Exp Brain Res (1988) 73: 225–235

Experimental
Brain Research

Kinematic variability of grasp movements as a function of practice and movement speed

W.G. Darling[1,*], K.J. Cole[1,*], and J.H. Abbs[1,2]

[1] Speech Motor Control Laboratories, Waisman Center, University of Wisconsin, Madison, Wisconsin, USA
[2] Departments of Neurology and Neurophysiology, University of Wisconsin, Madison, Wisconsin, USA

Summary. Grasp movements were studied in six female subjects to determine the effects of practice and movement speed on kinematics and movement variability. Subjects performed four-joint pinch movements of the index finger and thumb, with 200 repetitions at each of three durations (100, 200, and 400 ms). As observed previously, movements of high velocity were performed with bell-shaped, single-peaked velocity profiles. In contrast, slower movements (~200, 400 ms) were performed as a series of two to four submovements with multiple peaks in the associated joint angular velocity profiles. With practice, only the slowest movements (400 ms duration) showed significant reductions in variability of joint end-positions. Surprisingly, variability of finger and thumb joint end-positions did not increase with increasing movement speed as has been observed for arm pointing movements. This was apparently due to reductions in positional variability during deceleration of the movement which offset increases in positional variability during acceleration. Neither practice nor movement speed affected variability of the location of fingertip contact on the thumb, which always occurred on the thumb distal pulpar surface.

Key words: Grasp – Kinematics – Variability – Hand – Motor control

Introduction

The neural mechanisms underlying control of multiarticulate or compound movements are not well understood. The obvious functional importance of such movements is reflected in the recent focus on multiarticulate arm movements for reaching and pointing (e.g. Abend et al. 1982; Soechting and Lacquaniti 1981; Lacquaniti and Soechting 1982; Soechting 1984; Atkeson and Hollerbach 1985). These studies indicate that wrist trajectory and tangential velocity profiles are invariant for movements of different speeds and to different targets. Similarly, simple movements of single joints exhibit nearly invariant velocity profiles (Ostry et al., 1987). These apparently invariant features of arm reaching movements have been interpreted to reflect planning of the movement at spatial trajectory levels of the relevant structure (e.g., hand).

Studies of arm pointing movements, however, have shown that while endpoint variability (or accuracy) is proportional to movement speed (Woodworth 1899; Fitts 1954; Schmidt et al. 1979; MacKenzie et al., 1987; Fitts and Peterson 1964), it decreases with practice (e.g., cf. Ludwig 1982). The variability of elbow movement phase plane trajectories (plots of velocity vs position during movement) increases with increasing movement speed and amplitude, but also decreases with practice (Darling and Cooke 1987a). Thus, while movements may be planned in terms of a specific kinematic feature (i.e., velocity profile, spatial trajectory), with increased speed there are greater variations in spatial endpoints and in phase plane trajectories of movements.

However, results from studies of single and multiple joint arm pointing movements may not generalize to movements of structures with different mechanical properties or movements that are organized to serve other functions. Precise grasp of objects, for example, is a seemingly simple skill associated with most everyday tasks. However, these multiple digit movements must be controlled in concert to properly locate an object within the grasp and to apply the appropriate forces. In previous investigations of rapid grasp movements of the finger

---

[*] Present address: Department of Exercise Science, Field House, University of Iowa, Iowa City, IA 52242, USA

Offprint requests to: W.G. Darling (address see footnote) and thumb (Cole and Abbs 1986, 1987), significant variability in the finger and thumb movements across trials was observed. However, these variations reflected a coordination among the constituent movements apparently organized around the task-related feature of preserving distal contact sites of the finger on the thumb. Additionally, velocity profiles of the constituent movements were invariant.

In the present investigation, the effects of practice and different movement speeds on finger-thumb grasp movements were studied. In this way, it was possible to investigate whether (1) grasp movements of different speed exhibit invariant velocity profiles and (2) kinematic variability is related to movement speed and practice as has been observed for arm pointing movements. Additionally, the movements studied here involved four joints (two each of the index finger and thumb) and thus permitted evaluation of more natural thumb movements than those studied previously (Cole and Abbs 1986).

Material and methods

Subjects

Six normal healthy females, ranging in age from 18 to 30 years served as subjects for these experiments.

Apparatus

Subjects were seated in a dental chair with the right forearm supported by a table surface and placed in a splint to restrict wrist movement. The hand was comfortably clamped to restrict thumb movement proximal to the metacarpo-phalangeal) MP joint and in a position such that thumb movement occurred in the horizontal plane. Adhesive tape was placed around the distal interphalangeal joint of the index finger to maintain a fixed, relaxed position of this joint, about 0.1 to 0.3 rad in flexion. Thumb and finger movements were not coplanar. Depending on the subject, the plane of finger movement was elevated 0.2 to 0.8 rad relative to the plane of the thumb movement. Subjects were instructed to begin movements from a relaxed, open-hand position with fingertip and thumb tip aligned with targets indicating the starting position. Depending on the hand size of the subject, distances between the pulps of the index finger and thumb at the starting position varied from 4 to 6 cm.

Angular positions of the finger metacarpo-phalangeal joint (MP) and proximal interphalangeal joint (PIP) and the thumb interphalangeal joint (IP) were transduced in the flexion-extension plane with planar electrogoniometers (cf. Cole and Abbs 1986). Each of these transducers was of exoskeletal linkage design, with the linkages being two parallelograms connected in series to drive a miniature precision potentiometer (Thomas and Long 1964). With this design, joint rotation is transduced without potential artifact from joint translation. For these experiments, the linearity of the transducers was within 1% and resolution was about 0.002 rad.

Two dimensional movements of the thumbtip and fingertip within the horizontal plane were transduced using an infrared photoelectric tracking system, based upon a distributed photodiode of Schottky-barrier design. Light emitting diodes (LEDs) were attached to the radial side of the finger near the tip and to the ulnar side of the thumb, proximal to the nail in order to avoid contact or optical occlusion during the pinch. LEDs were also attached to the skin overlying the thumb IP joint, and on the hand over the second metacarpal to serve as reference for overall hand movement. The distributed photodetector was oriented parallel to the plane of thumb movement onto which the light source was focused by a conventional 50-mm camera lens system. The photodetector and associated circuitry produced voltage signals porportional to the LED positions in a two-dimensional Cartesian coordinate system referenced to the fixed camera position. This optical system has a bandwidth of about dc-150 Hz with a resolution of about 0.5 mm.

Since finger movement was not in a plane parallel to that of the photoelectric tracking system, recorded fingertip trajectories were subject to error. However, the fingertip LED did reflect fingertip position in the plane of thumb movement at the time of finger-thumb contact (i.e., at the end of the pinch). In this way, fingertip position at contact could be measured both relative to the camera and in relation to the thumb nail base and thumb IP LEDs; this latter measure allows for determination of the location of fingertip contact on the thumb.

Thumb MP movement was calculated using trigonometric techniques based on three signals including: the trajectories of the LEDs placed on the thumbtip and over the thumb IP joint and the thumb IP angle measured by the electrogoniometer. These calculations assumed a fixed joint center of rotation for the thumb MP. Accuracy of measurement of thumb MP angle was about 0.01 rad. In one of the six subjects, the thumb LEDs were covered by the finger movement, precluding the calculation of thumb MP movement.

The pressure between the thumb and finger pulpar surfaces at contact was measured in two of the six subjects with a pressure transducer consisting of a small disc (3-mm diameter) placed on the distal pulp of the index finger. In two other subjects, the time of finger-thumb contact was determined using a small pad (4 mm diameter) placed on the fingertip which, upon finger-thumb contact, completed a circuit that yielded a corresponding step change in voltage. In the final two subjects, the experimental task was performed with no contamination of the finger or thumb pulpar surface.

Procedures

The experimental task was to bring the pulpar surfaces of the thumb and index finger together from an open-hand starting position in response to a tone, maintain a light pinch for a short time, and then return the thumb and finger to the start positions. Subjects were instructed to produce about the same contact pressure for each trial by reproducing the same sensation of pressure. For subjects in which contact pressure was transduced, visual feedback was provided following each pinch trial. Although contact pressure was not measured in all subjects, movement kinematics with and without this visual information to the subject appeared to be similar (Cole and Abbs 1986).

In a single experimental session, each subject performed 200 consecutive pinch movements at each of three movement durations (100, 200, and 400 ms); the desired movement was signalled by the duration of the tone. The order in which the different duration movements were performed was counterbalanced across subjects. To aid subjects in moving for the desired duration, verbal commentary was provided by the experimenter regarding whether the movements were too slow or too fast based on the velocity profiles of the finger MP and PIP joints displayed on an oscilloscope. Other than the instructions to maintain a consistent contact sensation and to adhere to movement duration specifications, no particular instructions were given for reducing the variability of the movements or for adopting any particular location for fingertip contact on the thumb. With this experimental design, it was possible to evaluate the influence of both movement speed and practice on the performance of the pinch task.

Data recording

Following suitable amplification, the movement signals were digitized at 500 samples/s/channel (12-bit resolution) using a DEC PDP-11/44 laboratory computer system. Data were transferred to a SUN microcomputer-network system for analysis.

Data analysis

Movement signals were filtered digitally to remove noise using a sixth order, maximally flat low-pass filter with a cutoff of 20 Hz and zero phase shift. Instantaneous angular velocities were obtained by numerical three-point differentiation. Onset of movement was measured from velocity records as the time at which velocity rose above 5% of peak velocity for that movement. Movement termination was measured as the time of contact (4 subjects) or was estimated as the time at which either MP or PIP angular velocity first decreased below 10% of peak velocity (i.e., whichever fell to 10% of peak velocity earliest). This measure was chosen based on measurements of actual time of contact relative to MP and PIP velocities for subjects in which time of contact was measured. Variability in the movements of individual joints was measured both at contact and throughout the movements. Variability in fingertip and thumbtip spatial positions at contact were also measured. Effects of practice were evaluated by dividing the 200 movements performed at each of the three movement durations into 8 groups of 25 consecutive movements. Statistical significance of the effects of movement speed and practice were evaluated with two-way, repeated-measures analysis of variance and subsequent paired t-tests.

Results

Individual joint movements

The general characteristics of these movements were similar to those described in a previous study of rapid pinch movements (Cole and Abbs 1986). Angular position records for each of the four joints for one subject are shown in Fig. 1 for movements of 100, 200, and 400-ms duration. Figure 2 shows joint angular velocity records for the finger MP and PIP joints and the thumb MP joint for a single movement trial performed by another subject. Joint movements of 100-ms duration were made smoothly from onset to finger-thumb contact with bell-shaped single-peaked velocity profiles (Fig. 2). Contact of the fingertip with the thumb occurred well after deceleration of both digits had begun. In contrast to the previous study (Cole and Abbs 1986) in which thumb movement was limited to the IP joint, there was little thumb IP movement observed in the present task. Indeed, only one of the six subjects moved the thumb IP joint more than 0.1 rad. This difference reflects the constraints on thumb movement imposed in the previous work.

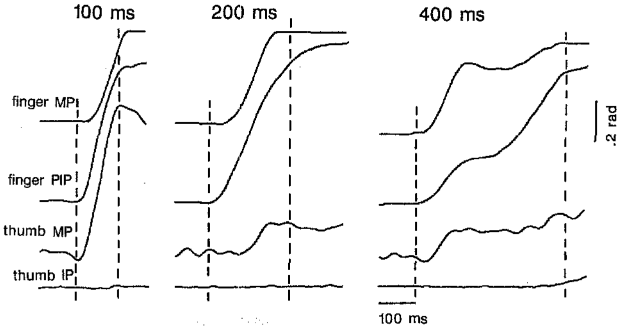

Fig. 1. Joint position records from grasp movements of different durations. The position records were low-pass filtered (20 Hz cutoff, 0 phase shift). Data are from one subject. The dashed vertical lines indicate finger PIP onset and finger-thumb contact

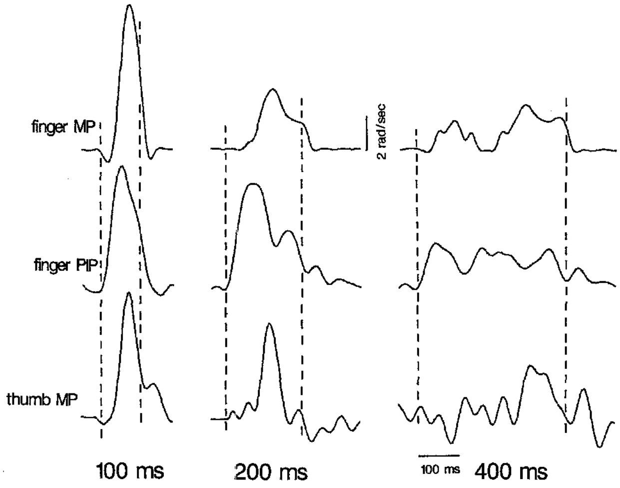

Fig. 2. Joint velocity records from grasp movements of different durations. The velocity records were obtained by three-point digital differentiation of filtered position records. Data are from one subject. The dashed lines show PIP onset and finger-thumb contact

While movements of 200-ms duration also appeared to be made smoothly from onset to contact, multiple peaks were often present in the velocity profiles (Fig. 2). These slower movements apparently were not made as a single smooth movement from onset to completion, but rather consisted of two or more sub-movements as indicated by multiple peaks in the movement velocity profiles. Joint movements for 400-ms duration trials likewise were not produced smoothly. The finger MP and PIP movements shown in Fig. 1 (400 ms movements) each consisted of two sub-movements. However, the two finger joints did not always exhibit the same number of sub-movements within a single pinch movement. As shown in Fig. 2 for movements by a different subject, two major peaks occurred in the finger MP velocity profile, whereas three peaks occurred in the PIP velocity profile. As many as four sub-movements were observed in the joint angle and velocity profiles of 400-ms duration pinch movements.

Effects of practice and speed of movement on sub-movements

The mean number of sub-movements associated with the first and last 25 grasp movements in the 200- and 400-ms duration conditions for the finger MP and PIP were estimated visually for each subject. This was done by simultaneously displaying joint position and velocity records of individual trials and estimating the number of major peaks in the velocity trace (smaller velocity peaks embedded within the larger peaks were not included – i.e., Fig. 2 – finger MP has 6 identifiable peaks but only two major peaks were identified). Thumb MP sub-movements were not measured because of the greater noise in the associated velocity signals (the noise resulted from lower accuracy of the thumb MP angle measures calculated from two-dimensional data). Overall, 200-ms duration movements were produced with fewer sub-movements than 400-ms duration movements (means of 1.5 and 2.1 sub-movements for 200- and 400-ms duration movements, respectively). Also, there were small and inconsistent changes in the mean number of joint sub-movements with practice.

Effects of practice and speed on variability of individual joint movements

Figure 3 shows group data for the effects of practice on end-position variability of finger MP (A) and PIP (B) and thumb MP (C) movements for the different target durations. Practice effects on the variability of finger MP and PIP end-positions depended on movement duration as shown in Fig. 3 and confirmed by significant duration-practice interaction effects [MP – F(df = 14,70) = 3.34, $p = 0.0004$; PIP – F(df = 14,56) = 2.32, $p = 0.0134$]. Specifically, for the 400 ms movements, significant ($p < 0.05$) reductions in variability occurred for the MP and PIP end-positions within 75 movements (Fig. 3). The effects of practice on variability of thumb MP end-positions were less clear. Overall, thumb end-position variability decreased with practice (F(df = 7,21) = 2.59, $p = 0.0429$). However, the reductions were not statistically significant for any of the individual movement duration conditions.

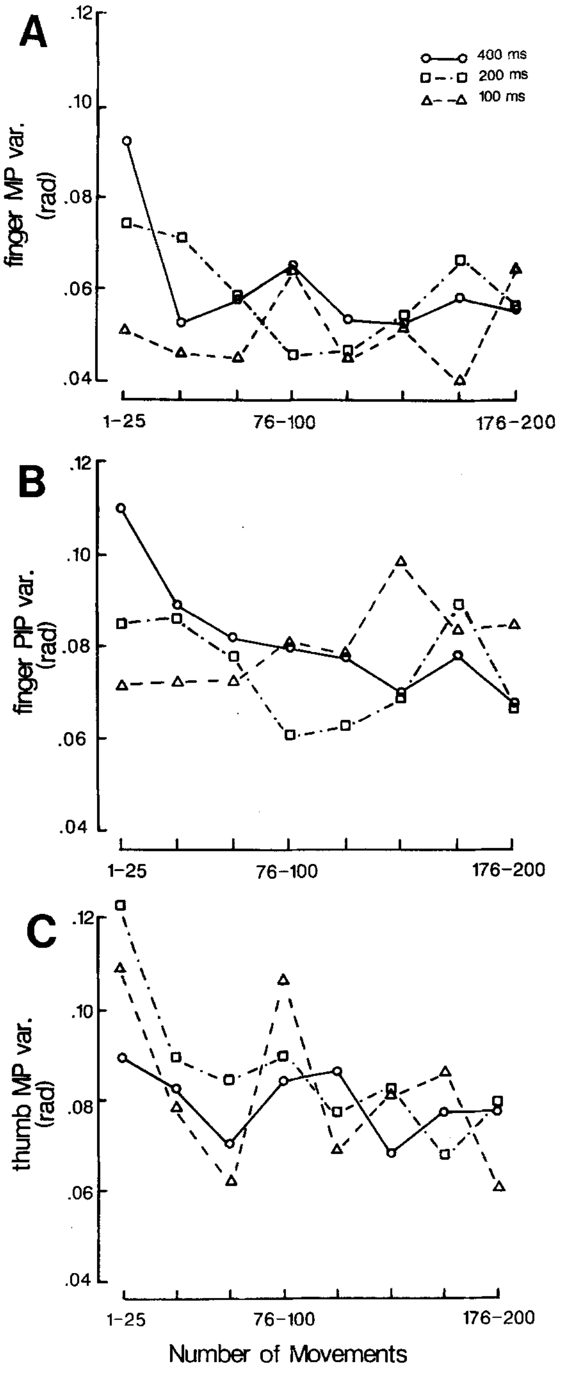

Fig. 3A–C. End-position variability of finger MP (**A**) and PIP (**B**) and thumb MP (**C**) movements throughout practice of grasp movements of 3 different durations. Each plotted point is the mean variability (SD) across subjects of joint end-positions for 25 consecutive movements during practice. Data are for six subjects (finger joint movements) and four subjects (thumb MP movements)

Table 1. Results of t-tests comparing joint end-position variability of movements of different duration

	t-values					
Joint	100–200 ms		100–400 ms		200–400 ms	
	1–25	176–200	1–25	176–200	1–25	176–200
finger MP	–2.24[a]	0.84	–3.40[a]	1.41	–1.38	0.86
finger PIP	0.25	–0.29	–2.00	0.31	–3.30[a]	0.18
thumb MP	–0.39	–1.35	0.48	–1.90	1.67	0.18

t-values from paired comparisons of end-position variability of movements of different duration for either unpracticed (1–25) or practiced (176–200) movements

[a] t-value significant ($p < 0.05$)

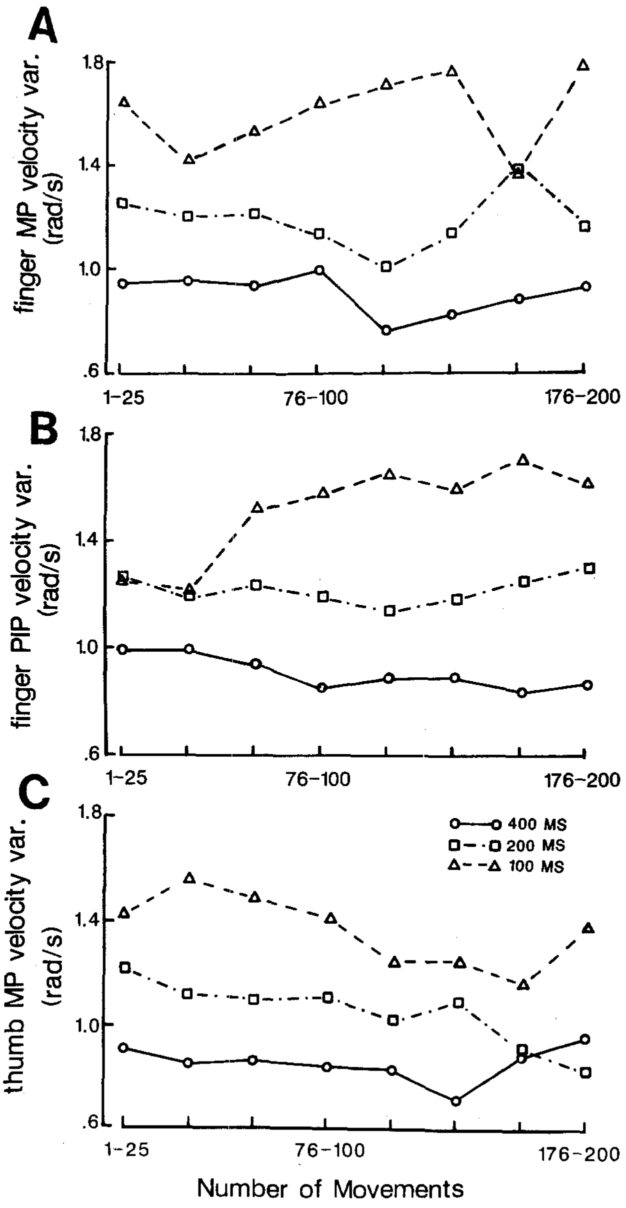

Fig. 4A–C. Variability in finger MP (**A**) and PIP (**B**) and thumb MP (**C**) peak angular velocities throughout practice of grasp movements of 3 different durations. Each plotted point is the mean variability (SD) across subjects of the joint peak angular velocities for 25 consecutive movements. Data are for six subjects (finger joint movements) and five subjects (thumb MP movements)

Further inspection of end-position variability for movements of different speed indicates that, surprisingly, finger MP and PIP movements were *more* variable for slow than for fast unpracticed movements (1–25) (Fig. 3A, B and Table 1). Moreover, practiced MP and PIP movements (176–200) were not significantly different in end-position variability for the different duration conditions. Finally, end position variability of thumb MP movements was independent of both movement duration and amount of practice (Fig. 3C). These results are striking, given previous work indicating that fast arm movements are associated with greater spatial variability than slow movements (Woodworth 1899; Fitts 1954; Schmidt et al. 1979).

Spatial variability at movement end-point must depend in some way on variability in movement velocity. That is, movements with more variable peak velocities would be expected to exhibit greater variability in movement amplitude and end-position (cf. Schmidt et al. 1979; Meyer et al. 1982). Thus, the observation that the spatial variability of fast movements was less than or equal to variability of slower pinch movements could be explained if velocity variabilities were comparable for movements of different speed. However, for movements of different mean durations but with the same velocity profile, end-position variability would depend on relative variability of peak velocity (i.e., coefficient of variation of peak velocity). Velocity profiles differed for movements of different mean durations studied here (Fig. 2). Thus, we have presented data on absolute velocity variability (Fig. 4). These data show that variability of peak finger and thumb joint angular velocities increased with increasing speed of the movements [finger MP – $F(df = 2,10) = 16.15$, $p = 0.0007$; finger PIP – $F(df = 2,8) = 7.85$, $p = 0.013$; thumb MP – $F(df = 2,8) = 6.25$, $p = 0.023$]. Practice did not influence variability of peak velocities (Fig. 4); thus the observed changes in end-position variability due to practice or speed effects were not a consequence of changes in velocity variability.

Variability throughout movements

The variability exhibited at the end of movements must result from variations in the torques that

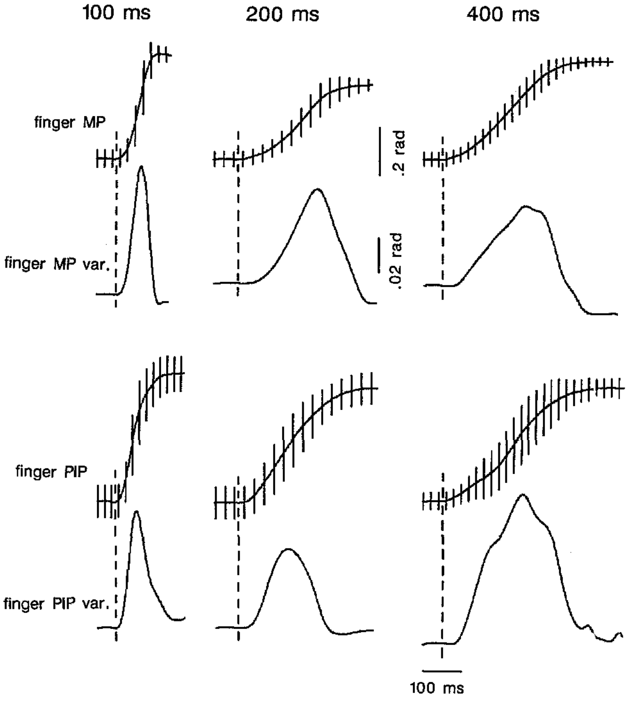

Fig. 5. Joint positional variability throughout grasp movements of different durations. Averaged finger MP and PIP joint position records of practiced grasp movements are shown with superimposed SD bars at 20-ms intervals throughout the movements. Below these averaged records are plotted the time-course of changes in joint positional variability (SD) throughout the movements. These point-to-point variability records were generated by calculating the SD of joint positions at 2-ms intervals throughout the movements and plotting these against time. Data are from one subject

produced the movements (cf. Schmidt et al. 1979; Meyer et al. 1982; Darling and Cooke 1987c). In an attempt to explain the dependence of velocity variability on speed of the movements, and the paradoxical independence of joint end-position variability from movement speed, the time-course over which joint positional variability developed was further analyzed. As shown in Fig. 5, angular position variability increased during the initial part of the movement, as indicated by the length of the vertical bars on the averaged position curves and by the smooth plots of variability throughout the movement. The rate of rise of variability during this phase of the movement, indicated by the slope of the continuous variability plots, exhibited a clear dependence on movement speed, with greater rates of increase for faster movements. During the latter part of the movement, as finger-thumb contact was approached, positional variability decreased at a rate porportional to the speed of the movements.

These results were confirmed by measuring the peak increase in variability during acceleration and the decrease in variability during deceleration for groups of 25 consecutive movements for each subject. Correlation analyses were performed and yielded negative correlations (Table 2) indicating that the greater the increase in variability during acceleration of the movements, the greater the decrease in variability as finger-thumb contact was approached. As a result, the end-position variability of fast movements did not differ from the slower movements.

Table 2. Correlations of peak changes in variability during acceleration and deceleration of movements

	Correlations	
Subject	finger MP	finger PIP
1	–0.36[a]	–0.48[a]
2	–0.74[a]	–0.63[a]
3	–0.39	–0.69[a]
4	–0.31	–0.64[a]
5	–0.45[a]	–0.60[a]
6	–0.76[a]	–0.33

– note that for these data movements from all durations were pooled for each subject

[a] correlation differs significantly from zero ($p < 0.05$)

Variability in spatial location of finger-thumb tip contact

In previous studies of the effects of movement speed and/or practice on spatial variability, variability has been examined in terms of an absolute spatial target for the movements. That is, the variability in spatial location of the movement end-point in relation to a target, or the number of hits and misses of the target have been studied in relation to, for example, average movement speed. In the case of the pinch task studied here, the spatial target is not a constant position in space but rather is a dynamic target based on the relative locations of the finger and thumb pulpar surfaces. As noted previously (Cole and Abbs 1986), individual fingertip and thumbtip absolute spatial locations could vary considerably at contact, but contact always occurred at the respective distal pulpar surfaces. In the present study, the variability in finger-thumb contact locations as a function of movement speed and practice was studied quantitatively using the infrared photoelectric tracking system. Although tip movements could be transduced in the horizontal plane of thumb movement only, location of the fingertip and thumbtip at the time of contact could be accurately measured.

Figure 6a shows trajectories of the fingertip, thumbtip (nail base, cf. Material and methods), and

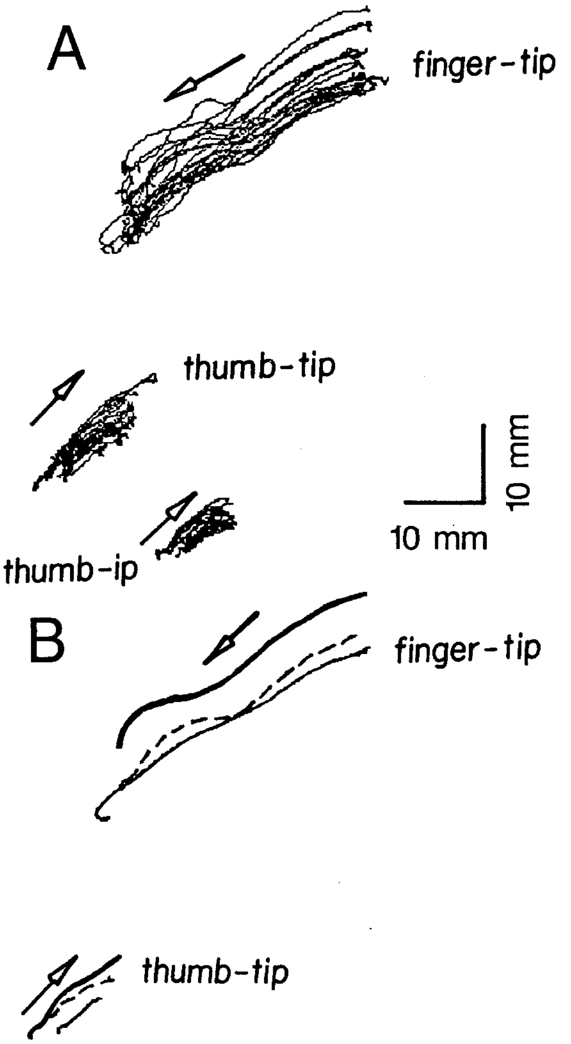

Fig. 6A, B. Trajectories of fingertip, thumbtip (nail base), and thumb IP LEDs during grasp movements. In **A** are shown superimposed trajectories from 25 consecutive pinch movements at the beginning of practice of 200-ms duration movements (movements 1–25). In **B** are shown superimposed trajectories of the fingertip and thumbtip from three movements of the 25 shown in A. Note that the distance between thumbtip and fingertip LEDs at contact results from the positions of the LEDs on the digits. Data are from one subject. Note that finger movements for this subject were made at an angle of about 0.2 rad above horizontal; thus the actual fingertip trajectories differed only slightly from those shown

thumb IP LEDs in the horizontal plane superimposed for 25 consecutive movements. Note that contact of the fingertip on the thumb always occurred distal to the thumb nail base in the region of the pulp. The finger and thumbtip trajectories were curvilinear (Fig. 6b) and thus differed from the near linear trajectories described for the wrist during arm movements (Morasso 1981; Soechting and Lacquaniti 1981; Atkeson and Hollerbach 1985). Also, there was considerable trial-to-trial variability in these trajectories, due in part to different tip locations at movement onset.

Variabilities in relative spatial location of the fingertip and thumbtip LEDs at contact of the finger and thumb were calculated as the areas of ellipses with radii equal to 1 SD in the x and y dimensions, as indicated in Fig. 6. Thus, greater variability in endpoint location would produce an ellipse of greater area. Similar methods have been used to quantify two-dimensional variability of arm movements in monkeys (Georgopoulos et al. 1981) and phase-plane trajectories in human arm movements (Darling and Cooke 1987a). The variability in location of the fingertip LED relative to the thumb nail base LED at contact was calculated in a similar fashion. The variability of the separation of the fingertip and thumbtip LEDs in the x and y dimensions was used to calculate a variability ellipse for fingertip contact relative to the thumbtip.

Variability in spatial locations of the fingertip and thumbtip were typically greater than the variability of fingertip locations relative to the thumbtip at contact. This is shown in Fig. 7 by plots of the variability of the fingertip location relative to the thumbtip at contact (plotted as circles) as a function of practice and movement speed. The squares represent the simple sum of the individual variabilities of the fingertip and thumbtip locations (areas of ellipses) at contact. Note that the sum of fingertip and thumbtip variability was always greater than the variability of the fingertip relative to the thumbtip.

How could variations in fingertip and thumbtip locations be greater than variations in the location of the fingertip relative to the thumbtip at contact? This could occur only if finger and thumb movements were organized such that variability in movements of one structure were associated with complementary variations in movements of the other structure, as has been shown previously for simple pinch movements (Cole and Abbs 1986, 1987). Such a relationship is illustrated in Fig. 6b by plots of trajectories of fingertip and thumbtip LEDs for three movements taken from the 25 movements shown in Fig. 6a. Note the reciprocal positioning of the fingertip and thumbtip at the end of the movements.

Effects of practice and movement speed on finger-thumbtip variability at contact

As previously discussed, the location of fingertip contact on the thumb may be considered to be a dynamic target for the pinch task. Variability in the location of contact may therefore be related to

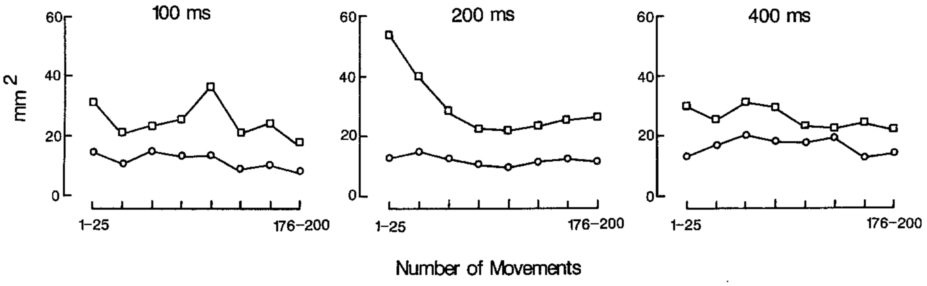

Fig. 7. Variability of location of fingertip contact on the thumb (circles) during practice of grasp movements of 3 different durations. Plotted as squares are the summed variabilities of individual fingertip and thumbtip locations in space at contact. Each plotted point is the mean variability (SD) across subjects of 25 consecutive movements during practice. Note that variability is measured in mm^2 as the area of an ellipse with radii equal to 1 SD in the x and y dimensions of finger and thumbtip spatial locations at contact (see text for details). Data are for five subjects

variability about a target, or error, in a pointing task (cf. Schmidt et al. 1979). With practice, one might therefore expect a reduction in such variability; whereas with increases in movement speed one would expect greater variability in contact location. Figure 7 shows, however, that there was no effect of practice or speed (duration of the movements) on variability in fingertip location on the thumb at contact (circles). Thus, as observed for movements of the digit joints, movement speed had no effect on spatial variability in this task.

Discussion

The effects of practice and different movement speeds on the variability of thumb and index finger grasp movements were investigated. Previous studies of movement variability have largely concerned upper limb pointing tasks. The present data invite speculation concerning the mechanisms which might underlie control of grasp or other oppositional movements, and how these mechanisms may differ from those underlying movements involved in tasks such as pointing or reaching to a location in space.

In the present investigation little or no thumb IP movement was observed in 5 of the 6 subjects. This was in contrast to previous work in which thumb movement was limited to the IP joint (Cole and Abbs 1986). The observed differences are probably due to the constraints on thumb movement imposed in the previous research. The present observations suggest that there is relatively little thumb IP motion during natural precision grasp in which thumb movement is unconstrained.

Invariant properties of grasp movements

As observed in previous work (Cole and Abbs 1986), fast movements (~100 ms duration) of the digits toward grasp exhibit bell-shaped velocity profiles for the individual joint movements. This finding was confirmed in the present study in which thumb MP joint angular velocity profiles were also studied. The near symmetrical bell-shaped velocity profile has been suggested to reflect movement programming (Brooks et al. 1983) and occurs consistently in single and multiple joint arm movements over a wide range of movement speeds and for hand movements to different locations in the work space (Bouisset and Lestienne 1974; Cooke 1980; Morasso 1981; Soechting 1984; Atkeson and Hollerbach 1985; Ostry et al., 1987). However, in the present experiment, slower digit movements were executed as a series of submovements reflected by multiple peaks in the joint angular velocity profiles. The shape of velocity profiles is, therefore, not an invariant property of grasp movements. Multiple peaks in velocity profiles have been interpreted to indicate movements that are under feedback control (Brooks et al. 1983). Such differences in fast and slow movements may reflect the mechanical properties of the digits in comparison to the arm. Since the digital joints have relatively high stiffness and low inertia, it is probable that such a system is optimized for performance of fast movements. In this regard, the slow movements studied here may be considered a series of fast, small amplitude movements rather than a single slow movement.

An apparently invariant property of precision grasp is indicated by the preference for contact on the distal pulpar surfaces of the digits (Landsmeer 1962; Napier 1956; Cole and Abbs 1986, 1987). Indeed, an extremely low variability in the location of fingertip contact on the thumb (about 20 mm^2) was observed, and was maintained for movements of different speeds. As noted by Cole and Abbs (1986, 1987), the regular contact at the distal pulpar surfaces of the digits probably reflects the greater density of cutaneous mechanoreceptors at these sites (cf. Johansson and Vallbo 1979a, b).

Variability of movements of different speeds

Given the well-known effects of movement speed on variability of movements, it was particularly surprising to observe that fast finger joint movements in the present study were less variable than slow movements at the beginning of practice, and that there were no significant differences in variability after practice. Several possible explanations can be considered. As noted in Results, positional variability in movements must depend in part on variability in movement velocity. However, spatial variability of the movements was similar for movements of different speed despite velocities that were more variable for fast movements than for slow movements. This finding rules out an explanation for the low spatial variability of fast movements based on mechanical limit or saturation effects in which fast movements could be relatively invariant because they were at or near maximum possible speed. The observation that finger-thumb contact occurred well after peak velocity also argues against such an explanation. Finally, the absence of movement speed effects was not due simply to the oppositional nature of the pinch movements since oppositional movements of the lips and jaw exhibit greater variability as speech rate is increased (Hughes and Abbs 1976).

A possible explanation for the finding that positional variability was similar for movements of different speed was indicated by increases in positional variability during acceleration that were compensated by nearly equivalent decreases in variability during deceleration. The reduction in joint angular position variability as finger-thumb contact was approached is especially noteworthy when one considers that there were no targets for the individual joint angles as is typical for paradigms in which variability of targeted movements is studied. That is, the reductions in joint angular position variability occurred in the absence of any constraints on final joint angles. As noted by Cole and Abbs (1986) consistent finger-thumb contact could be attained with considerable variability in finger and thumb joint angles.

The interpretation of the time-course of positional variability throughout movement is, however, difficult because of variations in movement duration, peak velocity and the movement profile (e.g., velocity profile). It is important, therefore, to determine whether the observed reductions in angular position variability during the latter part of the movements could be attributed simply to a factor such as variations in movement duration. This possibility was studied by simulating movements with the same velocity profile (minimum jerk profile – Hogan 1984) with: (1) constant peak velocity while duration was varied and (2) constant duration while peak velocity was varied. The results of these simulations are shown in Fig. 8 which contains plots of the time-course of position, velocity and positional variability for the simulations. When peak velocity is varied and movement duration held constant, positional variability increases throughout the duration of the movement (Fig. 8 – left hand side). In contrast, when duration is varied while peak velocity is held constant the time-course of positional variability is more complex (Fig. 8 – right hand side). Positional variability increases during the initial part of the movement, then decreases for a short period of time and then again increases sharply until the end of the averaged movement. Variations in both peak velocity and movement duration were evident in the movements studied in these experiments. The simulations show that variations in these two parameters combined would be expected to produce only a small

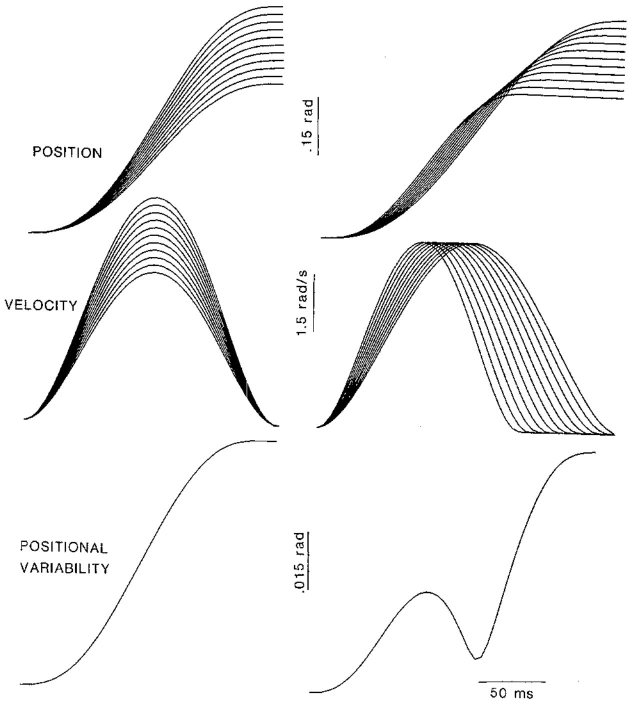

Fig. 8. Results of movement simulations. On the left side are shown movement simulations in which duration was maintained constant while peak velocity was varied. On the right side are shown simulations in which peak velocity was held constant while duration was varied. Superimposed traces of the time-course of position and velocity of the simulated movements along with the time-course of positional variability associated with each of the simulations are shown

decrease in positional variability at the end of acceleration followed by a sharp rise in variability unless the variations in velocity and duration were correlated appropriately. Thus, the observed reductions in variability as finger-thumb contact is approached cannot be attributed simply to variations in movement duration or velocity.

A direct relationship between movement speed and the rate of increase in positional variability during the early part of the movement is consistent with findings of a previous study of phase-plane variability (Darling and Cooke (1987a) and with impulse variability models (Schmidt et al. 1979; Meyer et al. 1982). The assumption underlying such models is that end-position variability results from variations in the forces or torques produced by muscles. The variability of targeted, rapid isometric torques has been reported to be directly proportional to the target torque (Schmidt et al. 1979; Sherwood and Schmidt 1980). Thus faster movements, which require larger acceleration torques, would be expected to exhibit a more rapid rise in kinematic variability during acceleration of movement. A reduction in positional variability during the latter part of the movement shows that torques produced in later parts of the movement compensate somewhat for movement variability produced by variations in accelerative torques (cf. Darling and Cooke 1987b, 1987c). In studies of targeted single and multiple joint arm movements, reductions in variability as the movement target is approached have been observed consistently (Soechting and Lacquaniti 1981; Soechting 1984; Darling and Cooke 1987a).

The finding that spatial variability did not depend on speed of movement provides some insights into the processes controlling digit movements during grasp. One possibility is that corrections to the movements could be made on the basis of afferent signals received early in movement. The initial joint motion may yield information for the predictive control of later parts of the movement. This may be true particularly for slower movements, which were made as a series of sub-movements. Indeed, the use of proprioceptive and visual feedback has been postulated to underlie control of such sub-movements (Crossman and Goodeve 1963; Keele 1968). It has been proposed recently that movement corrections based on sensory feedback may occur even in saccadic eye movements of fast movements of the speech articulators (see, for example, Abbs et al. 1984). However, in a recent study, disturbances applied to the thumb during rapid grasp movements comparable to those in the present study evoked functional compensations of the thumb and index finger only for disturbances introduced just *prior* to movement onset, but not after movement was initiated (Cole and Abbs 1987).

Alternatively, the use of efference copy of motor commands to digital muscles could underlie the reductions in positional variability observed during deceleration of joint movements as contact is approached (cf. Darling and Cooke 1987b, c; Hore and Vilis 1984). Thus, for example, variability in motor commands for initiation of the movement may be compensated by appropriately corresponding variations in commands to muscles which decelerate the movement through an efference copy mechanism. Finally, the predominance of multiple joint muscles controlling digital movements may provide a biomechanical linkage which tends to reduce kinematic variability as has been suggested for gait (cf. Winter 1984). The opposing actions of muscles acting at the hip and knee or knee and ankle joints (i.e., quadriceps femoris contraction produces knee extension and hip flexion torque) produce the necessary linkage to reduce kinetic and kinematic variability of gait. Likewise, for movements of the index finger, the lumbrical and ulnar (palmar) interosseous exert opposing actions at the MP and PIP joints and thus provide a similar linkage.

Effects of practice on performance of the pinch movement

In previous studies, it has been shown that practice reduces variability of end-positions and trajectories of arm movements (Ludwig 1982; Darling and Cooke 1987a; Georgopoulos et al. 1981). Interestingly, in the present experiment, consistent changes in joint end-position variability during practice occurred only for the slowest movements. These slow movements of the digits were jerky in appearance and appeared somewhat unnatural. Thus, it is possible that requiring subjects to make such movements slowly represented a novel situation that required practice for improved performance. Because fast movements were, initially, less variable than slower movements, this may indeed be the case. Likewise, variability of finger-thumb contact location was not influenced by practice of the task and was, in any case, very low for all movement speeds. Since the task studied in the present experiments was relatively simple and common, one might not expect changes in movement variability with practice.

The properties of digit movements of the hand differ greatly from those of arm movements in many respects including movement variability and control of movements of different speed. In particular, the finding that end-point spatial variability was about the same for movements of different speed is indicative of different control properties from those of arm movements. Also, the finding that slower finger movements during grasp (200- and 400-ms duration) were made as a series of sub-movements rather than as a single movement from onset to completion suggests quite a different control strategy for slow as compared to fast movements. Only the consistency of location of fingertip contact on the thumb proved to be nearly invariant for movements of different speed. Indeed, it is the specific task of prehension in which may reside the crucial difference in the mechanisms of control of arm and hand movement.

Acknowledgements. The authors wish to thank Richard Konopacki for his technical assistance and Deborah Hoffman for the editing of this manuscript. Research supported in part by National Institutes of Health grants NS-16373, NS-13274, and HD-03352.

References

Abbs JH, Gracco VL, Cole KJ (1984) Control of multimovement coordination: sensorimotor mechanisms in speech motor programming. J Motor Behav 16: 195–232

Abend W, Bizzi E, Morasso P (1982) Human arm trajectory formation. Brain 105: 331–348

Atkeson CG, Hollerbach JM (1985) Kinematic features of unrestrained arm movements. J Neurosci 5: 2318–2330

Bouisset S, Lestienne F (1974) The organization of simple voluntary movement as analyzed from its kinematic properties. Brain Res 71: 451–457

Brooks VB, Kennedy PR, Ross HG (1983) Movement programming depends on understanding of behavioral requirements. Physiol Behav 31: 561–563

Cole KJ, Abbs JH (1986) Coordination of three-joint digit movements for rapid, finger-thumb grasp. J Neurophysiol 55: 1407–1423

Cole KJ, Abbs JH (1987) Kinematic and electromyographic responses to perturbation of a rapid grasp. J Neurophysiol 57: 1498–1510

Cooke JD (1980) The organization of simple, skilled movements. In: Stelmach GE, Requin J (eds) Tutorials in motor behavior. North-Holland, Amsterdam, pp 199–212

Crossman ERFW, Goodeve PJ (1963) Feedback control of hand movements and Fitt's Law. Paper presented at the meeting of the Exp. Psychol. Society, Oxford, July, 1963. Published in Q J Exp Psychol [A] 35: 251–278, 1983

Darling WG, Cooke JD (1987a) Changes in the variability of movement trajectories with practice. J Motor Behav 19: 291–309

Darling WG, Cooke JD (1987b) Movement related EMGs become more variable during learning of fast accurate movements. J Motor Behav 19: 311–331

Darling WG, Cooke JD (1987c) A linked muscular activation model for movement generation and control. J Motor Behav 19: 333–354

Fitts PM (1954) The information capacity of the human motor system in controlling the amplitude of movement. J Exp Psychol 47: 381–391

Fitts PM, Peterson JR (1964) Information capacity of discrete motor responses. J Exp Psychol 67: 103–112

Georgopoulos AP, Kalaska JF, Massey JT (1981) Spatial trajectories and reaction times of aimed movements: effects of practice, uncertainty and change in target location. J Neurophysiol 46: 725–743

Hore J, Vilis T (1984) A cerebellar-dependent efference copy mechanism for generating appropriate muscle responses to limb perturbation. In: Bloedel J, Dichgans J, Precht W (eds) Cerebellar functions. Springer, Berlin Heidelberg New York, pp 24–35

Hughes OM, Abbs JH (1976) Labial-mandibular coordination in the production of speech: implications for the operation of motor equivalence. Phonetica 33: 199–221

Johansson RS, Vallbo AB (1979a) Detection of tactile stimuli. Threshold of afferent units related to psychophysical thresholds in the human hand. J Physiol (Lond) 297: 405–422

Johansson RS, Vallbo AB (1979b) Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptor units in glabrous skin. J Physiol (Lond) 286: 283–300

Keele SW (1968) Movement control in skilled motor performance. Psychol Bull 70: 387–403

Lacquaniti F, Soechting JF (1982) Coordination of arm and wrist motion during a reaching task. J Neurosci 2: 399–408

Landsmeer JMF (1962) Power grip and precision handling. Ann Rheum Dis 21: 164–170

Ludwig DA (1982) EMG changes during acquisition of a motor skill. Am J Phys Med 61: 229–243

MacKenzie CL, Marteniuk RG, Dugas C, Liske D, Eickmeier B (in press) Three dimensional movement trajectories in Fitt's task: implications for control. Q J Exp Psychol [A] 39: 629–647

Meyer DE, Smith JEK, Wright CE (1982) Models for the speed and accuracy of aimed movements. Psychol Rev 89: 445–482

Morasso P (1981) Spatial control of movements. Exp Brain Res 42: 223–227

Napier JR (1956) The prehensile movements of the human hand. J Bone Joint Surg [Br] 38: 902–913

Ostry DJ, Cooke JD, Munhall KG (1987) Velocity curves of human arm and speech movements. Exp Brain Res 68: 37–46

Schmidt RA, Zelaznik H, Hawkins B, Franks JS, Quinn JT (1979) Motor-output variability. A theory for the accuracy of rapid motor acts. Psychol Rev 86: 415–451

Sherwood DE, Schmidt RA (1980) The relationship between force and force variability in minimal and near-maximal static and dynamic contractions. J Motor Behav 12: 75–89

Soechting JF (1984) Effect of target size on spatial and temporal characteristics of a pointing movement in man. Exp Brain Res 54: 121–132

Soechting JF, Lacquaniti F (1981) Invariant characteristics of a pointing movement in man. J Neurosci 1: 710–720

Thomas DH, Long C (1964) An electrogoniometer for the finger: a kinesiologic tracking device. Am J Med Electron 96–100

Winter DA (1984) Kinematic and kinetic patterns in human gait: variability and compensating effects. Hum Movement Sci 3: 51–76

Woodworth RS (1899) The accuracy of voluntary movement. Psychol Monogr [Suppl] 13: 1–114

Received October 1, 1987 / Accepted April 29, 1988