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The use of overlapping submovements in the control of rapid hand movements

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Abstract Rapid targeted movements are subject to special control considerations, since there may be inadequate time available for either visual or somatosensory feedback to be effective. In our experiments, subjects rapidly rotated a knob to align a pointer to one of several targets. We recognized three different types of movement segments: the *primary movement*, and two types of submovement, which frequently followed. The submovements were initiated either *before* or *after* the end of the primary movement. The former, or “overlapping” type of submovement altered the kinematics of the overall movement and was consequently difficult to detect. We used a direct, objective test of movement regularity to detect overlapping submovements, namely, examining the number of jerk and snap zero crossings during the second half of a movement. Any overlapping submovements were parsed from the overall movement by subtracting the velocity profile of the primary movement. The velocity profiles of the extracted submovements had near-symmetric bell shapes, similar to the shapes of both pure primary movements and nonoverlapping submovements. This suggests that the same neural control mechanisms may be responsible for producing all three types of movement segments. Overlapping submovements corrected for errors in the amplitude of the primary movement. Furthermore, they may account for the previously observed, speed-dependent asymmetry of the velocity profile. We used a nonlinear model of the musculoskeletal system to explain most of the kinematic features of these rapid hand movements, including how discrete submovements are superimposed on a primary movement. Finally, we present a plausible scheme for how the central nervous system may generate the commands to control these rapid hand movements.

Keywords Hand movements · Kinematics · Submovements · Model · Human

Introduction

When healthy adults make unconstrained voluntary reaching movements, they are usually smooth and accurate. The velocity profile in the “end space” of the motor task (i.e., the path of the hand) contains a single peak, and is bell-shaped and nearly symmetric (Morasso 1981; Abend et al. 1982; Atkeson and Hollerbach 1985; Flash and Hogan 1985; Uno et al. 1989). However, in stroke patients (Krebs et al. 1999), infants (Berthier 1997), and adult subjects when they attempt to move with high spatial precision (Crossman and Goodeve 1983; Milner and Ijaz 1990; Novak et al. 2000), movements are often irregular, with multiple velocity peaks and asymmetric, non-bell-shaped velocity profiles. One explanation for the irregularities in movements is that they are due to discrete movement segments. The first segment, called the primary movement, usually contributes the largest velocity peak. Subsequent movement segments (submovements) each contribute another velocity peak. A large number of investigators, beginning with Woodworth in 1899 (Woodworth 1899; Keele 1968; Morasso and Mussa Ivaldi 1982; Crossman and Goodeve 1983; Meyer et al. 1988; Flash 1990; Milner 1992; Pratt et al. 1994; Berthier 1996; Krebs et al. 1996; Lee et al. 1997), have described irregularities in movements as a series of discrete submovements.

While earlier work assumed submovements were made at fixed, nonoverlapping intervals (Crossman and Goodeve 1983), or immediately following one another (Meyer et al. 1982, 1988), later work allowed for the possibility that the submovements overlap the primary movement (Flash and Henis 1990; Milner and Ijaz 1990; Milner 1992; Berthier 1997; Lee et al. 1997; Krebs et al. 1999). These later investigators generally decomposed a movement into separate overlapping movement segments by curve-fitting. Foremost of the assumptions in

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this process was that the basic *shape* of each movement segment was invariant, but its amplitude and duration could be scaled. Many experimenters (Flash and Henis 1990; Berthier 1997; Lee et al. 1997) have assumed that each segment has the minimum jerk velocity profile, but others have attempted to determine the shape empirically (Milner 1992; Krebs et al. 1999). Whatever the exact shape may be for different subjects and movement conditions, none of these previous models allows for trial-to-trial variability in the shape, and none has a direct, objective means of identifying when overlapping submovements are present. We attempt to deal with these and other issues in the present study.

In our experiment, subjects were required to rotate a knob rapidly with their fingers and wrist to align a pointer with a target. Close examination of the kinematics revealed that the primary movement varied in amplitude and often did not end in the target window. Consequently, subjects frequently made corrective submovements during (“overlapping submovements”) or after (“delayed submovements”) the primary movement. In a previous account of this work (Novak et al. 2000), we described an algorithm for objectively detecting the occurrence of overlapping submovements based on the smoothness and regularity of the kinematics, and we analyzed the kinematics of movements that were not complicated by these overlapping submovements. The work presented here focuses instead on the properties of overlapping submovements and the effect they have on the speed, accuracy, and kinematic trajectories of rapid hand movements. We examined the kinematics of rapid hand movements in order to gain insight into the neural mechanisms underlying the planning and correction of movement.

We test the hypothesis that irregularities in movement can be well described by a series of discrete segments of the same scaled shape. Discrete corrective submovements are presumed to be generated centrally, by a process that monitors efference copy and afferent feedback, from a variable primary movement, and then generates additional commands as required to correct for predicted or actual errors in the primary movement. We investigated, with both modeling and analysis, whether the presumed corrections are a continuous adjustment of the primary movement (for instance, its duration) or whether the corrections are discrete commands that lead to submovements. Finally, we discuss the notion that subjects plan to generate multiple movement segments, perhaps to reduce the variability caused by larger, faster movements. Our results are consistent with the hypothesis that the central nervous system (CNS) monitors and predicts the effects of previous movement commands, generating discrete corrections that are apparent in the kinematics of movement.

Materials and methods

Six subjects participated in the experiment after giving their informed consent, following a review and approval of the study by

the Northwestern University Internal Review Board. The subjects had previously participated in similar experiments (Novak et al. 2000). Subjects had no history or symptoms of neurological disease and appeared to be healthy individuals with normal motor skills. They ranged in age from 24 to 50 years; and there were five men and one woman. One subject was left-handed, while the others were right-handed. Subjects sat with their forearms resting on a horizontal armrest, with their elbows flexed 90°, and they were instructed to rotate a knob rapidly and accurately in a single motion, using their fingers and wrist, in order to align a pointer to light-emitting diode (LED) targets spaced above it. While subjects were encouraged to keep their upper arm still and to rotate the knob using only their fingers and wrist, no restraints were used, and no means were available to record all the individual joint motions that may have contributed to the overall movements. However, visual inspection of their movements during a practice session confirmed that most subjects kept their upper arm still and rotated the knob with coordinated motion of the following joints: finger flexion and/or extension and rotation, wrist ulnar and/or radial deviation, and small amounts of forearm pronation and/or supination.

The rapid, targeted rotation task was difficult in its timing and accuracy constraints. Subjects moved between three LED targets, each spaced 30° apart in an arc above the pointer. After one of the three target LEDs was pseudorandomly chosen and lighted, subjects had 400 ms to turn the knob pointer from the prior target into an 8°-wide area centered on the currently lighted target, either 30° or 60° away. Experiments were performed in the dark, and the pointer LED was extinguished as soon as subjects began to move. Visual feedback was thus removed during the movement and was returned after the trial ended by relighting the pointer LED. Subjects were informed of the results of their movements by an audible tone given at the end of a successful trial. Trials were performed in blocks of 240, taking 8 min to complete, and subjects were informed of their success rate at the end of each block. Subjects rested for as long as they wanted in between blocks of trials, usually for a few minutes.

As the subjects made these rapid movements, the pointer's angular position was measured with a potentiometer and velocity with a tachometer. These signals were digitized at 200 samples per second by a computer for later analysis.

Data analysis

Data were filtered digitally with a 3-point sliding boxcar filter, and derivatives of velocity (acceleration, jerk, and snap) were calculated through numerical differentiation. Overlapping submovements were detected as described previously (Novak et al. 2000), by looking at the regularity of the second half of the primary movement. Figure 1 shows the kinematics of three trials. The knob pointer's angular position is shown in the top row as the subject moves from one target to another, with each of the three targets shown as shaded horizontal bars. Irregular movements like the one in Fig. 1B had sizable inflections in the acceleration traces, detected as extra zero crossings in the jerk and snap records. On the other hand, pure primary movements (Fig. 1A) were smooth and regular. They were presumably generated by a single force pulse that created a single acceleration pulse without inflections.

The symmetry and shape of the velocity profile were quantified by the values K and C , respectively. K represents the relative time to peak velocity, with perfectly time symmetric movements having a K -value of 0.5. C represents the ratio of peak velocity to mean velocity. The K - and C -values were used primarily to describe the shape of single movement segments. In the case of a trial composed of both a primary movement and one or more overlapping submovements, the peak velocity of the *primary* movement was used. However, on some trials we examined K - and C -values for the whole movement, in order to compare the results with previous studies. The beginning and end of the movement were defined as the time when velocity crossed above or below 10% of the peak velocity of the movement.

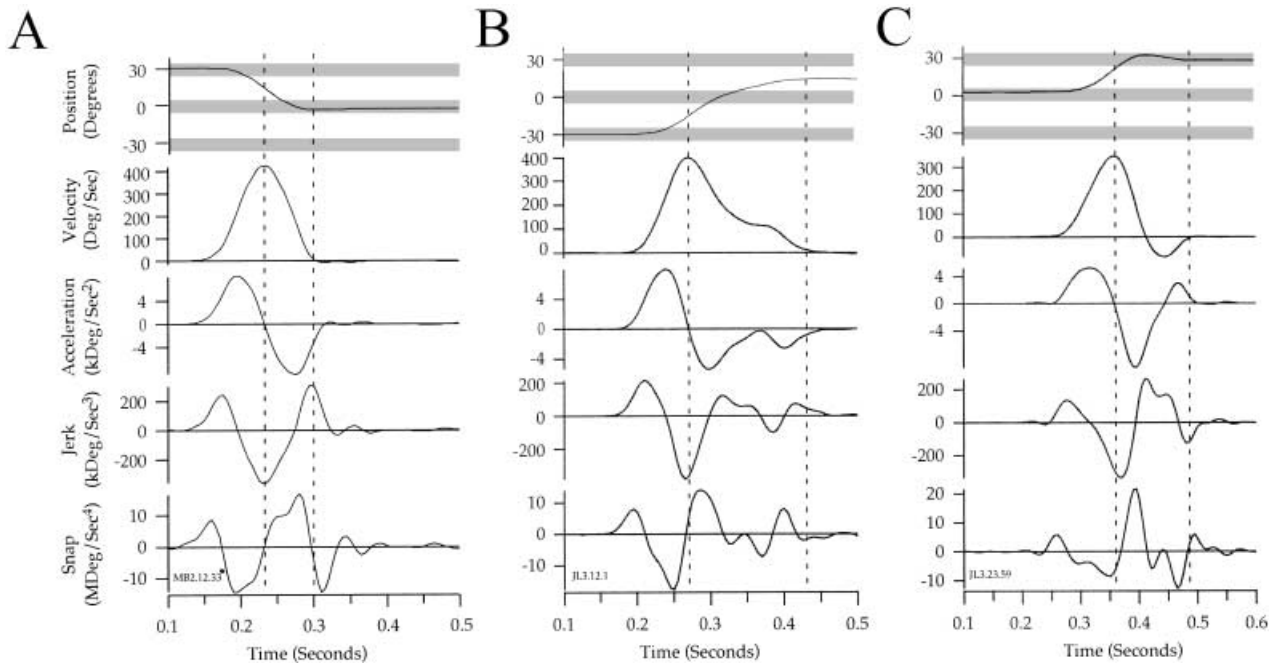


Fig. 1A–C Method for detecting overlapping submovements by examining the regularity of the second half of movements (*dashed lines*). The angular position of the knob pointer is shown on the *top row*, and its time derivatives *below it*. The *gray-shaded areas* represent the location of the three targets. **A** A single primary movement from top to middle target. It had just one jerk zero crossing and one snap zero crossing during this period, indicating a smooth and regular movement. **B** Movement from bottom to top target, composed of a primary movement followed by an overlapping submovement (second velocity peak). The movement had two jerk zero crossings and two snap zero crossings, indicating its irregularity and the presence of the overlapping submovement. **C** A movement from middle to top target. It had an overlapping submovement in the direction opposite the primary movement, again causing more than one jerk and snap zero crossing (M mass, k spring)

Neuromusculoskeletal model

In order to understand how discrete, central motor commands may overlap and alter the kinematics of movement, we used the same nonlinear mass-spring model of the neuromusculoskeletal system as in our previous publication (Novak et al. 2000). Briefly, the hand was modeled as a mass (M) and spring (k) with a variable equilibrium position (x_{eq}) and nonlinear viscous damping (b):

$$M\ddot{x} + \text{sign}(\dot{x})b|\dot{x}|^{1/5} + k(x - x_{eq}) = 0 \quad (1)$$

We used the same parameters of $M=1$, $b=3$, and $k=30$ as before, but modified the damping term to be bidirectional, taking the absolute value of velocity before taking the 5th root and making the damping force consistently in the direction opposite movement. In our previous use of the model, the damping term was unidirectional, intended only for positive velocities. Because here we wanted to simulate situations with negative velocities, we needed to add this slight modification (Karniel and Inbar 1999).

The mass-spring model of Eq. 1 incorporates the lambda-type equilibrium point control theory of Feldman (1986), in which force is generated by setting the slack length of the spring (the equilibrium position, x_e , or the threshold of the spinal stretch reflex, λ). The input to the system is the equilibrium position and the output, the motion. The input was set first to a high level to generate the initial acceleration, and then a lower, maintained level, which was required to maintain the final endpoint position.

The combination provided a simple pulse-step movement command, a control strategy that has been observed in an experimental study of force production in the cat (Ghez and Vicario 1978). While setting the slack length of the spring generated the initial acceleration, there was no explicit command for decelerating the mass. Instead, the model relied on the nonlinear viscous damping produced by the stretch reflex (Gielen et al. 1984).

Results

The rapid hand movements of this study were composed of a primary movement and, often, one or more corrective submovements with which it overlapped. In a previous study (Novak et al. 2000), we developed a direct, objective means to detect overlapping submovements. Since we assumed that each submovement was caused by a discrete force pulse and had an associated acceleration pulse, we searched for overlapping submovements by looking for inflections in the acceleration traces of the movements. Using this method, illustrated in Fig. 1, overlapping submovements were detected in approximately two-thirds of all trials.

Separation of overlapping submovements

If a trial contained an overlapping submovement, it was separated from the primary movement by subtracting out the primary movement from the overall movement. Because the underlying primary movement was obscured by the overlapping submovement, its shape was estimated based on our previous analysis of the shapes of pure primary movements (Novak et al. 2000). Since the pure primary movements were typically symmetric, we subtracted a symmetric estimate of the primary movement. An analysis of the possible errors of this estimate is presented later. For each trial, a primary movement velocity

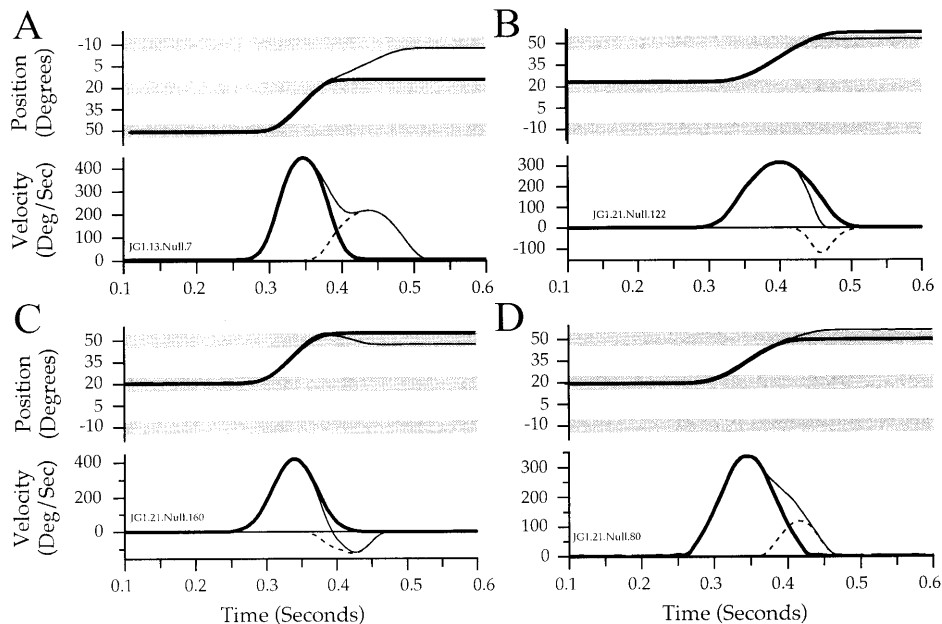


Fig. 2A–D After overlapping submovements (*dashed lines*) were detected, they were parsed from the whole movements (*thin lines*) by subtracting an extrapolated, symmetric representation of the primary movements (*thick lines*). **A** A trial starting at the bottom target and moving to the top one. It had two clear velocity peaks, both in the same direction. The overlapping submovement corrected the initially inaccurate primary movement before it ended. **B** Movement from middle to top target. The subject made an overlapping submovement in the direction opposite the primary movement, again correcting the primary movement, which was too large. **C** Movement from middle to top target. This trial gives an example of a corrective submovement in the opposite direction as the primary movement. The submovement caused the overall velocity profile to reverse direction. **D** Trial from the middle to top target. The movement contains a smaller overlapping submovement that did not create a clear second peak in the velocity profile. This submovement was unusual in that it moved the pointer out of the target – not an appropriate choice

profile was created by flipping the acceleration phase about the time of peak velocity to approximate the deceleration phase. Figure 2 shows a few examples of how overlapping submovements are extracted. Three trials are shown in Fig. 2A–C, with the angular position traces on the top axis and the reconstructed velocity traces of each submovement on the bottom.

The trial of Fig. 2A had two clear peaks in the velocity profile, one for the primary movement and one for the overlapping submovement. After subtracting the estimated velocity profile of the primary movement from the overall movement, the estimated overlapping submovement remains. This overlapping submovement was made in the same direction as the primary movement, termed the positive direction. The submovement turned an initially short primary movement into a successful, accurate movement, reducing the endpoint error from an estimated -26° (thick position trace) to a final error of only -3° .

The trial in Fig. 2B contained an overlapping submovement in the direction opposite to the primary movement, the negative direction. Subtracting the expected

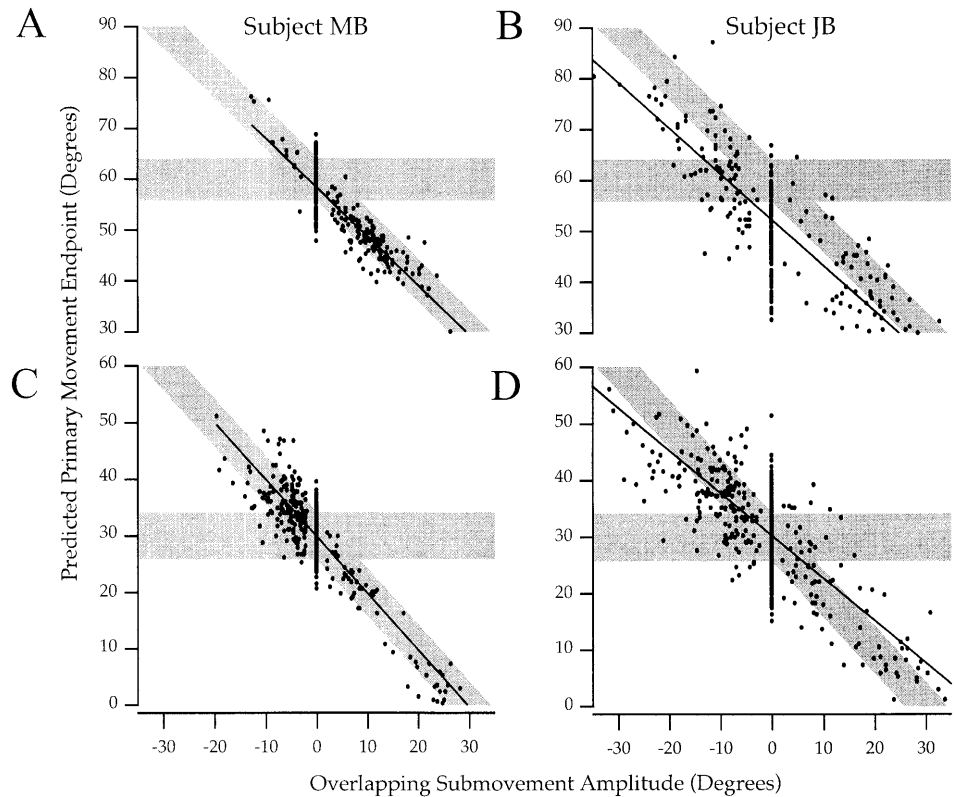
primary movement velocity profile from the overall movement, the negative overlapping submovement is seen. Like the trial in Fig. 2A, this submovement also was corrective, turning what would have been a 7° overshoot into an accurate trial, with only a 2° overshoot.

Figure 2C shows another negative overlapping submovement, which actually caused a reversal in direction and negative velocity. This corrective submovement was barely necessary, since the uncorrected primary movement would have ended 4.6° past the center of the target, outside of the target by 0.6° . Finally, the trial in Fig. 2D shows the rare case of an overlapping submovement that was inappropriate, turning an initially accurate primary movement (-0.4° endpoint error) into an unsuccessful trial, with an endpoint error of 5.6° . Although there were exceptional trials like this one, most of the overlapping submovements were corrective in nature, improving the endpoint accuracy of the primary movements.

Overlapping submovement properties

Figure 3 examines the accuracy of the overlapping submovements for two subjects. The predicted primary movement endpoint is plotted against the amplitude of the overlapping submovement for each trial. Results for subject M.B. are shown on the left and for subject J.B., on the right in Fig. 3. The 60° trials are separated from the 30° trials below them. If the knob pointer was supposed to reach the target 30° away but would have achieved only 20° with the primary movement, an overlapping submovement of 10° was required to land the pointer perfectly on the target center. The diagonal-shaded region shows the range of amplitudes of the overlapping submovements that would reach the target. A large majority of the overlapping submovements fell within this region and thus accurately corrected for errors in the amplitude of the primary movements. Subject M.B. was

Fig. 3A–D Accuracy of overlapping submovements for two subjects. The predicted endpoint of the primary movement is plotted against the amplitude of the overlapping submovement for each trial. The 60° trials are on the top (A, B) and the 30° trials on the bottom (C, D). The diagonal gray-shaded region represents trials in which the pointer landed in the target after the submovement, while the horizontal gray region represents movements which would have landed in the target after the primary movement. The lines represent the best line fit through the data and show how the overlapping submovements tended to correct the inaccuracy of the primary movements, landing the pointer inside the target



better than subject J.B. (75% of submovements were accurate versus only 40%) at making overlapping submovements that resulted in accurate final endpoints. Across subjects, 55% of all overlapping submovements were accurate, including 60% of the 30° trial submovements and 44% of the 60° ones.

Subject M.B. had a tendency on the 60° trials (Fig. 3A) to undershoot the target with the primary movement and make an overlapping corrective submovement in the same direction. Conversely, on the 30° trials (4°C), there was a tendency to overshoot the target with the primary movement, followed by an overlapping submovement in the opposite direction. Other subjects showed similar tendencies. When an overlapping submovement was present, the mean predicted 30° trial primary movement endpoint error was a 2.7° overshoot, while that of the 60° trials was an 8.2° undershoot.

The amplitudes of the corrective submovements were inversely related to the predicted primary movement endpoint errors for all subjects. In a system which perfectly corrects for errors in the primary movements, a line fit through the points in Fig. 3 would have a slope of -1.0 and an r of -1.0 . In fact, the line fit through the 30° trials for subject M.B. (Fig. 3A) had a slope of -1.0 and an r of -0.9 , while the 60° trial fit (4°C) had a slope of -0.97 with an r of -0.94 . Thus, the amplitude of the corrections was finely tuned for final endpoint accuracy. The data from the other subjects also indicated a strong inverse relation between the amplitude of the corrective submovement and the predicted primary movement endpoint errors. The mean slope was -0.86 for the 30° trials

and -0.79 for the 60° trials. Subjects tuned the amplitude of the overlapping submovements in order to correct for errors in the primary movement end positions. However, some subjects were more accurate with their corrections than others. Subject J.B., for instance, made less accurate corrections than subject M.B.. The slope of the fit for the 30° trials of subject J.B. (Fig. 3B) was only -0.75 , with an r of -0.87 . This decreased slope indicates that this subject often made corrections that were too big, or made submovements in the wrong direction, increasing the primary movement endpoint error instead of correcting it.

On a fairly high percentage of trials, subjects did not make an overlapping submovement even though the primary movement was inaccurate. These trials are represented in Fig. 3 by a submovement amplitude of zero, but with the primary movement out of the target zone. Subject M.B. failed to make an overlapping correction on 15% of all trials, compared with 32% for subject J.B. and a six-subject mean of 28%. Although subjects did not always make a correction before the primary movement ended, they often made discrete corrective submovements afterward, as described previously (Novak et al. 2000). In addition to omitting overlapping corrections when they were needed, on 4% of trials, subjects made corrections that moved the pointer out of the target region.

The data from Fig. 3, as well as that from other subjects not included in the figure, show that the overlapping submovements corrected for errors in the primary movement. Since the mean (predicted) primary move-

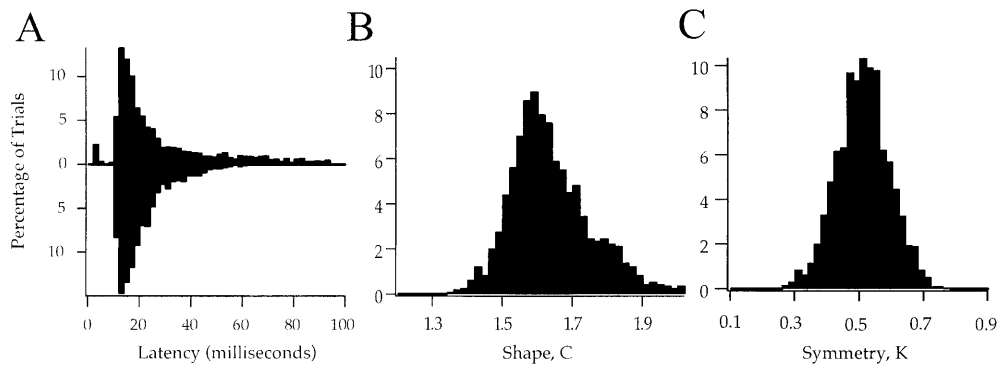


Fig. 4A–C Properties of overlapping submovements, combined from all six subjects. **A** Histogram of latencies of overlapping submovement onset measured from the primary movement peak velocity. Overlapping submovements in the same direction as the primary movement are on *top*, and those in the opposite direction are on the *bottom*. **B** Shape of overlapping submovements determined to be single overlapping submovement via the jerk and snap zero-crossing method. The shape C is the ratio of peak velocity to mean velocity. **C** Symmetry of pure overlapping submovements. K equals the relative time to peak velocity

ment endpoint error for trials with overlapping submovements was a 4.1° undershoot, the mean amplitude of the overlapping submovements averaged positive 3.9° – i.e., in the same direction as the primary movement. The corrective submovement thus improved the constant error of the primary movements from a 4.1° undershoot to a 0.2° undershoot. Trials without overlapping corrections had primary movements that were more accurate, with a 1.3° mean undershoot and a standard deviation (SD) of 6.3. Subjects made overlapping corrections predominantly in the situation where the primary movement would have been inaccurate, and not when the primary movement was accurate.

The corrective submovements were initiated over a range of times following the peak velocity of the primary movement, as indicated in the histogram of all subjects' latencies in Fig. 4A. Latencies were calculated by subtracting the time of peak velocity from the time of overlapping submovement onset (when the overall movement first deviated from the symmetric by more than $10^\circ/\text{s}$). Overlapping submovements in the same direction as the primary movement are shown above the zero axis, and submovements in the opposite direction below it. The overlapping submovements began within 100 ms after the peak velocity of the primary movement, with the majority in the 10- to 40-ms range. Since the mean time to peak velocity was approximately 70 ms, most submovements were generated 80–120 ms after the primary movement onset. The small number of submovements occurring just 5 ms after the primary movement represented trials in which the primary movement was smaller than the overlapping submovement.

The trials shown in Fig. 2 were composed of a primary movement and a single overlapping submovement, but this was not always the case. On approximately 58% of trials with overlapping submovements, the velocity re-

maining after subtracting the primary movement was not smooth and regular, and was determined to contain more than one overlapping submovement. The properties of the overlapping submovements in these multisubmovement trials were not included in the analysis. The symmetry is defined as the relative time to peak of the velocity profile, while the shape is the ratio of peak velocity to mean velocity (see Materials and methods). Figure 4B shows that the range of overlapping submovement velocity profile shapes had an approximately normal distribution, with a mean of 1.64 and a SD of 0.16. The symmetry of the overlapping submovements in Fig. 4C had a mean of 0.51 and a SD of 0.08. These measures were similar to those reported previously for primary movements ($K=0.53\pm 0.05$; $C=1.58\pm 0.06$) and for delayed submovements ($K=0.52\pm 0.07$; $C=1.57\pm 0.16$; Novak et al. 2000). However, the mean values were statistically different ($P<0.001$). The shape (C) of the overlapping submovements was increased, indicating a more vertically elongated velocity. The symmetry value was decreased slightly, indicating that the peak velocity of the overlapping submovements occurred earlier. There was also more variability in the shape and symmetry of the overlapping submovements.

The overlapping submovements altered the symmetries and shapes of the overall movements quite appreciably. Figure 5 examines the effect of overlapping submovements on the symmetry of the overall velocity. The acceleration period was defined as the time from movement onset (when velocity increased more than 10% of peak velocity) to the primary movement peak velocity, and the deceleration period from primary movement peak velocity to the end of movement (velocity less than 10% of peak). Figure 5A, B shows, for 30° and 60° trials, the symmetry of the pure primary movements compared with the overall movements as a function of primary movement peak velocity. The pure primary movements have a small range of symmetry values that are clustered around 0.52 and are independent of speed. However, the overall movements, which include overlapping submovements, have symmetry values that vary considerably with the speed of movement. For instance, a relatively slow movement like the one in Fig. 2A required a corrective submovement which prolonged the deceleration period and shifted the relative time to peak velocity (K) below 0.5. A relatively fast movement that

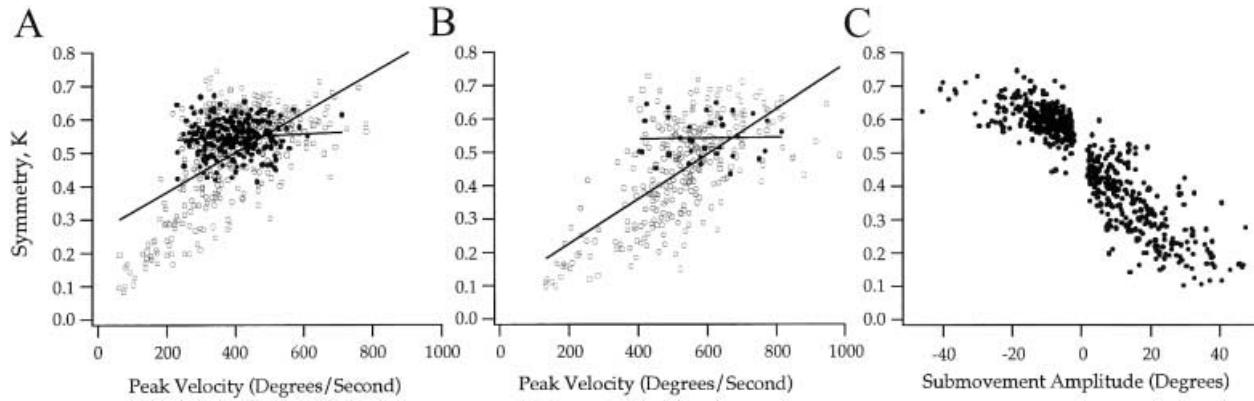


Fig. 5A–C Symmetry of whole movement was affected by presence of overlapping submovements. **A** 30° and **B** 60° trials for subject J.B. Trials without submovements (*filled circles*) had symmetry values (mean $K=0.52$) that were independent of speed, while trials with overlapping submovements (*empty circles*)

showed the previously reported dependence of symmetry on speed of movement. Slower movements had lower K -values, and faster movements had higher K -values. **C** Dependence of symmetry on size of overlapping submovement

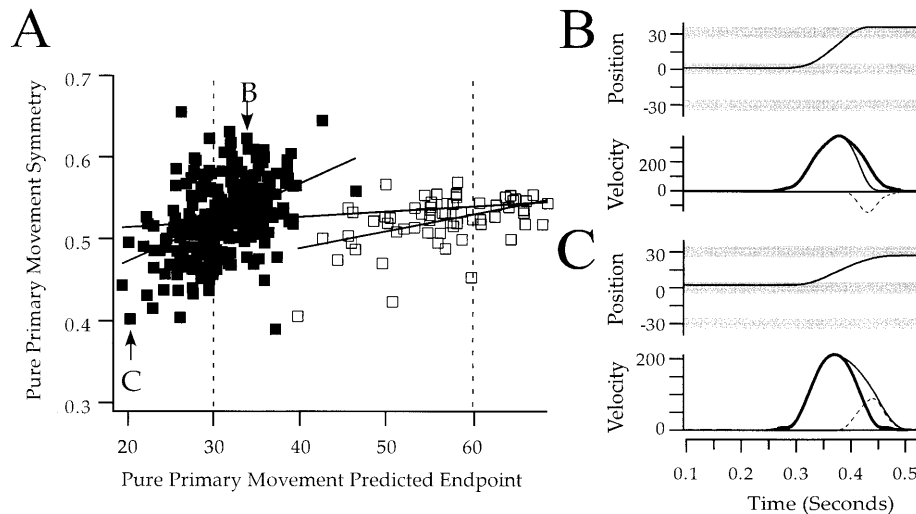


Fig. 6A–C Examination of whether movements are adjusted continuously or with discrete submovements. **A** Symmetry of pure primary movements as a function of predicted endpoint, estimated as twice the distance from movement start to primary movement peak velocity. *Filled squares*, 30° trials; *empty squares*, 60° trials. Symmetry changed as a function of predicted endpoint within each group of targets, as shown by the slope of the *solid lines* fit to the data. Movements predicted to be short of the target, like trial **C**, had low symmetry values, while those predicted to overshoot the target had high symmetry values, like example **B**. **B**, **C** Kinematics of trials labeled **B** and **C** in **A**. Although no submovements were detected with the irregularity criteria examining higher-order derivative zero crossings, these trials could be well explained by a primary movement (*bold line*) and overlapping submovement (*dashed line*)

would have overshoot the target, as in Fig. 2B, was often accompanied by a correction in the opposite direction which effectively ended the movement sooner and increased the relative time to peak above 0.5. Figure 5C shows that the time symmetry of the overall movement was inversely related to the size and direction of the overlapping submovements. Movements with high

K -values were composed of large submovements in the opposite direction, while movements with low K -values tended to have submovements in the same direction as the primary movement. The linear relationship between movement asymmetry and the size of the overlapping submovements was strong ($r=-0.89$).

It is clear from Fig. 3 that the overlapping submovements accurately corrected for errors in the primary movement. Subjects apparently used feedback or efference copy information about errors or anticipated errors in order to generate discrete corrections. However, subjects might also have been continuously monitoring and modifying a single primary movement. To explore this possibility, we examined the time symmetry of pure primary movements, those determined not to contain an overlapping submovement using the jerk and snap zero-crossing method described in Fig. 1, as a function of the predicted endpoint, estimated as twice the distance covered during the first half of movement. Figure 6A shows that the primary movement velocity symmetry was dependent on the predicted endpoints. For all 342 pure primary movements for subject J.B., a line fit through the

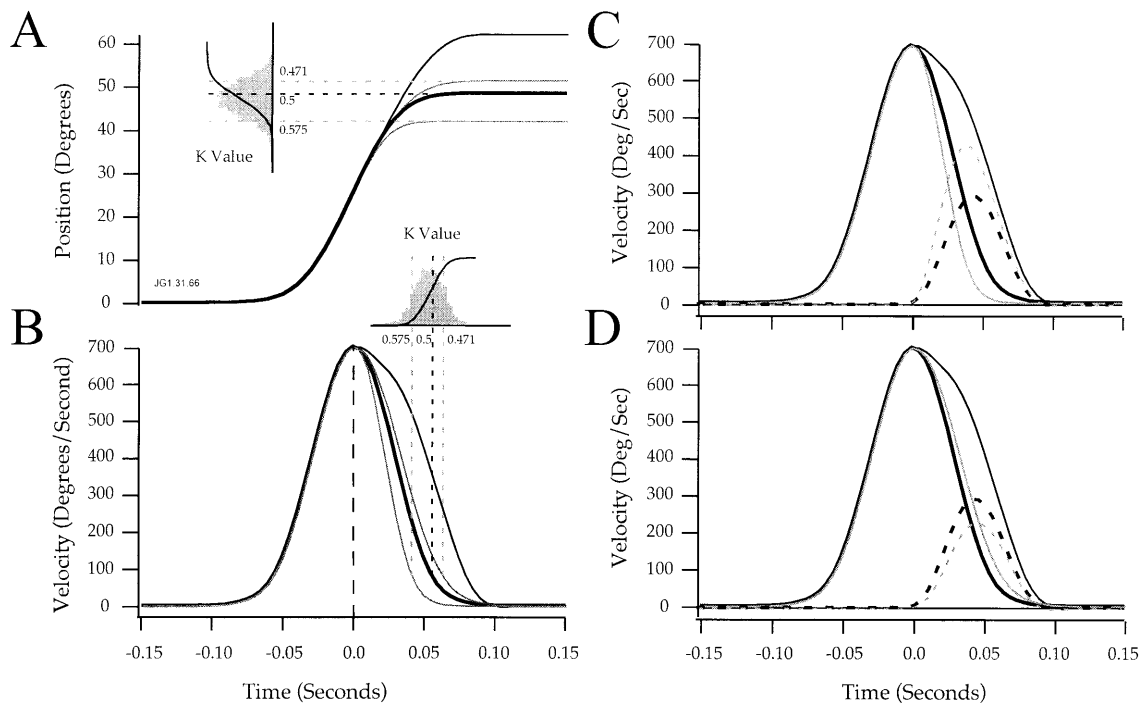


Fig. 7A–D Effects of time-symmetry assumption on the overlapping submovement analysis. Estimation of the shape of the primary movement position (**A**) and velocity (**B**) by flipping the acceleration phase about the time of peak (*dashed vertical line* at time zero), giving a symmetric representation (*thick line*). Slightly asymmetric primary movements are shown as *thin gray lines* to either side of the symmetric in the velocity profile (**B**), or *above* and *below* the position traces (**A**), while the overall movement is drawn with *thin black lines*. Histograms show the distribution of *K*-values from pure primary movements, from which the two asymmetric primary movements were chosen. **C–D** Separation of the overlapping submovements, using the same conventions as in Fig. 2. **C** Using a slightly asymmetric primary movement ($K=0.575$; *gray trace*) resulted in a slightly different shape for the overlapping submovement (*dashed gray trace*) compared with that obtained (*thick black dashed line*) by subtracting a symmetric primary movement. **D** Using a slightly asymmetric ($K=0.471$) primary movement velocity profile (*thin gray trace*) gave the overlapping submovement shape shown with the *thin gray dashed line*

data shows that the relationship was significant ($r=0.16$, $P<0.004$), but the effect of predicted error on symmetry was small (low slope). When analyzing the relationship between symmetry and predicted error for just the 30° trials, or 60° trials alone, the correlation was stronger ($r=0.43$, $P<0.001$ for 30° trials, $r=0.46$, $P<0.001$ for 60° trials) and the size of the effect was greater. For the 30° amplitude trials, when the primary movement would have ended short of the target (trial labeled C), the relative time spent during deceleration was extended, such that *K* decreased. On the other hand, when the primary movement would have ended past the target (trial labeled B), the relative time spent decelerating decreased, and *K* increased.

Examples of each of these scenarios are shown in Fig. 6B for a predicted overshoot and rapid deceleration, and in Fig. 6C for a predicted undershoot and prolonged

deceleration. Although the jerk and snap zero-crossing algorithm did not detect any overlapping submovements, these figures show that the observed velocity profiles *could* be explained by an overlapping submovement summing with a symmetric primary movement. If an overlapping submovement was truly present in each of these trials, they were difficult to detect because they were small and smoothly blended into the primary movement, without creating inflections in the velocity trace that could be detected with the jerk and snap zero-crossing algorithm.

Variability analysis

Much of the analysis of overlapping submovements relies on the assumption that pure primary movements have time-symmetric velocity profiles. Although the average pure primary movement was highly symmetric (Novak et al. 2000), with a relative time-to-peak velocity (*K*-value) equal to 0.52, the histograms inset in Fig. 7 shows the range of symmetry values of pure primary movements. The effects of this slight variation in symmetry on the velocity and position traces are shown in Fig. 7. In addition to the perfectly symmetric velocity profile, two more velocity profiles were created which had symmetry values near the extremes of the observed range. Only 15% of the pure primary movements had *K*-values of more than 0.575. This choice of symmetry resulted in the thin, gray trace to the left of the thick, symmetric trace (Fig. 7B). Likewise, the gray trace to the right of the symmetric trace had $K=0.471$, a value at the lower 15% of the distribution. Thus 70% of the movements had symmetry values within these two extreme cases.

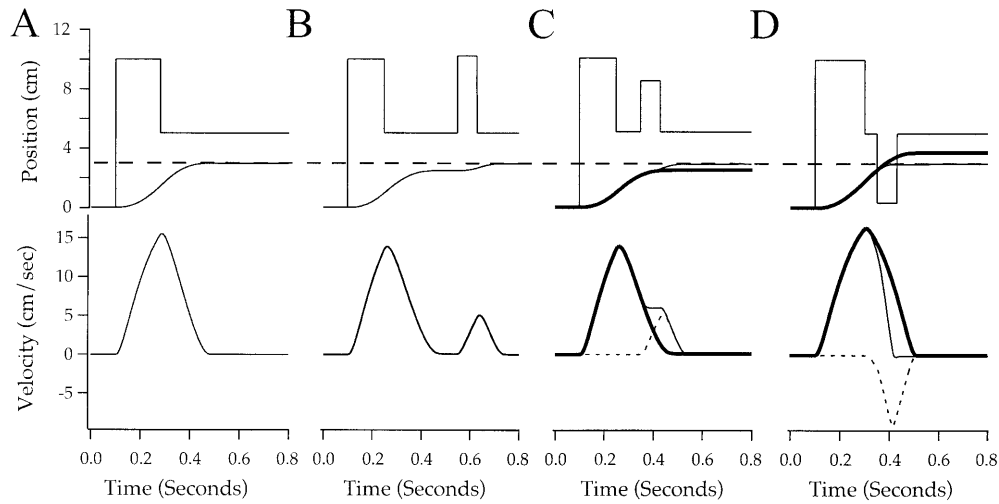


Fig. 8A–D Simulation with the nonlinear neuromusculoskeletal model. The pulse-step command (shown unfiltered) commanded the slack length of the spring, and the mass moved accordingly. The position (*top*) and velocity (*bottom*) of the mass are shown. **A** This movement had a time-symmetric velocity and reached the desired endpoint (*dashed horizontal line*). **B** Shortening the pulse duration caused the primary movement to fall short of the target. A delayed submovement was commanded with a second pulse 300 ms after the first ended to accurately correct the error. **C** After the same error following the primary movement as in **B**, a second pulse was generated sooner, resulting in an overlapping corrective submovement (*dashed line in the velocity trace*). **D** An overlapping corrective submovement (*dashed line in the velocity trace*) in the direction opposite the primary movement (*bold lines*) corrected for the predicted target overshoot

Next, these two asymmetric versions of the primary movement were each used to extract the overlapping submovement (Fig. 7C and D). The higher K -value primary movement (thin gray trace of Fig. 7C) resulted in a somewhat different submovement shape (thin, gray dashed trace, $K=0.40$, $C=1.67$) than when a symmetric primary movement was used (thick dashed trace, $K=0.51$, $C=1.65$). However, by using the lower K -value primary movement (Fig. 7D), the overlapping submovement shape was almost identical ($K=0.51$, $C=1.64$) to that obtained from the symmetric primary movement. Hence, only one of these two extreme examples had an appreciable effect on the shape of the overlapping submovement. In most cases, the effect will be even smaller. As such, errors in the estimation of submovement shape resulting from assuming a symmetric primary movement are likely to be rather small.

Figure 7A examines the movement amplitude estimation errors resulting from the same assumption. While the symmetric primary movement was estimated to have an amplitude of 48.5° , if it was not perfectly symmetric its amplitude could have varied from 42.2° ($K=0.575$) to 51.6° ($K=0.471$). When a primary movement is obscured by an overlapping submovement, it is impossible to say with certainty how large it would have been in the absence of the submovement. However, estimates of amplitude for the low and high K -values range across 9.4° , or

approximately 20% of the amplitude of the movement. Although the small variability in observed symmetry introduces some error in the primary movement amplitude estimates, we chose the most likely amplitude, namely that resulting from a symmetric primary movement.

Model of discrete, overlapping submovements

The effect of discrete, centrally generated, corrective submovements on movement kinematics was investigated with a nonlinear model of the motor plant. The model utilizes pulse-step commands to control the equilibrium point, or slack length, of a spring attached to a mass with nonlinear viscous damping attributed to the stretch reflex (Gielen et al. 1984). Figure 8A shows the results of the model using a single, pulse-step movement command. The command was filtered in the model but is shown unfiltered here for purposes of clarity. As a result of the command, the mass moved near to the final equilibrium position, sticking at the final end-point. One feature of this system is that, because of the fractional power damping, the mass decelerates to a position well short of the final step command and continues to drift only very slowly. For simplicity, we assume the mass has stopped moving at this point. The velocity of the movement, on the bottom of the figure, was time-symmetric ($K=0.5$) and approximately bell-shaped.

In Fig. 8B, the switch point from the pulse to the step portion of the command occurred 30 ms sooner than in Fig. 8A, so the primary movement fell short of the desired endpoint. Consequently, a delayed, corrective submovement was generated with a second command pulse 300 ms after the primary movement command in order to bring the mass to the desired final endpoint. Alternatively, Fig. 8C shows a second command pulse generated just 100 ms after the primary command pulse ended, causing an overlapping submovement in the same direction as the primary movement. The overlapping submovement summed with the primary movement to produce the overall movement velocity. The combination brought the mass to the desired endpoint, similar to the

real movements in Fig. 2A. The overlapping submovement in the model caused the velocity profile to become irregular, with three snap and jerk zero crossings (not shown), and skewed the symmetry of the velocity profile. Such rapid corrections might need to rely on a prediction of the anticipated endpoint error based on efference copy information.

The final simulation in Fig. 8D shows the effect of an overlapping submovement in the direction opposite the primary movement, similar to the actual movement in Fig. 2B. In this model trial, the pulse duration was too long by 20 ms, and the primary movement would have gone considerably past the desired target. A second, discrete command pulse in the opposite direction corrected this predicted overshoot. As with the previous model trial, the overlapping submovement caused an irregularity in the velocity profile that was detected by more than 1 snap zero crossing during the second half of the movement (not shown). The corrective submovement also skewed the symmetry of the whole movement velocity profile, $K > 0.5$.

This simple model of discrete, centrally generated overlapping submovements captures many features of the actual data. Although the nonlinear viscosity requires that a smaller command be used when the primary movement has not yet ended (second pulse of Fig. 8C) compared to a command generated when the primary movement has ended (second pulse of Fig. 8B), the resulting velocity profile from the overlapping submovements sums linearly with the primary movement velocity profile in both cases. The overlapping submovements cause irregularities in the kinematics that alter the shape and symmetry of the velocity profile, which can be detected by jerk and snap zero crossings. These submovements generally correct for errors in the amplitude of the primary movement. They also cause the normally symmetric pure movements to become asymmetric, an effect which depends on the speed of the primary movement and predicted error. We conclude that the CNS appears to monitor and predict the outcome of the primary movement, often generating early, pulse-like commands to correct for errors in a noisy initial command.

Discussion

In the absence of visual feedback, subjects attempting to align the position of a knob pointer with a target frequently made small corrective submovements. When these submovements were generated before the primary movement ended, they caused irregularities in the kinematics of the overall movement. The overlapping submovements were often apparent as second peaks in the velocity profile, or as a rapid deceleration and reversal of direction of the knob pointer. We detected the movement irregularities caused by overlapping submovements by analyzing the higher order derivatives of movement, jerk and snap, as described previously (Novak et al. 2000) and shown in Fig. 1. After identifying the overlapping

submovements, we used a technique similar to previous studies (Flash and Henis 1990; Milner 1992; Berthier 1996; Lee et al. 1997; Krebs et al. 1999) to separate them from the primary movements. Simply subtracting the estimated primary movement from the overall movement in the velocity space left a good estimate of the underlying submovement. In order to gain insight into the neural mechanisms responsible for producing corrective submovements, we analyzed the kinematic properties of the overlapping submovements and compared them with the properties of the primary movements and nonoverlapping, delayed submovements reported previously (Novak et al. 2000).

Shape of “pure” movements

Although there exists some variability in amplitude and speed for repeated attempts to make the same movement, the primary movements produced by the subjects on average had bell-shaped and near time symmetric angular velocity profiles (Novak et al. 2000), as has commonly been observed in other movement studies (Abend et al. 1982; Flash and Hogan 1985; Gordon et al. 1994a). The particular shape of the velocity profile of single, targeted movements has been widely studied. When several investigators (Soechting 1984; Atkeson and Hollerbach 1985; Gordon et al. 1994b) manually varied the amplitude and duration of velocity profiles of primary movements to achieve the same scale, the shapes of the traces were very similar. We quantified the degree of this invariance in the shape of the velocity profile over varying speeds, amplitudes, and durations with the parameters C and K , describing the ratio of peak velocity to mean velocity and the relative time symmetry, respectively. All three types of movement segments that subjects made in our task (single primary movements, delayed submovements, and overlapping submovements) had similar shapes, despite a tenfold range of speeds. While our study did not determine whether different joint motions produced the different movement segments, the basic similarity of the shapes suggests that essentially the same neural control mechanisms are involved in their production. Future examination of the central motor control signals commanding each type of segment should determine whether this hypothesis is true.

Previous studies examining the shape of individual movement segments all found the same kinematic profile, despite different methods. Krebs et al. (1999) have examined the arm movements of stroke patients, reasoning that the ability to coordinate movement segments is lost after brain injury and the segmented movements that result are composed of isolated submovements. They found the elemental submovement to be bell-shaped (similar to the Gaussian density function and the minimum-jerk trajectory; Flash and Hogan 1985) and near symmetric, with $K=0.52$ as reported here. Milner (1992) has assumed that movements with the lowest accuracy constraints have no corrective submovements, and deter-

mined that the shape of the elemental movement is near-symmetric and bell-shaped, and varies slightly from subject to subject. Finally, Flash and Henis (1990) have looked at how individual arm movements overlap during double-step target presentations. During some movements between two targets, a third target was given, and subjects simply added a second movement to the original. After subtracting the primary movement, the remaining submovement also had a minimum jerk velocity profile. All these results are compatible with the hypothesis that movements are composed of a series of approximately minimum-jerk overlapping submovements.

Most of the other studies of overlapping submovements have not included a direct test of the shape of the overlapping submovements, but make assumptions regarding the shape of the basic movement segment or "primitive." Morasso and Mussa-Ivaldi (1982) have used mathematically formulated "strokes," Milner (1992) and Krebs et al. (1998) have used empirically determined templates of each subject's simplest movements, and others (Berthier 1996; Lee et al. 1997) have assumed the minimum-jerk trajectory. Our method uses our finding that, in the absence of overlapping submovements, the mean primary movement was symmetric. We made no further assumption about the shape of the primary movement beyond its demonstrated symmetry, and we did not fit a predefined shape to the data. The resulting evidence that the single primary movements and single submovements have a relatively invariant shape is strong.

However, we showed that the symmetry of *whole movements* composed of a primary movement and an overlapping submovement varied systematically with speed (Fig. 5), as has been reported previously (Moore and Marteniuk 1986; Nagasaki 1989; Wiegner and Wierzbicka 1992). Our experimental and simulation data indicate that the main reason for the speed dependence of overall movement symmetry is the presence of overlapping submovements, which act either to hasten or prolong the deceleration phase of the movement. Overlapping submovements are probably responsible for most of the movement asymmetries previously reported.

While the majority of the movement asymmetry can be explained by overlapping submovements, sometimes it was difficult to distinguish between when subjects made discrete overlapping submovements and when they made continuous adjustments (see Fig. 6). This study emphasized the occurrence of a discrete corrective process, yet we showed that a continuous process might also have been used. Thus, the brain may use continuous monitoring and modification of the primary movement in addition to discrete corrective commands.

Two prior studies have also addressed the issue of whether subjects produce compensatory adjustments to deal with errors in the first part of a movement. Gordon and Ghez (1987) have examined elbow force pulse production, and Messier and Kalaska (1999) have examined horizontal arm-pointing movements. Both have examined how the initial variability in movements relate to the final endpoints or force levels. Each has used the

same multivariate analysis to suggest that subjects continuously adjust the duration of their movements or force pulses to compensate for the initial errors and achieve the desired target endpoint or force level. We applied the same multivariate statistical and graphical analysis of Gordon and Ghez on our movement data (data not shown in Results section), and got the same general result as Messier and Kalaska. Adding target amplitude to the regression equation of movement amplitude as a function of peak velocity significantly increased the variance accounted for. The same result has been interpreted by previous authors to mean that subjects adjust movements to compensate for initial errors in peak velocity or force scaling. Another interpretation for these and other results is that subjects plan for both the peak velocity (force rate) and duration of movement (force pulse production) together in order to reach a desired target location, as suggested by Hoffman and Strick (1986). Thus it is difficult to ascertain whether or not what appear to be continuous, compensatory adjustments to movements are planned that way in advance or are true corrections.

One potential ambiguity in our analysis of discrete movement segments concerns their muscle effector origins. Because of the mechanical complexity of the hand movements, it was difficult to say which muscles and joint motions caused the movement. While we interpreted the discrete submovements to be the result of a single set of effectors, another explanation also is possible. Subjects may have been using multiple effectors, each with staggered timing. For instance, the subject may have made the primary movement by pronating the forearm and the smaller submovements by rotating the thumb. Because we did not measure the motion of each joint in this movement, the parallel effector control scheme cannot be ruled out. However, since movements often were composed of a single segment, the CNS clearly is capable of synchronizing parallel effectors, if they are indeed used. It is unclear in this scheme why some movements would thus be made synchronously, and others asynchronously. Abend et al. (1982) have described how subjects varied the timing of movements about the elbow and shoulder joints in order to generate a single, smooth movement of the hand. Their finding suggests that subjects do utilize parallel effectors with staggered timing, but do so in a way that generates a single, smooth movement of the hand in space. It is likely that the subjects are using the same control scheme for the movements studied here and that any deviation in the single, smooth movement is due to a discrete correction.

Summation of submovements

Given that movements are composed of simpler, elemental segments that may overlap in time, it is critical to understand how the submovements sum together and why this strategy of overlapping submovements may be used by the CNS. It has been suggested by many (Morasso

and Mussa Ivaldi 1982; Milner 1992; Berthier 1997; Krebs et al. 1999) that the elemental submovements may be building blocks for more complex motor behaviors. Submovements may also be used as an iterative corrective process (Meyer et al. 1982; Crossman and Goodeve 1983; Meyer et al. 1988), in which the CNS constantly monitors the state of the limb and, knowing the desired endpoint, generates the necessary, discrete corrective submovements to reach the final endpoint rapidly and accurately. Here, we show that subjects produce overlapping submovements to correct for predicted errors in the primary movement.

All of the previous related studies have assumed that each elemental submovement superimposes linearly but have not directly tested the assumption. The majority of studies have just tweaked submovement kinematic parameters objectively with an algorithm (Morasso and Mussa Ivaldi 1982; Flash and Henis 1990; Berthier 1996; Lee et al. 1997) or subjectively by eye (Milner and Ijaz 1990; Milner 1992) until the error of the fit approaches zero. With such an approach, great care must be taken that the technique for separating overlapping submovements does not become reduced to an exercise in curve fitting. For instance, one could perform a Fourier analysis on the velocity waveform, fitting a sequence of different-frequency sinusoids to the velocity profile, but this would not prove that movements are composed of overlapping submovements with a sinusoid shape. Our study avoided the curve-fitting trouble by examining only the trials with a single overlapping submovement, as determined by the objective zero-crossing algorithm. We did fit the trials containing more than one overlapping submovement with a series of symmetric velocity profiles, but since this analysis did not give insight into the true shape of the overlapping submovements, these trials were excluded from the study.

Despite the possible pitfalls of the assumption of linear superposition of velocity profiles, evidence for its viability comes from the relative ease and accuracy with which this simple model can be fit to the kinematic data (Milner 1992). A stronger argument for the linear superposition of overlapping submovements has been made by Flash and Henis (1990), who looked at the superposition of two movements to two targets and found that the movements could be well fit by exactly two minimum-jerk velocity trajectories. In the present study, we realized that, while the shape of a single submovement was somewhat variable, the mean shape of single overlapping submovements (those with no remaining movement irregularities) was similar to that of both single primary movements and single delayed submovements. This supports the idea that movements are composed of a set of bell-shaped velocity profiles which superimpose linearly.

Although the overall movement can be well modeled as a linear summation of overlapping velocity profiles, our modeling results suggest that, because of the nonlinearities of the motor plant, the summation of motor commands is not linear. If the same command pulse given 300 ms after the primary movement (Fig. 8B) was given

200 ms sooner, before the primary movement ended, the mass would have gone far past the target. Thus, in order to achieve the desired endpoint, the CNS must take into account the position and speed of the limb. It then performs a nonlinear transformation to generate the appropriate command pulse to reach the target. While the kinematics of movement can be described as a linear summation of bell-shaped velocity profiles, the motor control system is nonlinear.

Beyond the nonlinear control problem, another consideration that the nervous system must take into account is the mechanical properties of the environment in which the limb moves. The knob-turning apparatus had relatively low friction and inertia ($0.013 \text{ N}\cdot\text{cm}/\text{s}^2$). The subjects were able to produce relatively smooth, single-peaked velocity profiles in this environment. In another experiment, we changed the viscosity of the apparatus with a torque motor attached to the shaft of the knob, and the subject had to adapt (Novak et al. 1996). Surprisingly, the adapted movements displayed essentially the same kinematics as before the mechanical load was added (unpublished observation). While the mechanical environment has an effect on the kinematics of movement, the CNS is able to adjust its commands adaptively in order to generate smooth, accurate movements.

In addition to the kinematic studies previously discussed, a recent study of isometric motor control also supports the notion of linear summation of motor primitives. Kargo and Giszter (2000) show how modules in the spinal cord of the frog generate force fields at the ankle that sum linearly. They have looked especially at "correction responses," spinal reflex-mediated responses to cutaneous feedback caused by obstacle collision. The feedback-based corrections sum linearly if it is assumed that the original movement force field continues unaltered. Previous work on the spinal frog with electrical stimulation of the spinal cord (Mussa-Ivaldi et al. 1994) has suggested that control may be simplified by activating a small number of spinal force field modules whose effects sum linearly. These studies, combined with previous studies of overlapping submovements in targeted human movements, strongly support the notion that complex movements are composed of more basic submovements that sum linearly.

Besides being building blocks for complex movements, submovements are perhaps more importantly involved in correcting errors and controlling the final accuracy of movements. Because of the variability inherent in the rapid primary movements in the dark, subjects frequently made one or more corrective submovements when it was likely that the primary movement would not have reached the target. These corrections were seldom made when not needed (only 5% were inappropriate), were almost always in the proper direction (95%), and generally were of the proper amplitude (60% of submovements finish in the horizontal gray zone of Fig. 3). These data suggest that the nervous system predictively monitors the anticipated effects of motor commands and then transmits discrete update commands to correct the errors.

Brain processes underlying corrective submovements

What central processes might be responsible for initiating and regulating these discrete, corrective submovements? It is possible that spinal dynamics may contribute to movement segmentation. However, our hypothesis is that the brain detects the need for and generates the commands required to produce the corrective submovements. Figure 9 provides a schematic summary of the functional anatomy subserving voluntary limb movement control. The two main brain regions that ultimately give rise to descending voluntary motor commands are the primary motor cortex and the magnocellular red nucleus (Houk et al. 1993). Specific channels through the basal ganglia and the cerebellum are available for the regulation of these commands (Hoover and Strick 1999). The channel through the basal ganglia is thought to be particularly important in the selection and initiation of an appropriate command (Houk 2001). Observations from patients with basal ganglia deficits support this notion. In Parkinson disease, when the inhibitory output of the basal ganglia is hyperactive, patients have trouble initiating movements (Flash et al. 1992). In contrast, in Huntington disease, when inhibitory basal ganglia output is decreased, subjects tend to produce many more unnecessary corrective submovements (Smith et al. 2000). While the basal ganglia may be important for regulating the initiation of the commands for primary movements and corrective submovements in motor cortex, the cerebellum is believed to regulate the dynamics of the commands (Houk 2001; Miller et al. 2002). Upon transmission to the spinal cord, interneuronal circuits regulated by the stretch reflex translate these commands into muscle activations and limb movements.

In 1899, Woodworth (1899) described rapid movement production with two phases: an “initial adjustment phase” and a “current control phase.” These dual phases correspond roughly to our rapid primary movement, and one or more small corrective submovements. The information available to the brain during the current control phase, for monitoring when corrections are necessary, consists of efference copy and then sensory afference. In our task, subjects produced submovements as soon as 80 ms after primary movement onset. Because of the 100-ms delay in the forward path, the movement must have been commanded 20 ms before the primary movement began and must have been based on efference copy. The afferent information from Golgi tendon organs and the initial burst discharge of muscle spindles would be the next available information. Subjects may use this initial phasic discharge to predict roughly whether the primary movement will be too big or too small, thus aiding in a quick decision on whether to initiate a corrective submovement before the primary movement has ended. This prediction may take place in the cerebellum as a forward model of the motor system (Miall et al. 1993), or as a direct, adaptive, predictive controller (Barto et al. 1999). Finally, position sense during and after the primary movement could determine whether the pointer is in

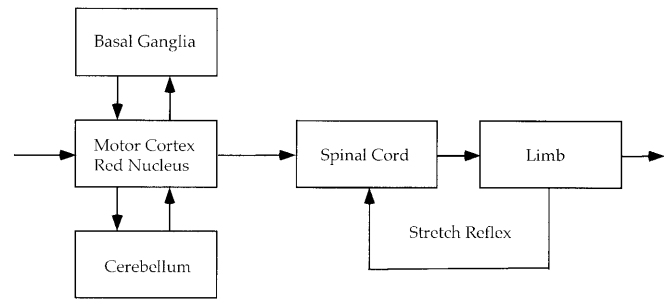


Fig. 9 Schematic representation of the functional anatomy for the control of voluntary movement. The main sources of descending motor commands are the motor cortex and red nucleus, which project to interneurons and motor neurons in the spinal cord, which in turn ultimately control muscle activity of the limb and the resulting movement. The spinal stretch reflex is important in the control of limb movements. The production of movement commands is regulated by recurrent loops with the basal ganglia and cerebellum

the target and whether an additional, delayed submovement is required to bring the pointer into the target window. Information becomes available at different times, so, it follows that submovements will be initiated at various times – as is shown by our data (Fig. 4A). Other studies that systematically varied the timing of final target information (Hening et al. 1988; Flash and Henis 1990) found similar results compatible with this hypothesis.

A limiting factor in the brain’s ability to produce rapid and accurate movements is the speed-dependent noise in the CNS, known as the “speed-accuracy trade-off” (Plamondon and Alimi 1997). Because of noise in the movement-production system, rapid movements are inherently variable. A recent “minimum variance theory” by Harris and Wolpert (1998) proposes that the CNS chooses commands so as to minimize the variability in movements. Although they provide no biological mechanism beyond trial-and-error learning, the authors briefly mention that the CNS may learn from “the consequences of the inaccuracy,” perhaps the occurrence of corrective submovements, as others have proposed (Berthier et al. 1993; Schweighofer et al. 1996; Fagg et al. 1998).

Several theories of learning thus suggest that the brain tries to make movements which are as fast and accurate as possible. However, limitations imposed by the speed-accuracy trade-off often require subsequent corrective submovements. In this study, we have shown how these corrective submovements may overlap the primary movement and thereby change the kinematics of the overall movement. We have modeled corrective submovement production with a nonlinear model of the motor plant and speculated on the plausible brain mechanisms behind their production. Further studies of the activity in brain areas involved in the production of movement are required to test the motor control hypotheses raised by Fig. 9 and to further elucidate how the brain controls accurate, rapid movements.

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