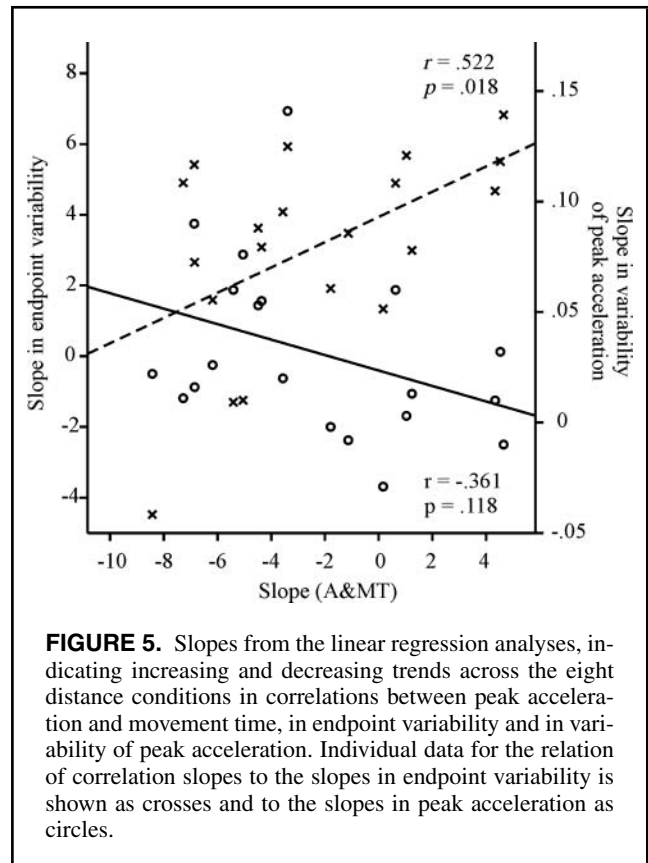


FIGURE 5. Slopes from the linear regression analyses, indicating increasing and decreasing trends across the eight distance conditions in correlations between peak acceleration and movement time, in endpoint variability and in variability of peak acceleration. Individual data for the relation of correlation slopes to the slopes in endpoint variability is shown as crosses and to the slopes in peak acceleration as circles.

of correlation indicating trajectory corrections (i.e., between acceleration and movement time) with distance. For both variability measures most of the values were positive, indicating an increase of the variable error with distance (see also previous analyses). Slopes for acceleration with movement time regression, in contrast, were negative for the majority of participants indicating an increase in negative correlation between acceleration and movement time with distance (cf. Figure 2). That is, participants with more negative slopes used progressively greater corrections over target distance compared with participants with slopes near zero. Positive slopes indicate an opposite trend toward applying fewer corrections with an increase in distance.

The slopes of the correlations between peak acceleration and movement time correlated positively and significantly with slopes in endpoint variability values ($r = .522, p = .018$). This result suggests that participants using progressively more corrections with distance tended to have a relative decrease in final movement variability with distance as compared to participants showing a less pronounced increase (or a decrease) of corrections with an increase in distance.

For the variability measures of peak acceleration a negative trend was observed ($r = -.361, p = .118$), indicating a tendency to apply more trajectory adjustments with distance in response to an increase of variability in acceleration with distance.

Discussion

We asked participants to perform linear hand movements to memorized visual targets and analyzed kinematic movement characteristics. The main purpose of the present analyses was to examine a possible dependency of preprogrammed and online control mechanisms on movement amplitude and duration. Maximal acceleration is an early kinematic marker that is assumed to be widely specified before movement initiation. A number of studies showed that this measure is predictive for final movement position and it may serve as a signature of preprogrammed scaling of responses (e.g., Gordon & Ghez, 1987a; Messier & Kalaska, 1999). Moreover, it has also been demonstrated that maximal acceleration (or velocity) may negatively correlate with movement time (Gordon & Ghez, 1987b; Gordon et al., 1994; Martin et al., 1995; Messier & Kalaska). This has been interpreted as evidence for a mechanism of trajectory adjustments serving to compensate for initial force pulse variability (Gordon & Ghez, 1987b). We used this rationale as the basis for the correlation analyses performed between peak acceleration and movement distance and between peak acceleration and movement time.

Negative correlations between maximal acceleration and movement time were rather rare and low, when short movements were performed. This suggests that the type of trajectory corrections mentioned previously has only seldom been used. Simultaneously, the kinematics of the same movements were characterized by maximal correlations between peak acceleration and final movement distance, as compared with other target ranges. These results appear to indicate a dominant role of central planning processes in movements of small amplitude and speak to the preference for an open-loop mode of control. As movement distance increased, the magnitude of negative correlations between peak acceleration and movement time increased, whereas positive correlations between peak acceleration and movement distance decreased (cf. Figure 2A). This predicted results pattern suggests a change of processing from a rather preplanned to a more corrective control with an increase in movement magnitude. Moreover, it seems to support the assumption of a mechanism that is applied in order to counteract an increase in movement variability associated with an increase of noise in the motor system.

The results of additional analyses appear to confirm this conclusion. We used the variability in peak acceleration and in movement distances as markers of signal-dependent noise. The acceleration variability was assumed to reflect imprecision in the initial motor command (e.g., Schmidt et al., 1979), whereas the final movement variance was assumed to reflect noise in preplanning as well as in online control (e.g., Gordon & Ghez, 1987b). An increase in target distance was associated with an increase in variability of both measures, suggesting that larger motor commands were noisier as predicted by the minimum variance theory (Harris & Wolpert, 1998) and the impulse-variability model (Schmidt

et al.). More importantly, when relative variable errors were considered, we observed that variability in movement amplitude decreased at a higher rate than the variability in peak acceleration (cf. Figure 3 and Additional Analysis Point 1). That is, an increase in target distance was associated with a successive decrease in variability of movement distance as compared with variability in peak acceleration. Thus, there was a trend toward a nonproportional decrease in endpoint variability that can be explained neither by the imprecision of the initial motor command alone nor by a constant relation between preplanning and online control mechanisms. This result can be considered as evidence that endpoint variability was increasingly reduced with target distance during movement execution. We assume that this occurred through online corrections increasingly applied as target distance and motor noise increased.

Moreover, we observed moderate correlations between the amount of online corrections and endpoint variability as well as between the amount of online corrections and variability in peak acceleration. Participants showing substantial online adjustments of trajectory tended to have less variability in the movement distances, but more variability in the initial acceleration than participants who rarely used online corrections (cf. Figure 4 and Additional Analysis Point 2). This result further confirms the idea that online adjustments of trajectory are indeed used to counteract errors (i.e., noise) in the initial motor program and to improve response accuracy as originally proposed by Gordon and Ghez (1987b). Moreover, it points to interindividual differences in relative weighting of preplanning and online control mechanisms.

Interindividual differences were also observed in respect to the changes in correlation across the distance conditions. Although the described pattern of the main analysis was rather consistent, the individual patterns deviated more or less from it, and were even reversed in some participants. Nevertheless, we observed a considerable interdependence between distance-specific trends in measures of preplanning and of trajectory corrections, suggesting that the amount of distance specific changes of online corrections was dependent on the amount of distance-specific changes of preplanning (cf. Figure 2B). Thus, the deviating behavior observed in some participants may have been determined by noise in the initial command that, however, did not increase with distance as predicted. We explored this possibility by relating individual slopes, indicating increasing and decreasing trends in correlations of peak acceleration with movement time across the target distances to corresponding trends in variability of peak acceleration and of movement distance. As a consequence of the assumed reciprocal relation between trajectory corrections and the precision of the initial motor command, we expected a positive relationship between the tendency to apply more adjustments with distance and the tendency to express more variability in peak acceleration with distance (i.e., an increase in corrections with movement magnitude was assumed to take place in response to an increase of the imprecision of the initial motor command). However,

because trajectory adjustments are assumed to enhance final movement accuracy, an increasing tendency to apply more adjustments with distance should be accompanied by a progressively lower increase in the variable endpoint error. The results were compatible with these predictions. Participants who showed a strong increase in correlation between peak acceleration and movement time across the eight distances showed a less increasing (or more decreasing) trend in final movement variability than did participants whose correlation values of peak acceleration and movement time tended to increase to a lesser extent or even to decrease with distance. For the analyses of peak acceleration, the predicted pattern has also been observed, however, as not significant (cf. Figure 5 and Additional Analysis Point 3). Thus, the results appear to delineate that the distribution of noise in the initial motor command across the distances affected the application of trajectory adjustments, which on their part led to the modulation of the endpoint variability. This appears to further support the assumption that the magnitude of trajectory adjustments may depend on the magnitude of noise in the initial motor command. However, the observed interindividual differences indicate that motor noise was not exclusively determined by the movement magnitude in the present task.

The amount to which visually guided movements are planned in advance or controlled online has been controversially discussed. Three different types of models have been suggested to account for data in this research area (e.g., Desmurget & Grafton, 2000). According to feedforward approaches, movements are mainly controlled by a motor command that is specified before movement onset (e.g., Plamondon & Alimi, 1997). Feedback models, in contrast, emphasize the role of feedback loops and argue that motor commands are generated online during movement execution (e.g., Bullock & Grossberg, 1988). The third group of models (hybrid models) contains feedforward and feedback components, assuming that a crude motor plan is defined before movement onset and continuously updated through feedback loops (e.g., Desmurget & Grafton). Our results seem to highlight an aspect of how preplanned and corrective mechanisms may interact and, thus, indicate how feedforward and feedback processes are related to each other depending on movement amplitude and duration. Feedforward control appears to be best applicable to describe the observed kinematics of movements of small amplitude (cf. Schmidt et al., 1979). Feedback processes, in contrast, appear to be more valid the greater the movement magnitude is. According to our rationale, this tendency may arise as a consequence of neural noise, the magnitude of which depends on the magnitude of the initial motor command. If so, then the results would extend the hybrid principles by suggesting that the impact of a feedback component on the movement control may not be generally constant, but may depend on the precision or magnitude of the motor program and thus, may vary in different context conditions (cf. Meyer, Abrams, Kornblum, Wright, & Smith, 1988). Moreover, such a flexible control schema

may also be able to predict interindividual differences, such as those observed in the present study, as well as strategic influences on task outcomes, such as emphasis of accuracy or speed (cf. Gordon & Ghez, 1987b).

Given the findings suggesting that trajectory corrections may occur in a time range that may be assumed to be uninfluenced by visual and proprioceptive information (cf. Desmurget & Grafton, 2000), the involved feedback processes do not necessarily have to rely on sensory inflow. They may also depend on monitoring of motor outflow signals that allow trajectory corrections with negligible delays (e.g., Desmurget & Grafton 2000; Gordon & Ghez, 1987b). Moreover, there is increasing evidence that sensory inflow and motor outflow are integrated within one feedback module in the motor control system (e.g., Desmurget & Grafton; Miall & Wolpert, 1996; Wolpert, Ghahramani, & Jordan, 1995). Wolpert et al. suggested that efferent and reafferent information sources are combined, but are differently weighted depending on movement time. During an early part of the movement, motor outflow signals are predominantly used to estimate the present state of the effectors (e.g., position, velocity). In the course of the movement, however, the sensory feedback receives more weight. According to this and similar concepts, motor commands can be continuously updated (e.g., Desmurget & Grafton) and a strict distinction between planning and control mechanisms may be questioned (e.g., Guigon, Baraduc, & Desmurget, 2007). Our results are not inconsistent with these approaches, as no abrupt changes in the examined relationships and, thus, in the control mode were evident. A successively stronger involvement of online movement corrections may merely reflect a kind of response of the same feedback module to an increase of noise in the motor system.

It should be noted that our conclusions are based on the assumption that the CNS specifies a type of default trajectory and considers deviations from this ideal response as errors, which have to be corrected. Thus, if such corrective commands or temporal aspects of the response may be preprogrammed, the proposal of corrective trajectory adjustments as well as of contribution of motor program to the motor control may not be valid (Gordon & Ghez, 1987a, 1987b).

Another caveat is related to the fact that the relative variable error in acceleration as well as in movement distance tended to decrease with target distance (see also Gordon et al., 1994; Messier & Kalaska, 1999). Thus, the assumption that movements to near targets are associated with fewer errors and therefore require fewer corrections appears to be somewhat misleading, at first glance. However, the minimum variance theory (Harris & Wolpert, 1998), which we used here as a premise is grounded on Fitts's and Schmidt's laws (Fitts, 1954; Schmidt et al., 1979), which are based on the dependence of movement duration, movement amplitude, and the absolute variable error (or absolute target width). The problem has already been recognized by Schmidt et al., who speculated that such an effect (i.e., a decrease in relative variability with an increase in force) may be produced by

noise uncorrelated with the nature of the movement to be produced, and who also concluded that they did not feel that such a nonzero intercept detracted from their original thesis. Accordingly, there may be other variability sources than signal-dependent motor noise, which may affect the variability in the initial acceleration peak as well in the final distance and whose role as potential confounds has to be explored.

Finally, due to a strong interdependence of movement parameters an increase in movement distance is accompanied by variations of several kinematic markers. Accordingly, although the present data seem to correspond well with the idea of a compensatory response to the signal-dependent noise, alternative explanations are also possible. An increase in corrective adjustments for larger target distances may also be due to a greater capacity for corrective behavior with longer movement times (cf. Crossman & Goodeve, 1983; Keele, 1968). For closer targets, temporal constraints may make it difficult to substantially correct the trajectory. For further targets, movement times or the using of sensory feedback may be less constrained making more corrective adjustments possible. Thus, further studies are needed to examine the mechanisms underlying the observed tradeoff in more detail.

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NOTES

1. The minimum variance theory does not allow direct predictions in respect to online corrections of trajectory, as it was formulated to account for motor planning. However, it can explain Fitts's law as a consequence of signal-dependent noise (Harris & Wolpert, 1998). As suggested by Schmidt et al. (1979), Fitts's law may be assumed to well account for slower responses, in which error corrections are possible. In rapid movement tasks (with movement times shorter than 200 ms), an analogous speed-accuracy tradeoff can be explained by the variability of the initial force pulse and without the assumption of feedback-based corrective processes. Accordingly, our hypothesis is not inconsistent with the minimum variance approach. Moreover, a similar assumption can be derived from the work of Meyer et al. (1988) incorporating Fitts's as well as Schmidt's laws.

2. The data presented was collected within a comprehensive study aiming at the investigation of kinematic and electrophysiological correlates of planning and control of linear hand movements. In a previous article we reported a part of the results of this study (Kirsch & Hennighausen, 2010). In particular, we described electrophysiological markers of planning and control of one-dimensional hand movements associated with a varying degree of motion and their relation to the averaged kinematic trajectories. For the present report we used data collected in this study and focused on a single trial analysis of selected kinematic parameters.

3. One of the aims of the overall study was to investigate a possible dependence of visuomotor mapping on time delay inserted between stimulus and response. Based on the work on the relation between vision for perception versus vision for action (e.g.,

Goodale & Milner, 1992), we were primarily interested in EEG indicators of early stages of visuomotor planning. The purpose of the present analyses was quite different. Here, we focused on low-level motor control mechanisms, which may be assumed to be widely independent from the response delay, but dependent on the movement magnitude. Nevertheless, we included the factor delay in all analyses in order to ensure that the results are valid for all delay conditions.

4. Figure 2A gives an impression that the relationship between targets and correlations between peak acceleration and movement time is positive. Note, however, in Figure 2 the respective y-axis is reversed so that more positive values are at the bottom. Thus, the observed negative slopes are fully consistent with the data of the main analysis.

5. A similar analysis was also performed by Gordon and Ghez (1987b) to ensure that compensatory adjustments improve response accuracy. They estimated peak force variability, if peak d^2F/dt^2 were a perfect predictor of peak force. In their analysis, the coefficients of variability in peak force increased in respect to the observed values indicating that the overall accuracy was improved compared with a simulated case in which force rise time was constant.

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