Coordination of Three-Joint Digit Movements for Rapid Finger-Thumb Grasp

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SUMMARY AND CONCLUSIONS

1. Human thumb and index finger kinematics were examined for multiple repetitions of a simple grasp task as a means to evaluate motor planning and execution of these important hand movements. Subjects generated a rapid (~90-ms duration) pinch movement of the index finger and thumb from an open-hand position. Approximately 400 repetitions were obtained from four naive subjects.

2. The two-dimensional trajectory of the fingertip and the angular positions of the metacarpophalangeal (MP) and proximal interphalangeal (PIP) joints of the index finger were recorded along with the angular position of the thumb interphalangeal joint (TH). Individual joint angular positions were transduced using planar electrogoniometers of an exoskeletal linkage design.

3. Except for consistent single-peaked joint angle and digit trajectory velocity profiles, most kinematic features of the grasp varied considerably across trials, including 1) fingertip spatial position at contact, 2) specific finger paths, 3) finger and thumb path distances, 4) finger and thumb peak tangential velocities, and 5) individual joint rotation magnitudes and peak velocities.

4. However, this kinematic variability was not random. Variable TH angular positioning was paralleled by complementary two-dimensional variations in the finger path. These fingertip adjustments were accomplished by actively controlled, reciprocal angular positioning of the MP and PIP joints. Specifically, with natural reductions in thumb flexion, MP flexion was greater while PIP flexion was reduced and vice versa. These adjustments acted to minimize variations in the point contact of the finger on the thumb and yielded a robust and seemingly natural preference for finger-thumb contact at the more distal surfaces of the digits.

5. The kinematic variability was not due to the finger and thumb movements being controlled independently of digit contact. The variable appositional movements of the finger and thumb and the associated contact force were generated as a single action. This was indicated by 1) an absence of kinematic or force adjustments after contact, 2) smooth digit trajectories with a single peak in their tangential velocities, and 3) finger-thumb contact that consistently occurred well after peak velocity.

6. Likewise, because the variability in the kinematics of the grasp was systematic, it apparently was not due simply to sloppiness or noise in motor execution. Moreover, movements of greater amplitude were produced with greater peak velocities. The covariability among the multiple degrees of freedom for rapid grasp thus indicates that individual digit trajectories, joint angular positions, and muscle contractions were controlled subordinately to the specified site of digit contact.

7. Based on the variability in the digit trajectories, finger and thumb joint angular positions at contact, and variation of that contact point in space, these data indicate that motor planning may not operate exclusively in a spatial domain. Inasmuch as the somatic sensory site of thumb and fingertip contact was relatively consistent, despite spatial variability, an alternative and perhaps a more universal domain for motor planning may be in terms of...
of the multisensory experience associated with successful task performance.

INTRODUCTION

Recent work in voluntary motor control reflects a renewed emphasis on the kinematic characteristics of multijoint movement, particularly reaching movements of the arm (3, 6, 9, 25, 41, 57, 65, 66). A consistent finding in these studies has been that two-joint reaching movements to different targets show bell-shaped hand speed profiles and, except for some vertical reaching movements (6), manifest approximately straight hand paths (3, 6, 23, 30, 57, 65). These regularities in hand trajectory and tangential velocity typically were associated with variable rotations of the constituent joints (e.g., elbow and shoulder). Moreover, for movements of varying speed, distance, and load, the hand speed profile appeared scaled so as to simplify the computational problems posed by the underlying arm dynamics (6, 30). The kinematic regularities in hand trajectory and hand speed have been interpreted to indicate that for reaching tasks the terminal segment trajectory is planned first in hand spatial coordinates, with constituent joint kinematics and dynamics specified subordinately (3, 6, 29, 57). Other investigators have reported invariant relations between the instantaneous angular velocities of the shoulder and elbow during movement deceleration (40, 41, 65, 66). Predictably, these latter data were interpreted to indicate a planning strategy organized around constituent joint angle variables (also see Refs. 31, 41).

This recent work has offered valuable insights; however, it has been focused almost exclusively on the proximal joints of the arm and thus may not offer an optimal basis for understanding the control of other types of multiarticular movements. In particular, the movements of the digits toward grasp represent an important class of multiarticular actions that may be controlled differently from those of arm reaching. These hand movements require coordination of the wrist plus two or more kinetic chains in opposition, involving no fewer than seven joints, with the eventual requirement that precise segment forces be applied to the grasped object (35, 76). The trajectories and final positions of the constituent terminal segments in grasp need not be specified absolutely as long as apposition with the necessary grip forces is achieved. As such, the digital movements leading to acquiring, stabilizing, or manipulating an object by using multiple kinetic chains may not be planned in spatial trajectory terms as suggested for arm reaching movements.

Besides the obvious functional differences between grasp and arm reaching movements, a wealth of neuroanatomical and neurophysiological evidence indicates that proximal (shoulder, elbow) and distal (wrist, forearm, hand) movements of the upper limbs are controlled differently. These proximal-distal differences appear to include, for example, patterns of agonist-antagonist muscle activity (55), the functions of monosynaptic and long loop reflexes (48, 49, 54, 61), directness of projections from the large pyramidal cells of the primary motor cortex (20, 46, 61), and influences of lesions of the pyramidal tract, somatic sensory cortex, and dorsal columns (26, 46, 74). Furthermore, although the importance of afferent information for the control of normal grasp and manipulation is unassailable (35, 47, 56, 74, 76), its significance in control of proximal multijoint arm movements is not as well defined and has been argued by some to be unimportant for rapid movements (30). The muscular and ligamentous linkages of the hand also present the nervous system with biomechanical characteristics different from those of the arm (43, 44, 67). In addition, the underlying dynamics of hand kinetic chains are quantitatively different from the arm, based on the low inertia of the former. Overall, these differences ultimately may reflect the vastly different functions of the hand and arm, particularly with the hand viewed as a generalized but sophisticated apparatus of prehension. Indeed, Tubiana (71) has suggested that, "... the hand gives the upper arm its importance and originality."

Intrinsic and extrinsic hand muscle functions have been studied for individual finger movements (12, 14, 43, 44, 50, 51), precision handling, power grip, and reaching-grasping functions (5, 13, 33, 52, 58, 64); however, the kinematics of the constituent actions and coordination among the digits have not been examined. In this context, the purpose of the present study was to characterize the kinematics of the thumb and index finger in a simple but natural movement, a rapid pinch. Of
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particular interest were 1) the spatial and spatiotemporal relations among the constituent joint rotations and between the paths and trajectories of the tip of the thumb and index finger as well as 2) their relative degrees of variability in repetitions of this task. Thus, in contrast with recent studies of arm movements, the present study focused on the patterns of kinematic variation and regularity for repetitions of a single targeted action rather than examining movements to and from different positions in the work space. The movements were limited to flexion and extension of three joints: the interphalangeal joint of the thumb (TH), the proximal interphalangeal (PIP), and the metacarpophalangeal (MP) joints of the index finger. The trajectory of the fingertip was monitored along with angular position of these joints.

METHODS

Subjects

Subjects included four adult humans (2 males, 2 females), all reporting a right-hand preference and ranging in age from 18 to 27 yr. Because anomalous connections between flexor pollicis longus of the thumb and flexor digitorum profundus of the fingers occur in 0.5% of the population (21), subjects were screened for independence of flexion of the TH from flexion of the index finger. All subjects were naive with regard to the purposes of these experiments.

Apparatus

Subjects were seated in a dental chair with the right forearm supported by a table surface set at the height of the xyphoid process. The hand and forearm were placed in intermediate pronosupination and held in a cast made of orthotic plastic that was shaped and padded to restrict thumb movement to flexion and extension of only the interphalangeal joint. The distal interphalangeal joint of the index finger was fixed with adhesive tape at a relaxed position of about 20° of flexion. Thumb flexion was not coplanar with that of the finger but was elevated about 15° relative to that of finger flexion. The starting positions of the TH and finger MP and PIP joints for each movement trial were set at relaxed flexion (~20°). At these start positions the thumb and finger pulps were separated by ~4–7 cm, depending on the hand size of the subject. The movement starting points were indicated to subjects by a pointer for the thumb and by rigid stops for the proximal and distal phalanges of the index finger.

Angular position of the PIP, MP, and TH joints were transduced in the plane of flexion-extension.
with planar electrogoniometers. As illustrated for MP and PIP in Fig. 1, each of these transducers was of exoskeletal linkage design. The linkages consisted of two parallelograms connected in series to drive miniature precision potentiometers (69). This particular design permits transduction of the rotation of the joint while following joint translation, thus eliminating potential artifact from the latter. A constant instantaneous axis of joint rotation is assumed with this design; both the PIP and MP joints have flexion-extension rotational axes that are constant to within 1 mm (19, 77). The linkages were constructed of thin-walled aluminum tubing of small diameter (2.3 mm) and stainless steel shim stock (0.13-mm thick) with brass bushings supporting steel-wire pivot pins at each linkage joint. The flexible shim stock permitted limited abduction and adduction movements of the MP joint, which were not transduced. The transducers were mounted on the dorsal aspect of the hand with a combination of skin adhesive and tape on the saddles such that the transducer linkage spanned only the joint of interest allowing more distal joints (PIP) to be transduced independently of the proximal joints (MP). The linearity of these transducers was within 2.0% with a resolution of ~0.5°, as measured photographically with the transducer mounted on the hand (15).

For three subjects, linear movement of the thumb was transduced instead of TH angular position. A lightweight steel band was fitted around the thumb at the level of the nail bed and connected, via a sector arm and wire, to a rotational variable displacement transducer at the spindle of a torque motor. The wire was approximately perpendicular to the longitudinal axis of the distal thumb phalanx when the joint was at 0° flexion. Strain gauges bonded on the sector arm of the torque motor enabled transduction of a force nearly proportional (±3%) to that acting on the thumb in the direction of the wire. This force signal was used in a feedback control circuit to maintain a constant force of 0.2 N on the thumb band during movement (1, 16). The sector arm of the torque motor was designed such that the linear translation of the wire was proportional to the rotation of the torque motor shaft.

The two-dimensional trajectory of the fingertip was transduced by using an infrared photoelectric tracking system, based on a distributed photodiode of Schottky-barrier design. A light-emitting diode (LED) was attached to the side of the finger at the level of the pulp where finger-thumb contact was made. A conventional 50-mm camera lens system focused the light source onto the distributed photodetector, which was oriented parallel to the plane of finger movement. The photodetector and associated circuitry yielded two voltage signals proportional to the position of the LED in a two-dimensional rectangular coordinate system referenced to the fixed camera position. This optical system has a bandwidth of approximately DC–150 Hz and a resolution of <0.5 mm.

**Procedures**

Subjects were trained to bring the pulpar surfaces of the thumb and index finger together rapidly in response to the onset of the fourth of four equally spaced tones. Contact force was transduced for both training and experimental trials using a miniature (3 mm diam) encapsulated force transducer attached to the pulp of the index finger. A specified contact force level (0.75–1.25 N peak) was used to provide a general goal for task performance and to aid in the training process. For training, a two-channel oscilloscope was used to provide the subjects with information after each trial on the target and attained contact force levels. Subjects were instructed to monitor the sensation of contact and use the oscilloscope display only as an after-the-fact validation of their sensations for productions of on-target contact force. To further encourage learning of the sensation of contact, the oscilloscope was blanked on ~50% of the trials after ~25 practice trials. After ~50–100 training trials, subjects produced the contact force within the range specified with acceptably rapid movements toward contact. For one of the four subjects (subject 1), contact force was not transduced after the initial training period, thus providing finger-thumb kinematic data without the potential contamination of having a portion of the pulpar surface of the finger covered. After training, this subject was instructed to produce a brisk tap of the finger and thumb and to attempt to reproduce the sensation of the same contact force for each trial. Both qualitatively and quantitatively, the results from subject 1 were not different from those of the other three subjects. In particular, finger and thumb peak joint positions and angular velocities were no more variable than those of the other three subjects, as determined statistically (F tests of the ratios of the uncorrelated variances for individual subjects, α = 0.05). After training each of the four subjects produced ~100 repetitions of the specified task.

**Data recording and analyses**

Following amplification, all signals were digitized on-line at 800 samples s⁻¹ per channel (12-bit resolution) and stored on a Winchester 450 Mbyte disk via a Digital Equipment Corporation PDP-11/44 laboratory computer.

The contact force and movement signals were digitally low-pass filtered in both the forward and reverse directions using a four-pole Butterworth filter design with a cutoff of 20 Hz. Instant angular and tangential velocities also were obtained digitally by using three-point numerical differentiation. The thumb trajectory was computed based on the measured angular position and the length of the thumb from the interphalangeal crease to the distal pulp.
In three subjects the angular position of the thumb was calculated from the linear movement of the wire at the level of the nail bed. This calculation assumed that 1) during TH rotation the wire remained perpendicular to the line of the thumb when at 0° flexion, and 2) the movement of the thumb was simple planar rotation. The first assumption is valid for the long wire-to-sector length that was used in this experiment. For the second assumption, besides the distal phalanx undergoing 5–10° of pronation with flexion (36), the phalanx also translates slightly in the plane of flexion. These latter sources of error were not considered to be significant for the present purposes. Measures of peak angular position for all joints were obtained at the time of peak contact force.

RESULTS

Examples of finger and thumb tip paths; PIP, MP, and TH joint rotations, and pinch

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**FIG. 2.** Representative signals for a single trial from subject 4. **A.** upper 2 traces show 2-dimensional path of LED attached to the fingertip and 2-dimensional thumb tip path derived from the TH position signal measured with the planar electrogoniometer (see METHODS). Both paths are portrayed as occurring in the same plane: start positions are indicated by crosses; arrows indicate direction of movement toward contact. Spatial relation of finger path to thumb path is approximate. Remaining four traces: corresponding angular position signals from PIP, MP, and TH, and contact force signal, respectively. **B.** upper 2 traces, instantaneous tangential velocity (speed) profiles of finger and thumb trajectories (positive values assigned in the direction for contact). Three remaining signals, angular velocity profiles of PIP and MP, and interdigit speed profile, respectively. **Lowest** trace obtained by calculating vector difference of the instantaneous tangential velocity profiles of the thumb and fingertip trajectories.
force from a typical trial are shown in Fig. 2A. All subjects showed several consistent patterns in these movements. As illustrated in Fig. 2A, the duration of the rapid pinch gesture was \( \sim 90 \text{ ms} \), and subjects typically maintained the finger-thumb contact (as evidenced in the force trace) for an additional 100 ms. The paths of the distal thumb and finger pulps were curved slightly and smooth; e.g., there were no abrupt changes in the direction of the finger. The movements of the thumb and finger yielded a pinch force signal with a peak that was achieved at the peak angular position of the joints and likewise reflected no terminal corrections. Consistent with hand path trajectories for multijoint arm movements, the fingertip and thumb tangential velocities increased smoothly to single peaks (Fig. 2B). Likewise, the PIP and MP finger joints were characterized by a smoothly increasing angular velocity with a single peak. Finally, the net closing trajectory of the tip of the finger and thumb, which is the significant resultant motor output for this three-joint task, also manifests a single peak in its velocity profile (see Fig. 2B). This was calculated from the vector differences of the thumb and finger trajectories. This latter kinematic measure, the net result of the three-joint action studied, is analogous functionally to the hand trajectories described by Morasso (57), Abend et al. (3), and others.

In all subjects the magnitude of the constituent joint rotations varied from trial to trial. This variability is illustrated in Fig. 3 by a representative set of contact force, MP, PIP, and TH signals for multiple trials from subject 4. For all subjects the standard deviations of the PIP, MP, and TH joint peak angular positions averaged 4.3, 2.0, and 4.7°, respectively, and were similar across subjects. The ranges of peak angular position (difference between the minimum and maximum position) averaged across subjects were 20°, 10°, and 21° for the PIP, MP, and TH joints, respectively. Likewise, across subjects the mean range of the finger path distance was 14 mm (28% of the total amplitude), and the standard deviation was 5 mm. The path of the thumb had a range of 13 mm or 93% of the total amplitude with a standard deviation of 2 mm. Of the total distance traveled by the thumb and finger (from the point of movement onset to contact onset), the average thumb contribution was \( \sim 20\% \), and the average finger contribution was \( \sim 80\% \).

Although no instructions were given regarding relative speed or degree of thumb and fingertip movements, and despite the difference in the distances moved, the mean durations for thumb and fingertip movement were not different for three of the subjects (\( t \) tests, \( P > 0.5 \)) and varied by only 5 ms for the fourth subject. By contrast, the mean durations for MP and/or PIP joint movements were shorter than those of the TH or the fingertip path for all subjects (\( t \) tests, \( P < 0.05 \)). The variability in the amplitude and duration of the individual joint movements is in striking contrast with the nearly equal durations of fingertip and thumb movements; these kinematic patterns appear to indicate that control of these individual joints is subordinate to the control of the combined multijoint action.

The variability in the peak angular positions of the constituent finger and thumb joints at contact yielded corresponding variation in the thumb and fingertip positions in two-dimensional space. Figure 4A illustrates the variability of the spatial positions of the fingertip
FIG. 4. **Top:** positions of fingertip LED at thumb-finger contact (closed circles) and range of thumb tip positions (open circles) at contact. Data in each panel are for all repetitions of the task by all subjects (S1–S4). **Bottom:** positions of the tip of the finger and thumb at contact and associated paths for 3 trials (a, b, c), illustrating the covariable relation of the finger and thumb paths and the divergence of finger paths.

LED (filled circles) and the corresponding range of thumb tip positions (along the thumb paths; open circles) at the time of contact for each subject. As illustrated in Fig. 4B, the fingertip moved from right to left to the indicated end-path positions, and the thumb tip moved from left to right along the indicated path. The distance between extreme end-path positions of the finger shown in Fig. 4A ranged from 9.0 to 11.5 mm across the four subjects, and the thumb range was from 10.0 to 12.5 mm. Whereas the thumb tip was constrained to follow an arc of constant radius, the finger paths diverged to the indicated end points. Significantly, as illustrated in Fig. 4B, finger-path variation was not random but was covariable with the position of the tip of the thumb in achieving contact. Specifically, for instances of relatively larger or smaller peak thumb flexions (e.g., points c and a, respectively), the distal thumb pulp was positioned on an arc closer to or farther away from the palm. In complementary fashion, the tip of the finger traveled correspondingly different trajectories (paths a, b, and c) to follow the path of the thumb. As a result, the finger-path end points plotted in Fig. 4A show a prominent major axis oriented along the path described by the thumb tip.

This reciprocal positioning of the thumb tip and fingertips at contact was confirmed by examining the relations among the constituent joint positions. As shown in Fig. 5, with variations in TH flexion, the thumb tip is positioned along an arc at varying distances from the MP joint; i.e., with smaller TH flexions, the distance (d, d') from the MP joint to the thumb tip will be greater and vice versa. Based on the geometry of the two-joint finger, the distance from the fingertip to the MP joint can change in a like manner only with alterations in the angular position of the PIP joint. That is, changes limited to increased MP flexion in response to reduced TH flexion do not increase the finger length; MP flexion can only increase the rotation of the fingertip about the MP joint axis with a constant radius. The il-
A covariable relation between the positioning of the thumb and finger path endpoints will be manifest as a direct relation between the angular positions of the TH and PIP joints at contact. Distance \( d \) from thumb tip to MP joint will change with different TH angular positions. For example, reductions in TH flexion (arrow) will increase \( d \) to \( d' \). Distance from fingertip to MP joint can change only by changing PIP angular position, with \( d \) increasing with reductions in PIP (arrow). MP joint provides rotation to bring the finger tip into contact with the thumb, with, e.g., reduced PIP flexion requiring increased MP rotation (arrow).

Illustration in Fig. 5 thus implies that reduced thumb flexion should cause a corresponding reduction in PIP flexion. As shown in Fig. 6, this direct relation between the PIP and TH joint angular positions at contact was observed in all four subjects including subject 4, whose range of TH movement variation was much less than that of the other subjects. These data support the interpretation that trial-to-trial variations in thumb and fingertip positions (illustrated in Fig. 4A) tended to be patterned reciprocally. The direct relations between the PIP and TH also suggest a reciprocal relation between the PIP and MP joint positions at contact. That is, reductions in both TH and PIP flexion would, in turn, require increased MP joint flexion to bring the more extended fingertip into contact with the thumb anywhere along its length. Reciprocal relations between the PIP and MP joint positions at contact were observed. The Pearson product moment correlations between the MP and PIP joint angular positions at contact were \(-0.698\), \(-0.664\), \(-0.688\), and \(-0.863\) for the four subjects.

The functional significance of these MP-PIP-TH tradeoffs can be explored schematically by examining the joint configurations and resultant thumb tip and fingertip positions.

**Fig. 5.** Schematic representation of a 2-joint finger and 1-joint thumb illustrating that a covariable relation between the positioning of the thumb and finger path endpoints will be manifest as a direct relation between the angular positions of the TH and PIP joints at contact. Distance \( d \) from thumb tip to MP joint will change with different TH angular positions. For example, reductions in TH flexion (arrow) will increase \( d \) to \( d' \). Distance from fingertip to MP joint can change only by changing PIP angular position, with \( d \) increasing with reductions in PIP (arrow). MP joint provides rotation to bring the finger tip into contact with the thumb, with, e.g., reduced PIP flexion requiring increased MP rotation (arrow).

**Fig. 6.** Angular positions of PIP joint at thumb-finger contact plotted against TH position for the 4 subjects (S1–S4). Pearson product moment correlation coefficients \( r \) indicated in upper left corner of each plot.
FIG. 7. Schematic representation of 2-joint finger and 1-joint thumb system illustrating how the observed relations among joint angular positions at contact act to yield more distal sites of contact and thus minimize variations in the point of finger contact on the thumb. A: configuration of joint angles for thumb-finger contact at the distal surfaces with a large peak flexion of the thumb. B: hypothetical configuration (solid lines) showing that point of contact would be away from the distal thumb surface for instances of small TH flexion if PIP remained the same as for A (dashed lines) even with MP flexion increasing. C: observed reciprocal action of MP and PIP joints for instances of small TH flexion; i.e., PIP is reduced (A; dashed lines) and accompanied by a reciprocal increase in MP (A; dashed lines).

FIG. 8. Finger and thumb tip speeds and corresponding contact force signal from subject 2. Dashed line indicates approximate onset of finger-thumb contact.
TABLE 1. Pearson product moment correlation coefficients for path distance and peak speed for fingertip and movement amplitude and peak velocity for TH, PIP, and MP for all four subjects

<table>
<thead>
<tr>
<th>Subj. No.</th>
<th>Finger</th>
<th>TH</th>
<th>PIP</th>
<th>MP</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.592</td>
<td>0.751</td>
<td>0.554</td>
<td>0.751</td>
<td>25</td>
</tr>
<tr>
<td>2</td>
<td>0.632</td>
<td>0.760</td>
<td>0.447</td>
<td>0.619</td>
<td>39</td>
</tr>
<tr>
<td>3</td>
<td>0.876</td>
<td>0.841</td>
<td>0.789</td>
<td>0.577</td>
<td>25</td>
</tr>
<tr>
<td>4</td>
<td>0.803</td>
<td>0.847</td>
<td>0.431</td>
<td>0.590</td>
<td>63</td>
</tr>
</tbody>
</table>

n, no. for which correlations were computed; TH, interphalangeal joint; PIP, proximal interphalangeal; MP, metacarpophalangeal.

Contact force goal was not due to oppositional mechanical factors (saturation) but was the direct result of controlled digit movements. As shown in Fig. 8, contact of the thumb and finger, reflected in the onset of the pinch force, occurred during deceleration of the thumb and finger for all subjects. These data also indicate that contact force was not due to delayed corrective actions after contact. Indeed, the instructions to the subjects to produce the force target via a single tap of the thumb and index finger were intended to achieve continuity between the movement and contact force production. In this vein, although the task goal may not have involved control of position per se, the objective may have been to achieve contact at a time associated with the appropriate net velocity of the thumb and finger.

Additional observations indicating that the kinematic patterns observed are inherent components of an active control process are the relations between the magnitudes and velocities of the finger and thumb joint rotations. That is, the variations in movement amplitude were accompanied by proportional changes in peak velocity. Across subjects, the peak fingertip and thumb tip velocities averaged $118 \pm 21$ (SD) and $21 \pm 6$ cm/s, respectively. The peak joint angular velocities averaged $609 \pm$
139 (SD) and 509 ± 84°/s for the PIP and MP joints, respectively. The Pearson product moment correlation coefficients of the amplitude and peak velocities for the fingertip trajectories and the individual joint rotations for all subjects are summarized in Table 1. As is apparent, high positive correlations between peak amplitude and peak velocity were manifest regularly for the MP and PIP joint rotations, as well as for the finger and thumb trajectories. Note that the correlations in Table 1 were computed for each subject from a subset of all trials in which movement starting positions were highly consistent and, as such, amplitude variations were due solely to changes in the terminal positions of the joints. Thus, these latter data further indicate that the patterned variations in final position of the thumb and finger as well as their constituent joint rotations were intended at some level of movement production and not due solely to the oppositional requirements of the task.

As noted, a second alternative to active control of distal digit contact is that the MP and PIP joints were constrained biomechanically to interact in a reciprocal manner. If such constraints were operating, one might expect MP-PIP instantaneous joint velocities also to manifest consistent covariant properties during the course of movement. However, as illustrated in Fig. 9, the relation between the instantaneous angular velocities of MP and PIP rotation is not consistent, as has been reported in analyses of shoulder-elbow joint interactions (65). Indeed, in subjects 1 and 2, the trial-to-trial variations in the magnitude and timing relations of these PIP and MP velocity profiles yielded reversals in the directions of these loops, as shown (open vs. closed arrows). The data plotted for subjects 3 and 4 were from sequential trials, further indicating the absence of stereotyped position coupling between the PIP and MP joints.

DISCUSSION

The hand's multiarticulate prehensile actions permit the acquisition or grasp of objects as well as active exploration, manipulation, and stabilization of those objects within the grasp. The present study, although limited to finger-thumb grasp movements at three of a possible 16 joints, provides some insights into the control of this specialized motor apparatus. To evaluate this control, consider initially those features that were constant, those that were varied, and the manner of those variations.

Active control of invariant features of grasp

The major consistent kinematic feature for these rapid finger-thumb grasping movements was a robust and seemingly natural preference for finger-thumb contact at the more distal surfaces of the two digits. Paradoxically, with the exception of the single-peaked shapes of the joint angle and digit trajectory velocity profiles, almost all of the other kinematic parameters varied considerably across trials, including the fingertip position in space at contact, the distances traveled by the finger and thumb, the specific finger trajectories, the peak finger and thumb tangential velocities, and the magnitude and peak velocity of individual joint rotations. The manner in which such seemingly paradoxical invariance and variability operate provides insight into motor planning and control of these hand movements.

One explanation for the generation of acceptable thumb-finger contact force by variable finger and thumb movements is that these two components of the rapid pinch task were controlled independently. Contrary to this interpretation, evidence did not show either kinematic or contact force adjustments occurring after the time of contact. Moreover, the digit paths were characterized by a single peak in their tangential velocities. Even with a limited amount of training, subjects apparently were able to program these basic appositional movements and an acceptable contact force as a single smooth action. This observation implies that even several distinct subobjectives of a complex motor function can be unified to form a single, de novo gesture. Furthermore, although the force of contact presumably was related to the net speed of the two digits at the time of contact, the peak rates of the individual joint rotations varied. Despite these variations, there was evidence for temporal regulation in the generation of contact force: 1) finger-thumb contact occurred consistently from 20 to 30 ms after the peak velocities of both the finger and thumb trajectories, apparently reflecting prediction of the requisite time of contact; and 2) in any given trial the durations of the individual finger joint rotations differed
from the duration of the fingertip movement, although the durations of fingertip and the thumb tip movement were almost identical. Obviously, the durations of constituent MP and PIP joint movement were combined to yield a fingertip movement that was matched in duration to the movement of the thumb.

Consideration of the manner in which the finger-thumb contact was made at the distal surfaces, despite variations in the constituent joints, also offers insight into the control of this task. As was shown, with natural trial-to-trial variations in the magnitude of TH flexions, finger trajectories were adjusted in a complementary manner. These trajectory adjustments minimized variation of the site of fingertip contact on the thumb with apparent preference for a distal site of contact. The adjustments in finger trajectory were accomplished by reciprocal PIP and MP joint actions yielding the necessary combined rotation and translation of the fingertip. To fully interpret the significance of this pattern, it is important to ascertain that the observed reciprocal relation of peak MP-PIP angular position was under active control.

One explanation is that the reduced PIP flexion and the increased MP flexion associated with reduced TH flexion were not independent but rather were due to muscle and link interaction torques acting simultaneously to flex the MP joint and to exert net extensor torques on the PIP joint. Indeed, polyarticular muscle-tendon arrangements dominate the hand, and a muscle such as the volar interosseous may be situated to provide such reciprocal MP-PIP position coupling (73). However, for this grasp task, the instantaneous rotation rates of the MP and PIP joints were not codependent. This observation suggests that a source of additional net PIP extensor torque can be adjusted with some independence from MP flexion torques. Critically, the first lumbrical muscle, observed to be active for rapid pinch (Cole, unpublished observation) has been suggested to be capable of supplying extensor torque to the finger IP joints without increasing MP flexion torques over nearly the entire range of MP joint positions (70). By contrast, lumbrical electromyograms are conspicuously silent for digit flexion that does not require accurate positioning of the fingertip in the middle of the workspace, viz., for touching the finger to the palm (12, 51).

Taken together, these considerations indicate that finger-thumb contact at the distal pulps may involve partly independent adjustments of MP and PIP angular positions. In rapid precision grasp, these adjustments apparently are implemented to compensate for natural variations in TH rotation.

Preference for distal finger-thumb contact is consistent with the somatic sensory characteristics of the hand. That is, the distal digit pulps are more densely innervated than the remainder of the hand by mechanoreceptors that have small well-defined receptive fields (34). Similarly, in humans and in monkeys precision grasp is particularly dependent on the integrity of these sensory inputs (26, 35).

In some respects, the finger-thumb kinematic adjustments underlying contact at the sensitive distal surfaces are analogous to eye and head movements directed at positioning the visual target on the fovea of the retina. In the present experiment, this result is all the more remarkable inasmuch as subject instructions did not incorporate any indication as to where contact was to be made on the thumb.

Although the magnitudes of the individual joint rotations and the finger and thumb paths varied considerably in the present experiment, it obviously would be inappropriate to suggest that these kinematic variables were not influenced by movement planning. In particular, across trials there was a consistent relation between the amplitudes of those movements and their peak velocities. This observation indicates that the observed variations in joint angles and finger paths were controlled, although at a level that was subordinate to the site of that contact. In general, movement velocity increases when subjects are instructed to move rapidly to targets of greater distances (17, 24). These relations also have been observed for the path segments comprising curved trajectories in handwriting and arm reaching (23, 75) and for the oral movements of speech (38, 39, 68). As in handwriting, speech movement amplitude variations are implicit in the motor task. In the present study, variations in movement amplitude also were a natural aspect of the more general motor objective. The fact that velocity rather than movement duration increased in proportion to movement amplitude indicates a time-critical nature to the task, as...
indicated also from the timing of finger-thumb contact relative to peak digit velocities. These data, and those from other movements, suggest that positive correlations between velocity and amplitude may be a feature in the generation of many movements.

**Motor equivalence in hand kinematics**

The present data permit one to consider some characteristics of transforming a planned goal into the necessary joint torques. This transformation must account for the fundamental observation of motor equivalence in the present experiment; namely, a distal finger-thumb contact site that was achieved by variable actions at the individual joints. In essence, motor equivalence constitutes covariable patterning of the mechanical degrees of freedom that appear to be redundant in achievement of a particular goal. Motor systems with such apparent redundancies have been described as overcomplete (59) or overspecified (37). Although previous authors have identified these apparent redundancies as a potential complication (7, 72) or benefit (27, 37, 6) to motor control, motor equivalence has not been given much experimental attention (however, see Refs. 32, 41). The presumed value of exploiting such redundancies is that movement goals can be achieved nonstereotypically, and thus the control process may more easily accommodate changes in load, changes in muscle status (e.g., fatigue), or errors from any source that develop during the evolving movement (2, 22).

One possible mechanism for implementing motor equivalence variations may involve use of afferent information to adjust the constituent movements of a multiarticulate action (1, 2). Recent studies have documented that thumb perturbations during rapid thumb-finger pinch actions (the task in this study) yield both autogenic and nonautogenic compensatory adjustments of the finger (20, 16). In these experiments, the kinematic responses of the finger were combined with those of the thumb to yield a three-degree-of-freedom compensation for the load disturbances of thumb movement, thus exploiting the system's redundant degrees of freedom. Importantly, these compensations mirrored the motor equivalence patterns observed in the present study. Obviously, these data on sensorimotor contributions are not decisive; control processes operating independent of peripheral afferent information may be a major contributor to motor equivalence adjustments.

Aside from the underlying mechanisms, the observation that motor equivalence variation in multiarticulate movement control is a systematic phenomenon seemingly is inconsistent with recent control models derived from proximal arm studies (23, 57). That is, it is not clear how those recent models accommodate substantial and systematic motor equivalence variations. For example, trajectory specification may not greatly simplify the motor planning process if trajectories are adjusted systematically (as in the present study) in successful repetitions of the same motor task. A new trajectory or plan would have to be generated afresh for each iteration with task-related variations in the rules (23, 27). Alternative explanations for these variations have been brief and focused on the possibilities that 1) there is variability or random error in translation of the motor plan into muscle activity (23, 37) or 2) there are differences in subject perception of the task or target (23). It has also been suggested that motor equivalence may reflect the learning process of trajectory formation rules (27); however, motor equivalence is not limited to unpracticed actions (32).

The apparent inconsistencies between the data presented here and earlier studies may be related to differences between the proximal arm, the orofacial system, and the hand. The neurophysiological processes underlying control of these various muscle groups are different in many ways (48, 49, 54, 55, 61). Also, the motor task in the present experiment was different in several major respects from tasks studied in experiments on the proximal arm. In particular, the prespecified goal in the rapid pinch task did not involve a spatial target per se. The biomechanical constraints of grasp also differ from those of the proximal arm in that the fingers and thumb are substantially decoupled during closing movements, precluding their interaction. Aside from the source of the apparent differences between the present observations and those on proximal arm movements, these considerations may suggest that the models derived from analyses of the proximal arm cannot be generalized to different systems and different tasks.
Characteristics of motor planning

Based on interpretations from kinematic investigations of arm movement (29, 57), the results from the present experiment suggest that contact of the finger and thumb at the distal surfaces is near the top of the motor planning hierarchy for this task. That is, the constituent movements of the grasp, each alone showing substantial variation, combined in a manner to minimize variation in the site of finger-thumb contact. The relatively more variable kinematic parameters would appear to be specified subordinately. Because the movements in the present experiment were initiated from a single position to targets in a somewhat restricted area of the thumb-finger work space, regularities in finger and thumb kinematics such as single-peaked velocity profiles are difficult to assess in relation to arm-reaching studies. Nevertheless, these data on digit kinematics provide other insights into the nature of the motor planning process.

Regularities in hand trajectories for two-joint arm-reaching movements have been interpreted as indicative of movement planning in terms of the trajectories rather than the individual joint angles (3, 6, 57). A spatial command language has been hypothesized involving mechanisms to transform spatial commands into the requisite joint torque and movement specifications (6) or to define a “virtual trajectory” of equilibrium points of the arm (11, 28). This hypothesized spatial coding and planning is consistent with theoretical suggestions by Bernstein (8) and Lashley (45). Although the results from this study support the arguments that joint angle rotations and muscle contractions are specified in a fashion that is subordinate to the resultant movement goals (6, 30, 57), they raise questions regarding the planning of movement in a spatial domain. That is, for repeated trials of the pinch task, variability was considerable in the final spatial positions of both the fingertip and thumb and, hence, also variability in the spatial location at which these two digits made contact. Obviously, these digit movements were not generated consistently in relation to a spatial reference within the hand or to any portion of the body. Based on this variability and the tendency for finger-thumb contact at the distal digit surfaces, one must question whether spatial coding is functional as a basis for movement planning.

One possibility is that the first level of motor planning is not restricted to any single motor domain (e.g., spatial, temporal, or spatial-temporal) but instead varies in a manner that is wholly task specific. At some level such task specificity almost certainly operates. It does not require experimental data to argue that the highest level of the motor planning hierarchy consists of an intention to accomplish a particular objective, at least for so-called voluntary movements. However, if this is the only level of the motor control hierarchy above the processes of motor execution, the insights for motor planning and the generality implicit in the suggestions of Bernstein (8) and Lashley (45) clearly are lost.

A viable and still general alternative to spatial command codes or to variable task-dependent goals for motor planning may be in the sensory realm. Subjects in the present experiment consistently and naturally made finger-thumb contact on the distal somatic sensory surfaces without instructions to do so and independent of any consistent spatial reference. This contact, although varying significantly in the spatial coordinates at which it occurred, consistently excited a limited set of peripheral receptive fields. It thus seems reasonable to suggest that a more universal domain for the first level of motor planning is in terms of the multimodal sensory experience associated with successful accomplishment of intended motor tasks (cf. Refs. 4, 60). The planning of motor goals in terms of sensory consequences is fundamentally pragmatic and task specific and would appear to have the prerequisites for planning as well as learning almost all voluntary movements. To this point, for speech the planned motor goals are not absolute positions of the tongue, jaw, or lips or even stereotypic shapes of the oral-pharyngeal cavity, but particular acoustic patterns that correspond to auditory-perceptual categories of human speakers and listeners (42, 62). Similarly, in movements of the head and eyes, the significant goal is reception of light from an object on a sensitive region of the retina (63) in the same way as movements of the head and pinna in auditory localization are aimed at the reception of a difference in sound between the ears.
Thus, in two-joint arm-reaching tasks, sensory-based motor planning would be in terms of the somatic sensory and visual correlates of the hand position in space, independent of the combination of joint rotations involved in achieving that position. Costanzo and Gardner (18) reported convergence of afferent input to somatic sensory cortex that reflects hand position independent of individual joint angles. Moreover, areas of posterior parietal cortex receive similar converging somatic sensory input and associated visual information (53). Motor planning in sensory terms also permits one to consider how observed adjustments among the constituent elements in a multijoint motor action are scaled appropriately in relation to the combined movement goal (2). Namely, within a time frame allotted by the speed of the action, sensory input from the evolving multijoint movement may be processed comparatively relative to the sensory-based motor plan; moment-to-moment adjustments then can be distributed among the available elements in an appropriate task-dependent fashion.

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REFERENCES


