Human Finger Independence: Limitations due to Passive Mechanical Coupling Versus Active Neuromuscular Control

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Submitted 10 May 2004; accepted in final form 20 June 2004

Lang, Catherine E. and Marc H. Schieber. Human finger independence: limitations due to passive mechanical coupling versus active neuromuscular control. J Neurophysiol 92: 2802–2810, 2004. First published June 22, 2004; 10.1152/jn.00480.2004. We studied the extent to which mechanical coupling and neuromuscular control limit finger independence by studying passive and active individuated finger movements in healthy adults. For passive movements, subjects relaxed while each finger was rotated into flexion and extension by a custom-built device. For active movements, subjects moved each finger into flexion and extension while attempting to keep the other, noninstructed fingers still. Active movements were performed through approximately the same joint excursions and at approximately the same speeds as the passive movements. We quantified how mechanical coupling limited finger independence from the passive movements, and quantified how neuromuscular control limited finger independence using an analysis that subtracted the indices obtained in the passive condition from those obtained in the active condition. Finger independence was generally similar during passive and active movements, but showed a trend toward less independence in the middle, ring, and little fingers during active, large-arc movements. Mechanical coupling limited the independence of the index, middle, and ring fingers to the greatest degree, followed by the little finger, and placed only negligible limitations on the independence of the thumb. In contrast, neuromuscular control primarily limited the independence of the ring, and little fingers during large-arc movements, and had minimal effects on the other fingers, especially during small-arc movements. For the movement conditions tested here, mechanical coupling between the fingers appears to be a major factor limiting the complete independence of finger movement.

INTRODUCTION

The motor cortex and the corticospinal tract are crucial for the control of relatively independent finger movements (Lawrence and Kuypers 1968; Porter and Lemon 1993). The convergence and divergence of motor cortical cells onto the spinal motor- and inter-neurons affords the ability to selectively activate groups of muscles to perform complex finger movements. Despite this highly evolved control system, humans cannot move their fingers completely independently (Hagar-Ross and Schieber 2000) nor can they produce completely independent finger forces (Li et al. 1998a,b; Reilly and Hammond 2000).

In part, this lack of complete independence may arise from the corticospinal system itself. Synchronous firing of motor cortical cells (Baker et al. 1999; Matsumura et al. 1996) and the divergence of single motor cortical neurons to multiple spinal motoneuron pools (Buys et al. 1986; Fetz and Cheney 1980; McKiernan et al. 1998; Shinoda et al. 1981) result in common input to multiple muscles that move separate fingers, and could thereby limit complete finger independence. Short-term synchronization between pairs of motor units in different single-tendoned finger muscles (Bremner et al. 1991) and between different regions of multitenoned finger muscles (Keen and Fuglevand 2004a; Reilly et al. 2003; Winges et al. 2003) suggests that the motor cortex does not have completely independent access to move each finger. Active movement at one finger therefore may result in some movement at another finger.

Another factor contributing to the lack of complete independence in human finger movements is mechanical coupling produced passively by the architecture of the hand and forearm. In the hand, the fingers are coupled by the soft tissues of the web space, by the juncturae tendinum, which connect the extensor tendons on the dorsum of the hand (Von Schroeder et al. 1987). In the forearm, the fingers are further coupled by tendinous cross-connections between the flexor digitorum profundus tendons in the palm (Malerich et al. 1990), and by inconsistent tendinous slips that connect the flexor digitorum superficialis (Brand and Hollister 1993). Because of this mechanical coupling, passively imposed movement at one finger can produce movement at other fingers. Mechanical coupling therefore may be a major reason for the human inability to move the fingers completely independently.

We studied the extent to which mechanical coupling and neuromuscular control limit finger independence by studying passive and active individuated finger movements. Passive and active movements were examined using both large and small arcs to determine whether the magnitude of mechanical coupling depended on the range through which the joints rotated. We determined how much mechanical coupling limited finger independence in passive individuated movements, and then determined how much neuromuscular control limited finger independence using an analysis that subtracted the passive condition from the active condition. Given the complexity of the architecture of the hand and the complexity of the corticospinal system that controls it, we hypothesized that both mechanical coupling and neuromuscular control would limit finger independence and that their effects would be different across the 5 fingers.
METHODS

Subjects

Ten healthy, right-handed subjects (6 female, 4 male, age range 19–45 yr) participated in this study. None of the subjects had any history of neurological or orthopedic conditions that affected their hands or arms. The study protocol was approved by the Research Subjects Review Board of the University of Rochester Medical Center, Rochester, NY. Informed consent was obtained from all subjects before participation.

Experimental paradigm

We studied passive and active individuated finger movements in each subject. A custom-built device (Fig. 1) was used to passively rotate each finger, one at a time, around its metacarpophalangeal (MCP) joint axis. The device consisted of a computer-driven synchronous stepping motor (Superior Electronic, Bristol, CT) driven by a Micro stepping motor drive (Pacific Scientific, Wilmington, MA). The motor rotated a vertical shaft to which one finger at a time was attached by a C-arm paddle. The bottom, horizontal limb of the C-arm paddle (not visible in Fig. 1) ran from the shaft of the motor to the vertical limb of the C (vertical shaft in Fig. 1). The finger was attached to a paddle that formed the top, horizontal limb of the C, thus allowing the finger to rotate around its MCP axis. The finger was secured to the paddle from just distal to the MCP joint out to the fingertip on its palm surface. The proximal interphalangeal (PIP) and distal interphalangeal (DIP) joints of the instructed finger were fixed to the paddle in full extension during the movements. The position of the paddle could be adjusted vertically and horizontally to fit the height and length of each finger. The motor, shaft, and paddle were mounted on a stage that could be translated in 2 horizontal dimensions to align the paddle axis of rotation with the axis of rotation for each MCP joint. A rotational position encoder (U.S. Digital, Vancouver, WA) coupled to the vertical shaft measured the rotation of the motor and the corresponding angle of the MCP joint.

Subjects were seated beside a table with the shoulder in approximately 30° of flexion and 20° of abduction, and with the elbow flexed to about 60°. The forearm (in neutral pronation/supination) and wrist (in neutral flexion/extension) were stabilized in a vacuum cast (VersaForm, Sammons Preston, Bolingbrook, IL) attached to the metal forearm support on the device. An instrumented glove (CyberGlove, Virtual Technologies, Palo Alto, CA) was used to measure joint angles of all the fingers. Before testing, glove sensor output and goniometric joint measurements were obtained in standard positions to calibrate the glove sensors for each tested hand (Haggar-Ross and Schieber 2000). During passive movements, surface electromyograms (EMGs) were monitored and recorded from 3 extrinsic finger muscles to ensure that subjects did not assist the movement of the device and that passive movements did not evoke stretch reflexes. Disposable electrodes, 10 mm in diameter (VerMed, Bellows Falls, VT), were placed in bipolar configurations over the radial portion of extensor digitorum communis, the ulnar aspect of the flexor digitorum profundus, and the volar aspect of the flexor digitorum superficialis. EMG activity was amplified by a factor of 5,000–20,000 to produce a signal that fell within a ±5-V range. Spike2 software and a Micro 1401 interface (Cambridge Electronic Design, Cambridge, UK) were used to collect glove data, shaft rotational position data, and surface EMG simultaneously. Each glove sensor was sampled at the maximum rate of 78 Hz, shaft position data were sampled at the same 78 Hz, and EMG was sampled at 1,000 Hz.

For clarity, we hereafter refer to the tested finger as the instructed finger. In the passive condition, the instructed finger was secured to the paddle with self-adhesive wrap (Coban, Andover, Salisbury MA), such that rotation of the motor produced matching rotation at the MCP joint, with the PIP and DIP joints held in full extension against the paddle (Fig. 1, bottom left). The self-adhesive wrap was used to hold the finger firmly to the paddle and was more comfortable for the subject than rigid fixation methods. Each finger was secured to the paddle, one at a time, and rotated into flexion and extension at 20°/s. EMG recordings confirmed that stretch reflexes were not evoked at this slow angular velocity. Each instructed finger was moved through 2 ranges of MCP joint position, a large-arc and a small-arc range, where the range of the small arc was one half of the range of the large arc (Fig. 2A). The instructed MCP starting position was 0° for the large-arc range and 20° for the small-arc range for the 2nd to 5th fingers, and was 10° for both thumb ranges. Measured starting positions calculated off-line ranged from −5 to 6° for the large-arc range and 17 to 25° for the small-arc movements for the 2nd to 5th fingers, and 4 to 13° for both thumb ranges. Measured starting positions and joint excursion values (see Fig. 2A) indicated that individuated movements tested here were in MCP joint ranges typically used for normal finger movement, and not at the extremes of available motion. The large-arc range initially was set to 80° for the 2nd to 5th fingers, which represents about 75% of the available range of movement at the MCP joint. The initial large-arc range for the thumb MCP was set to 40°. Because subjects often had difficulty actively moving some fingers through this range in the experimental apparatus, the tested ranges were adjusted for each finger by reducing the required arc until the subject could do the task comfortably. In this manner, we ensured that the range used in the passive condition matched the range through which that finger would move in the active condition. In the passive condition, subjects were told to “relax the muscles in their hand and arm” and “to let the machine move the fingers” for each 30-s trial. EMG recordings were monitored during each trial. Any trial in which muscle activity was detected was aborted and the trial was redone. Subjects did not have difficulty relaxing, however, because <2% of trials had to be aborted.

In the active condition, the instructed finger was again splinted with the self-adhesive wrap to the paddle that was detached from the C-arm and shaft (Fig. 1, bottom right). With their forearm and wrist secured in the device and visual targets placed at the ends of the large- or small-arc range, subjects were told to actively rotate the instructed finger at the MCP joint, back and forth between the 2 targets, at the same rate at which the finger had moved in the passive condition, while trying to keep the other, noninstructed fingers still. Before recording a 30-s trial, subjects were given time to familiarize them-
Joint excursions values were used to derive 3 measures: the individuation index (II), the passive contribution index (PCI), and the active contribution index (ACI). The individuation index is a measure of how well a finger is able to move independently, that is, without the other fingers moving (Lang and Schieber 2003; Schieber 1991), and it was used to quantify the independence of the instructed finger in each trial, in each condition. Although we have previously used relative fingertip path distances to compute IIs (Lang and Schieber 2003), this method was not appropriate in the current experimental paradigm because the instructed digit was constrained to rotate at only the MCP joint. Rotating the thumb at the MCP joint, compared with the carpometacarpal joint as we did previously, substantially shortens the fingertip path of the thumb compared with the other 4 fingers. If we had calculated IIs using fingertip path distances, the relative motion of the thumb would have been artificially inflated compared with relative movement of the other fingers, resulting in indices that would not have reflected the observed movement accurately. We therefore calculated an II using joint angular excursions. Here, the II was calculated as 1 minus the relative joint excursions in the noninstructed fingers, or

\[ II = 1 - \left( \frac{E_{\text{noninstructed}}}{E_{\text{instructed}}} \right) \]

where \( E_{\text{noninstructed}} \) is the average joint excursion of all the joints (MCP, PIP, DIP) of the noninstructed fingers, and \( E_{\text{instructed}} \) is the average joint excursion of all the joints of the instructed finger. MCP joint excursion generally accounted for virtually all of \( E_{\text{instructed}} \) because the instructed finger PIP and DIP joints were constrained by the paddle. Because it was possible that the inclusion of all 3 joints in \( E_{\text{instructed}} \) might dilute the values of the IIs, we did an additional analysis computing IIs using only the MCP joint excursion in \( E_{\text{instructed}} \). This analysis produced similar results and is therefore not presented further. The II will be close to 1 for an ideally individuated movement in which the instructed finger moved with no movement of noninstructed fingers and closer to 0 the more noninstructed finger movement occurred simultaneously with instructed finger movement.

To quantify how mechanical coupling limited finger independence, we derived a PCI for each instructed finger from the joint excursion values in the passive condition. The PCI was calculated as the average angular excursion of the joints of the noninstructed fingers expressed as a fraction of the average excursion of the joints (chiefly the MCP) of the instructed finger, or

\[ PCI = \frac{E_{\text{instructed}}}{E_{\text{noninstructed}}} \]

The PCI will be 0 if the noninstructed fingers remained motionless and will increase with increasing movement of the noninstructed fingers in the passive condition.

To quantify how neuromuscular control limited finger independence, we derived an ACI for each finger using joint excursion values from the passive and active conditions. The ACI was calculated as the relative excursion of the joints of the noninstructed fingers in the active condition minus the PCI (i.e., minus the relative excursion of the joints in the noninstructed fingers in the passive condition) or

\[ ACI = \left( \frac{E_{\text{instructed}}}{E_{\text{noninstructed}}} \right) - PCI \]

The ACI will be 0 if the noninstructed fingers remained motionless or if they moved the same amount for both conditions. The ACI will increase as the movement of the noninstructed fingers increases in the active condition beyond that observed in the passive condition.

Statistical comparisons across fingers, ranges (large arc vs. small arc), and conditions (passive vs. active) were performed with Statistica (Statsoft, Tulsa OK) and significance levels were set at \( P < 0.05 \).

To test whether ranges of movement were the same across conditions, MCP joint excursions of the instructed fingers were compared using a repeated-measures ANOVA with 2 within-group factors (finger, condition). Separate ANOVAs were performed on data from the small-arc...
trials and large-arc trials. To test whether the rate of movement was the same across conditions, we subtracted the average speed in the passive condition (which was fixed by the constant speed of the motor, with little variance) from the average speed of movement in the active condition, and this difference was compared with 0 using single sample t-test for each finger. To test whether finger independence was different for the passive versus active individuated finger movements, Is were compared using a repeated-measures ANOVA with 2 within-group factors (finger, condition), with separate ANOVAs used for large- and small-arc movements. To test whether passive limitations to finger independence were different from active limitations, PCIs and ACIs were compared using a repeated-measures ANOVA with 3 within-group factors (finger, range, condition). When significant main and interaction effects were found, post hoc t-tests were used to identify the sources of the differences more specifically.

RESULTS

Joint excursions and movement frequencies

Motion of each instructed digit was similar in the passive and active conditions. Although the instructed MCP joint excursion tended to be slightly larger in the active condition (Fig. 2A), no significant differences were found between the active and passive conditions for either the large-arc (main effect of condition P = 0.590) or the small-arc movements (main effect of condition P = 0.162). Consistent with the anatomical range of rotation at the thumb MCP joint (about 50°) compared with the other MCP joints (−100°), the excursion of the thumb MCP joint was approximately one half that of the other MCP joints during the large-arc movements (main effect of finger P = 0.002).

The MCP joint of each instructed finger also moved at similar speeds during the passive and active conditions (Fig. 2B). In the passive condition, for both large-arc and small-arc movements the device was programmed to move the MCP joint at a constant 20°/s, but the average speed was slightly less (19°/s) because of millisecond pauses as the device switched between flexion and extension phases. During the large-arc movements, we found no differences in average speeds between the passive and active conditions (P values >0.05 for all fingers). During the small-arc movements, average speeds in the passive and active conditions were the same for the index finger (P > 0.05) but were 6–11° slower in the active condition compared with the passive condition for the thumb, middle, ring, and little fingers (P < 0.05 for these 4 fingers).

Movement of joints of the noninstructed fingers and finger independence

Although motion of each instructed digit was similar in the passive and active conditions, movement in the noninstructed fingers varied depending on both the instructed finger and the condition. Figure 3 shows joint position traces during single trials of instructed movement at each finger during small-arc movements in the passive condition. Each column shows the motion that occurred in the joints of all fingers during a given instructed movement, whereas each row shows the motion that occurred at the joints of a given finger during all instructed movements. During passive instructed thumb movement (1st column), virtually no movement occurred in the joints of the noninstructed fingers. During passive instructed movements of the index, middle, ring, and little fingers (columns 2–5), noninstructed movement was seen most often in the MCP joints (solid line) of fingers adjacent to the instructed finger. Figure 4 shows similar data during single trials in the active condition. Just as in the passive condition, active movement of the thumb typically did not produce movement in joints of the noninstructed fingers, but during instructed movement of the other 4 fingers, noninstructed movement was seen most often in the

![Image](https://www.jn.org)
MCP joints of fingers adjacent to the instructed finger. Although this subject’s data are generally representative of the sample, note that during instructed ring-finger movement (4th column), the noninstructed joints moved more in the active condition (Fig. 4) than in the passive condition (Fig. 3). Across the sample, this was typical during instructed large-arc ring-finger movements, but not during instructed small-arc ring-finger movements.

The independence of each finger in the passive and active conditions was quantified using the individuation index, where an II of 1 represents a finger that moves with no movement of the other noninstructed fingers (see METHODS). For the large-arc (Fig. 5A) and small-arc movements (Fig. 5B), the group II values for the thumb were close to 1 in both the passive and the active conditions, indicating that the thumb moved completely independently during flexion–extension movements. The group II values of the index, middle, and ring fingers ranged from 0.84 to 0.90 in the passive condition, and from 0.81 to 0.87 in the active condition. For the little finger, the II values in the passive condition were 0.95 (large arc) and 0.96 (small arc) compared with 0.90 and 0.93, respectively, in the active condition. Comparing passive versus active individuation indices during the large-arc movements (Fig. 5A), we found a significant main effect of finger \( (P = 0.008) \) where the II of the thumb was greater than the II values of the other 4 fingers. The condition by finger interaction did not reach statistical significance \( (P = 0.076) \), yet a trend can be seen in the data, where the active IIs were lower than the passive IIs for the middle, ring, and little fingers. Comparing passive versus active IIs during the small-arc movements (Fig. 5B), we found a significant main effect of finger \( (P < 0.001) \) with the IIs of the thumb again being higher than the IIs of the other 4 fingers. Thus during both large- and small-arc movements, passive mechanical coupling appeared to account for most of the joint rotation in the noninstructed fingers. Active neuromuscular factors produced some additional joint motion in the more ulnar fingers during the active, large-arc movements.
Passive versus active limitations on finger independence

We quantified the limitations on finger independence by calculating passive (PCI) and active (ACI) contribution indices using the relative joint excursion values in the 2 conditions (see Methods). During both large-arc (Fig. 6A) and small-arc movements (Fig. 6B), the PCI and ACI of the thumb were negligible, as illustrated by SE bars that were equal to or larger than the group means. PCIs were greatest in the index, middle, and ring fingers, suggesting that a major reason for the lack of independence in these fingers is mechanical coupling between the fingers. The ACIs were greatest in the ring and little fingers during the large-arc movements and were generally more variable across subjects than the PCIs.

Using an overall repeated-measures ANOVA to look for differences between fingers, conditions, and ranges (large arc vs. small arc), we found a significant main effect of finger (P = 0.026), a significant finger × range interaction (P = 0.016), and a significant finger × condition × range interaction (P = 0.024). Further statistical testing to determine where the differences existed revealed the following. For both the large-arc and small-arc ranges, the PCIs of the index, middle, and ring fingers were greater than the PCIs of the thumb and little finger (P values <0.05). Additionally, the PCIs were not statistically different for the large-arc versus small-arc ranges (P = 0.324). ACIs of the ring and little fingers were larger than ACIs of the thumb, index, and middle fingers (P values <0.05) in the large-arc range, whereas in the small-arc range, ACIs were not statistically different across the fingers (P = 0.585). When comparing across the 2 ranges, ACIs were unchanged in the thumb, index, and middle fingers (P values >0.05), whereas ACIs of the ring and little fingers was reduced in the small-arc range compared with the large-arc range (P_{ring} = 0.009, P_{little} = 0.006).

Last, we considered the possibility that the instrumented glove itself was a source of passive coupling between the fingers. The sensors on the dorsum of the fingers make movements feel slightly more cumbersome and compression of the soft tissues by the elastic spandex glove may make the hand feel stiffer. We tested the coupling of the glove itself by measuring passive individuated movements while the glove was filled with stuffing instead of filled with a human hand. Independence of the stuffed fingers was complete in many trials and nearly complete in others with an average II of 0.991 ± 0.003 (range 0.982–1.0). PCIs were 0.009 ± 0.003 (range 0.0–0.018). Thus our PCI values may have overestimated the passive coupling that truly exists between the fingers by this small amount. ACI values would not be affected because they are calculated from a subtraction analyses.

**DISCUSSION**

We examined how mechanical coupling and neuromuscular control limited finger independence in humans by studying passive and active individuated movements. Finger independence was generally similar during passive and active movements, except for a noticeable trend toward less independence in the middle, ring, and little fingers during the active, large-arc movements. Mechanical coupling limited the independence of the index, middle, and ring fingers to the greatest degree, followed by the little finger, and placed only negligible limitations on the independence of the thumb. In contrast, neuromuscular control primarily limited the independence of the ring, and little fingers in the large-arc movements, and had much smaller effects on the other fingers and during small-arc movements. The present findings are based on observations made during passive and active movements confined to the MCP joint. The current experiments do not allow us to determine the relative contributions of mechanical coupling versus neuromuscular control during movement at other finger joints, or various combinations of finger joints. Nevertheless, for the movement conditions tested here, mechanical coupling between the fingers appears to be a major factor limiting the complete independence of finger movement.

We did not explicitly constrain the starting positions of the noninstructed fingers, which could potentially affect the mechanical coupling. In the passive condition, the subjects were instructed to relax the entire hand, and let the device move the instructed finger. In the active condition, the subjects had to move only the instructed finger and may have used co-contraction of various unmonitored muscles to hold the other fingers in position. Thus the starting positions of the noninstructed fingers in both conditions represented a self-selected, comfortable position. It was not feasible to ask subjects to hold a particular starting position in the noninstructed fingers in the passive condition because, then, muscles would have been activated to maintain that position, thereby eliminating the passivity of those fingers. If a required starting position was achieved and then the subject relaxed all his fingers, the initial movement of the noninstructed fingers might have been a consequence of elastic recoil away from the starting position, independent of the movement of the instructed finger by the
device. Examination of the starting positions of the noninstructed fingers across fingers and across subjects shows that the noninstructed fingers were most often held in a semiflexed posture in both the active and passive conditions, where the specific semiflexed position was generally the same but not exactly constant across fingers, nor across conditions. Although our results might have been affected by variation in starting position of the noninstructed fingers, we would expect that the effect would be greatest if the noninstructed fingers were held at the extremes of MCP range (e.g., 15–20° of hyperextension, 85–90° of flexion), where tendons are most slack or most taut, and not in the midrange of available motion such as in our semiflexed starting positions.

Our analysis also assumes that active and passive effects sum linearly. During active movement, however, the passive coupling might change, especially at the slightly different movement speeds during the small-arc movements (see Fig. 2). One might hypothesize that the passive coupling could increase during the active condition compared with the passive condition, due to increased tension on the tendons from active muscle contractions. If this were the case, then our subtraction analysis would have overestimated the true ACI values. Given that our ACI values were quite small, we think this is unlikely.

**Causes of mechanical coupling between the fingers**

Independent control of the thumb and index finger is important for the dexterous manipulation of small objects. Our data show that the thumb can be considered completely independent during flexion–extension movements, given that more than half of our subjects had II values of 1.0 and ACIs and PCIs of 0.0 for the thumb. Interestingly, the independence of the index finger is limited chiefly by its mechanical coupling to the other fingers, and not by active neuromuscular control. Likewise, the lack of complete independence in the middle and ring fingers is attributed primarily to mechanical coupling rather than neuromuscular control. Mechanical coupling is lower in the little finger than in the index, middle, and ring fingers because the little finger has only one adjacent digit, whereas each of the other fingers has 2 adjacent digits.

Anatomical structures that mechanically couple the fingers include the flexor and extensor web spaces, the intertendinous connections of the multitendoned extrinsic finger muscles, and the muscle bellies of the extrinsic finger muscles. Although the web space produces considerable coupling when the fingers are hyperextended (von Schroeder and Botte 1993), the present movements were not performed at the extremes of MCP joint motion. The web space therefore would have remained relatively slack during the present movements and would not have pulled on adjacent fingers.

The intertendinous connections of the multitendoned extrinsic muscles likely contributed to the observed mechanical coupling. Our data suggest that structures on both sides of the hand contributed to the mechanical coupling because movement of noninstructed, adjacent fingers was similar in the flexion and extension phases during cycles of passive individuated movements (see Fig. 3). The juncturae tendinum of the extensor digitorum communis strongly couple the fingers on the dorsum of the hand (Von Schroeder and Botte 1993), whereas the intertendinous slips between tendons of the flexor digitorum profundus tendons (Leijnse et al. 1997; Malerich et al. 1987), and between flexor digitorum profundus and flexor pollicis longus tendons (Linburg and Comstock 1979) couple the fingers on the palmar side. How a tendon to one finger exerts passive force on a tendon to another finger is mechanically complex, and depends on multiple variables including the slack of the tendons, the insertion angle of the connections, and the stiffness of the connections (Leijnse 1997).

The bellies of the multitendoned extrinsic finger muscles also may couple the fingers to some degree. Depending on the how the regions of these muscle bellies serving different digits are coupled to one another, tension imposed on the tendon to one finger could pull on adjacent regions of the muscle belly, thereby unloading the tendons serving other fingers. Such unloading of the tendons to a noninstructed finger, resulting from movement of the instructed finger, could cause movement in the noninstructed fingers, driven by the existing tension in the tendons on the opposite (flexor vs. extensor) side of the finger.

The degree of mechanical coupling, as measured by the PCIs, did not change significantly from large-arc to small-arc movements. Note that this does not mean that absolute movement in the joints of the noninstructed fingers was the same for the 2 ranges, but that the relative movement was the same. Although we had expected that the degree of coupling would depend on the range through which the joint was rotated, the small- and large-arc ranges tested here both may have been sizable enough to pick up the slack in adjacent tendons, thereby producing movement in noninstructed fingers. Further testing of ranges even smaller than our small-arc range might find an arc at which imposed movement of one finger does not produce movement in adjacent fingers. We estimate that this arc would be approximately 10° (C. E. Lang, unpublished observations).

**Considerations about active movement and neuromuscular control**

During active, individuated movements, we found that finger independence was not the same across fingers, with the thumb being the most independent. In comparison, previous studies from our laboratory have found that either the thumb and index finger moved more independently (Hagar-Ross and Schieber 2000) or that all 5 fingers were equally independent (Lang and Schieber 2003; control group). These somewhat contradictory results may have resulted, in part, from the experimental constraints used in the different studies. Here we required subjects to move the instructed finger through a fixed arc (about 55–70° of the available range for the large-arc movements) by rotation of the MCP joint alone, whereas our previous studies either required a fixed arc but did not specify the joints at which rotation had to occur (Hagar-Ross and Schieber 2000) or did not specify either the arc or the joints (Lang and Schieber 2003). Furthermore, unlike our prior studies, here the distal joints of the instructed finger were fixed against the paddle. Taken together, these studies suggest that the independence of a given finger may vary depending on the arc through which the finger moves and on which joints are permitted to rotate.

The speed of movement in this experiment was chosen to avoid reflex responses during the passive movements. The chosen speed resulted in unnaturally slow movements during the active condition, as evidenced by the fact that subjects had...
difficulty matching the chosen speed (see Fig. 2B). Our results therefore may have underestimated the neural limitations on finger independence, given that reflexive responses may limit finger independence at more natural movement speeds. In pilot testing for this and for previous experiments on finger independence, however, we found that during active movements, finger independence was not a function of movement speed until movements were occurring at unnaturally fast speeds, where it becomes difficult for subjects to maintain the required rate. We therefore find it unlikely that lack of reflex responses led to underestimation of the neural limitations on finger independence in this experiment.

Neuromuscular control tended to reduce finger independence the most in the middle, ring, and little fingers during the large-arc movements. Three active processes may have coupled the more ulnar fingers. First, the corticospinal system may have less independent access to motor units acting on these digits, as suggested by greater short-term synchrony between motor units in the ulnar portions compared with the radial portions of multitudented extrinsic finger muscles (Keen and Fuglevand 2004a; Reilly et al. 2003; Winges et al. 2003). Second, active movements of the more ulnar fingers may have engaged multitudented motor units, the muscle fibers of which produced tension on more than one finger tendon (Keen and Fuglevand 2004b; Kilbreath et al. 2002; Schieber et al. 1997). Finally, active tension generated in one region of the muscle belly may have produced forces on adjacent regions, either by intramuscular connective tissue or by lateral force transmission (Huijing 1999; Maas et al. 2001). All these features of neuromuscular activation might have contributed to reducing the independence of the more ulnar digits during active as compared with passive large-arc movements. Given that the trend of greater neuromuscular limitations on the more ulnar fingers observed during the active large-arc movements was not present during the active small-arc movements, these 3 active factors may be quantitatively smaller when producing very small forces or movements (but see Fig. 2 of Zatsiorsky et al. 2000).

Although we found that mechanical coupling is a major contributor to the lack of complete independence during individuated finger movements, our data do not necessarily predict the extent to which mechanical coupling accounts for the force distribution across fingers during isometric finger force production tasks (e.g., Li et al. 1998a; Reilman et al. 2001; Santello and Soechting 2000). Intramuscular stimulation of small portions of the multitudented extensor digitorum communis has shown that some forces can be transmitted to adjacent fingers by the juncturae tendinum during an isometric task (Keen and Fuglevand 2003). However, force transmission to adjacent fingers may be less in an isometric task compared with an isotonic movement task, depending on how the slack is taken up across various tendons and their intertendinous connections. Interestingly, when subjects apply forces at different segments of a finger, thereby manipulating both the relative force contribution of various finger muscles and the influence of their intertendinous connections, the force sharing across the fingers stays relatively the same (Zatsiorsky et al. 2000). This result implies that the major reason for force sharing across fingers may be the corticospinal system’s ability to control the fingers independently, and not mechanical coupling, especially at high force levels. Likewise, because force synchronization during 5-digit grasping changes depending on whether the subject has to lift the object, 2 conditions in which the geometry of the hand remains the same (Rearick et al. 2003), the majority of the matching finger force profiles is likely explained by a coordinated motor command to all the fingers from the corticospinal system. Thus passive mechanical coupling of the fingers may have played a comparatively larger role during the present active isotonic finger movements with no load than during isometric production of higher finger forces.

In summary, passive mechanical coupling limited the independence of the index, middle, and ring fingers to the greatest degree, followed by the little finger, and placed only negligible limitations on the independence of the thumb. In contrast, active neuromuscular control limited the independence of the ring, and little fingers in the large-arc movements to the greatest degree and had much smaller effects on the other fingers and during small-arc movements. For the movement conditions tested here, mechanical coupling between the fingers appears to be a major factor limiting the complete independence of finger movement. Our findings highlight the importance of investigating how the anatomical structure of a body segment affects observed movements whenever investigating the neural system that controls that body segment.

ACKNOWLEDGMENTS

We thank K. T. Reilly for helpful suggestions throughout this project.

GRANTS

This work was supported by National Institute of Neurological Disorders and Stroke Grants F32 NS-44584 to C. E. Lang and R01/R37 NS-27686 to M. H. Schieber.

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