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Is the thumb a fifth finger? A study of digit interaction during force production tasks

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Abstract

We studied indices of digit interaction in single- and multi-digit maximal voluntary contraction (MVC) tests when the thumb acted either in parallel or in opposition to the fingers. The peak force produced by the thumb was much higher when the thumb acted in opposition to the fingers and its share of the total force in the five-digit MVC test increased dramatically. The fingers showed relatively similar peak forces and unchanged sharing patterns in the four-finger MVC task when the thumb acted in parallel and in opposition to the fingers. Enslaving during one-digit tasks showed relatively mild differences between the two conditions, while the differences became large when enslaving was quantified for multi-digit tasks. Force deficit was pronounced when the thumb acted in parallel to the fingers; it showed a monotonic increase with the number of explicitly involved digits up to four digits and then a drop when all five digits were involved. Force deficit all but disappeared when the thumb acted in opposition to the fingers. However, for both thumb positions, indices of digit interaction were similar for groups of digits that did or did not include the thumb. These results suggest that, given a certain hand configuration, the central nervous system treats the thumb as a fifth finger. They provide strong support for the hypothesis that indices of digit interaction reflect neural factors, not the peripheral design of the hand. An earlier formal model was able to account for the data when the thumb acted in parallel to the fingers. However, it failed for the data with the thumb acting in opposition to the fingers.

Keywords

finger; thumb; force; coordination; human

Introduction

Typical human hand activities, such as prehension, involve the coordination of the fingers and the thumb. Although in some languages, including the Icelandic and Russian, the thumb is referred to as “the big finger”, in other languages, including the English, it is considered as a special digit, a non-finger. There are anatomical and physiological reasons to separate the thumb from the fingers. The thumb has a very different muscular apparatus without multi-digit, multi-tendon muscles that are involved in finger action (Moore, 1992). Its brain representations are large and seemingly separate from those of the fingers (Penfield and Rassmussen 1950), although challenged recently (Schieber 2001). A major purpose of the current study has been to investigate whether the thumb interacts with other fingers differently from how fingers interact with each other.

In earlier studies, our group investigated indices of finger interaction during maximal (MVC) and submaximal force production tests (Li et al. 1998a, b; Zatsiorsky et al. 1998, 2000). In particular, these studies have identified three phenomena typical of finger force production tasks including (1) Sharing (total force is shared among the fingers in a stable way over a wide range of total force); (2) Force deficit (peak force produced by a finger in a multi-finger task is smaller than its peak force in a similar single-finger task, also see Kinoshita et al. 1995; Ohtsuki 1981); and (3) Enslaving (voluntary force production by a finger leads to involuntary force production by other fingers of the hand, also see Kilbreath and Gandevia 1994; Schieber 2001). These characteristics of coordination potentially reflect both the peripheral design of the hand musculature and its central neural coordination (Leijnse et al. 1993; Kilbreath and Gandevia 1994; Roullier 1996; Latash et al. 1998; reviewed in Schieber and Santello 2004). It has been unknown whether these characteristics of digit interaction apply to sets of digits that involve the thumb. If they do, this would provide crucial support for the hypothesis on the predominantly neural origin of finger interaction phenomena (cf. Latash et al. 2002; Goodman et al. 2003), taking into consideration the independent musculature of the thumb.

A formal description of finger force generation has been introduced using the notion of force modes, hypothetical central commands that lead to force generation by all four fingers (Danion et al. 2003). Within this description, a force mode vector is transformed by an inter-finger connection matrix with a coefficient that depends on the total number of explicitly involved fingers and reflects the force deficit phenomenon. Another goal of the study has been to investigate whether the same model can account for phenomena of digit interaction when sets of digits involve or do not involve the thumb.

The thumb is commonly used in two ways: In parallel with the fingers (e.g., pressing on an object) or in opposition to the fingers (e.g., grasping an object). We have been interested if changing the position of the thumb with respect to the fingers leads to changes in indices of digit interaction. We hypothesize that indices of thumb-finger interactions during MVC tasks are similar to indices of finger-finger interactions when the thumb acts in parallel to the fingers. However, special features of these indices may be expected in grasping tasks when the thumb acts as a force antagonist of the fingers (if one considers the normal forces).

Methods

Participants

Twelve, (6 men and 6 women) university students volunteered to participate in the study. Average age of the males was 27 ± 3.9 yrs; mean height 175 ± 9.6 cm; mean weight 73.7 ± 8.4 kg; mean length of the middle finger 11.2 ± 1.1 cm. Averages for the female participants were respectively 25.3 ± 3.3 yrs; 166.8 ± 3.7 cm; 64 ± 6.2 kg; and 10.7 ± 0.4 cm. All participants were healthy and right handed, according to their own preferential hand use during writing and eating. The purpose and procedures of the study were explained to the participants beforehand and they gave informed consent, according to the procedures approved by the Office for Regulatory Compliance of The Pennsylvania State University.

Apparatus

Five unidirectional piezoelectric sensors (model 208C02, PCB Piezotronics, Depew, NY) were used to measure the force generated by each digit. Analog output signals from the sensors were connected to separate signal conditioners (model 484B11, PCB Piezotronics). The signal conditioners operated in a direct-current-coupled mode, utilizing the sensor's discharge time constant, as established by the built-in microelectronic circuits within the sensors. The system involved ~1% error over the typical epoch of recording of a constant signal.

The sensors were mounted onto small metal platforms that were affixed to a horizontal wooden board (Fig 1B). The four finger force sensors were positioned on the top of the board such that each digit could be comfortably placed on the top of its sensor. The mediolateral distance between the sensors for the four fingers was 30 mm; the sensors could be moved in the anterior-posterior direction to fit every individual's anatomy. There were two thumb sensors. One of them was placed in opposition to the fingers. It was attached to a groove on the bottom side of the board in opposition to the middle finger. The other sensor was placed on the top of a horizontal extension to the wooden board. The extension was 25 mm below the level of the board to create a comfortable configuration for all five digits. The thumb was abducted 45° with respect to the index finger (Fig 1B). Double-sided tape was used to keep sensors in place once their position had been determined. A cotton pad was attached to the top of each sensor to increase friction and prevent effects of skin temperature. The board with the extension was attached to the table with strong clamps.

Subjects were seated in a chair facing the testing table and a monitor positioned 75 cm in front of them (Fig. 1A). The monitor displayed the total force of the explicitly involved (master) digits. The right forearm rested on a foam pad that was attached to the armrest of the chair. The forearm was placed on the pad such that the wrist was supported. The proximal part of the palm (beyond the metacarpophalangeal joints) rested on a wooden bar attached to the board to help maintain a constant position of the hand. The level of the palm support was 1.4 cm lower than the upper surface of the sensors. The right upper arm was at approximately 30° of abduction and 10° of flexion, the elbow was at approximately 120° of flexion and the wrist was at approximately 20° of extension. The metacarpophalangeal joints of the four fingers were in approximately neutral position while the proximal interphalangeal and distal interphalangeal joints were flexed by about 20° (Fig. 1). The left hand rested comfortably on the left thigh.

To monitor possible muscle co-contraction, electromyograms (EMGs) were recorded using surface electrodes. For the flexor muscles, electrodes were centered around the 50% point on the line joining the medial epicondyle to the styloid process of the ulna. These electrodes measure the summed activity of the flexor digitorum profundus (FDP) and flexor digitorum superficialis (FDS). For the extensor muscles, electrodes were centered around the 25% point on a line drawn from the lateral epicondyle to the styloid process of the ulna. These electrodes measure the activity of the extensor digitorum communis (EDC). Each electrode had a diameter of 1 cm, the distance between the electrodes within a pair was 2 cm. The EMG signals were amplified ($\times 3000$), high-pass filtered at 50 Hz and low-pass filtered at 500 Hz. For data acquisition and processing, a Dell Optiplex GX260 desktop computer with a 16-bit analog to digital converter (PCI-MIO-16XE-50, National Instrument, Austin, Texas) was used. Data were sampled at the rate of 1000 Hz using a Labview-based software.

Procedure

The participants were required to produce maximal voluntary force (MVC) by pressing down on force sensors with a subset of digits. The digits that participants were instructed to press down with will be addressed as “master digits” and the other, uninstructed digits will be addressed as “slave digits”. The participants were explicitly prohibited from lifting any of the digits off the sensors. They were instructed not to pay attention to possible force production by slave digits as long as the master digits reached their combined peak force.

MVC tests were performed in two conditions, with the thumb acting in parallel to the fingers and with the thumb opposing the fingers. For each condition, 21 tests were performed: I, M, R, L, T, TI, TM, TR, IM, RL, TIM, TML, TRL, IMR, MRL, TIMR, TIML, TIRL, TMRL, IMRL and TIMRL. The letters refer to explicitly involved (master) digits: I – index, M – middle, R – ring, L – little, and T – thumb.

Typically, one trial was performed for each digit combination to avoid fatigue. However, if a trial was considered “bad” by the participant or the experimenter, its data were deleted and the trial was repeated. Reasons for repeating a trial involved lifting digits off the transducers, pressing with a wrong set of digits, lifting the forearm off the armrest, or excessive co-contraction according to the EMG signal from the EDC muscle. Prior to the beginning of every test, two trials at maximal extension and maximal flexion force production by all four fingers were recorded. The maximal level of the rectified EMG signal from each muscle was used for reference. If in any of the further trials, the EMG signal recorded from the EDC muscle exceeded 40% of its maximal value, the trial was rejected and repeated. On average, two trials had to be repeated per subject due to one of the mentioned reasons.

All subjects got two practice trials before each set to get familiar with the position of the hand. Prior to each trial, the subject was instructed with which fingers to press. Each trial started with a “get ready” signal generated by the computer, and a trace showing the sum of the forces of the master digits started to move over the screen at a constant horizontal speed. The duration of every trial was seven seconds, and subjects were asked to produce maximal force within a three-second time interval marked by two vertical lines on the screen. The three-second interval was preceded and followed by two-second periods for preparation and relaxation. Following every trial, the EMG signal of EDC was viewed to determine whether excessive co-contraction had occurred. Subjects got a 30 second rest after each trial and 4 minutes of rest between the two conditions to prevent fatigue. Our previous studies have suggested that such rest intervals are sufficient to avoid effects of fatigue (Z-M Li et al. 1998; S. Li et al. 2001).

Data processing

The data were processed off-line using Matlab software (Mathworks, Inc). First, the force signals were low-pass filtered with a 4th order Butterworth filter at 30 Hz. Then, in each trial, individual digit forces were measured at the time when the combined force of the explicitly involved (master) digit reached its peak. Based on these values, a number of dependent variables were computed.

Enslaving forces were produced by the slave digits, i.e., by those digits that were not explicitly required to produce force. These forces were measured at a time when the explicitly instructed (master) digit(s) reached a peak force. For each slave digit, the enslaving force was expressed in percent with respect to this digit's MVC force in its single-digit task. For each task, these indices of enslaving were averaged across the slave digits for further comparisons.

Force deficit for a digit was defined as the difference between this digit's MVC force in its single-digit task and its force in a multi-digit task measured at the time of peak total force produced by all master digits. Force deficit was expressed in percent with respect to this digit's MVC force in its single-digit task. Thereafter, indices of force deficit were averaged across digits for further comparisons.

Force shares of master digits in multi-digit MVC tasks were computed as the ratio of the individual digit forces to the total peak force of all master digits.

Statistics

Standard descriptive statistics were used. The data are presented in the text as means and standard deviations. Figures show means and standard error bars. ANOVAs, with and without repeated measures and MANOVAs were used to test the effects of thumb involvement in multi-digit groups and thumb position on indices of digit interaction. The factors were *thumb* (two levels, involved and non-involved); *thumb position* (two levels, parallel and in opposition); *number of master digits* (five levels, one to five); and *digit* (five levels, I, M, R, L, and T). For

comparison of force sharing patterns, multivariate ANOVA was used and Rao's R was used to assess significance. In this analysis, shares of only four digits were used for five-digit tasks and of only three digits for four-digit tasks since the full set of individual shares does not constitute a set of independent variables (the sum of all the shares is always 100%). Planned comparisons and Tukey HDS post-hoc tests were used for post-ANOVA, -MANOVA analyses.

Results

During single-digit MVC tests, all subjects showed involuntary force production by other, explicitly uninvolved digits (enslaving, see the Methods). The two left panels of Figure 2 illustrate a typical performance in a single-digit task when the subject was required to produce maximal force with the index finger. Panel A shows the time series for the thumb acting in parallel to the fingers, while panel C shows the data for the thumb in opposition to the fingers. Note the smaller enslaved forces produced by the thumb and somewhat larger enslaved forces produced by the ring finger in panel A as compared to panel C.

In multi-digit tasks, the peak forces reached by the explicitly involved (master) digits were lower than during single-digit tasks, but only when the thumb acted in parallel to the fingers. Panel B of Figure 2 illustrates this for the TIM task (the thumb, index, and middle fingers being the master digits) performed by the same representative subject. Note the smaller peak force of the index finger in panel B as compared to panel A. When the thumb acted in opposition to the fingers, the force deficit was greatly reduced (compare the index finger forces in panels A vs. B and in panels C vs. D in Figure 2). Note also the difference in the magnitude of enslaving between panels B and D: The enslaving forces were somewhat higher when the thumb acted in opposition to the fingers (panel D).

The next sections present quantitative analyses of the indices of finger interaction. This analysis was based on data sets in individual subjects similar to those illustrated in Figure 2. We address such indices as maximal force (MVC), enslaving, force deficit, and force sharing described in the Methods.

MVC

In single-digit MVC tasks, peak forces reached by the master digits were typically higher when the thumb acted in opposition to the fingers. This difference was particularly pronounced for the thumb MVC force: It was, on average, 2.4 times larger when the thumb acted in opposition to the fingers as compared to tests when the thumb acted in parallel to the fingers. When acting in opposition to the fingers, the thumb was the strongest digit producing on average about 62 N force, while its MVC force was not different from MVC forces produced by any of the fingers when the thumb acted in parallel to the fingers (about 26 N). A smaller (about 17%) but significant difference between the peak forces observed in tests with different thumb positions was also observed for the index finger, which was also stronger when the thumb acted in opposition to the fingers. For the three other fingers, the differences between the peak forces observed at the two thumb positions were not significant.

These results are illustrated in Figure 3A, which shows averaged across subjects data with standard error bars. Two-way *thumb position* x *digit* ANOVA showed main effects of *digit* ($F_{[4,44]} = 42.72$; $p < 0.001$) and of *thumb position* ($F_{[1,11]} = 31.59$; $p < 0.001$) as well as a significant *thumb position* x *digit* interaction ($F_{[4,44]} = 19.31$; $p < 0.001$). Pairwise contrasts have confirmed the significant differences between the two thumb positions for the thumb MVC ($p < 0.001$) and for the index finger MVC ($p < 0.05$).

For the five-digit MVC tests, the peak forces of the digits showed a qualitatively similar dependence on the thumb position. The thumb showed the largest difference in its peak force,

which was nearly 4.4 times higher when it acted in opposition to the fingers. Smaller differences (on average, 32% to 53%) in the same direction were observed for the finger MVCs. These results are illustrated in Figure 3B. Two-way *thumb position* x *digit* ANOVA showed main effects of *digit* ($F_{[4,44]} = 33.88$; $p < 0.001$) and *thumb position* ($F_{[1,11]} = 48.92$; $p < 0.001$) and a significant *thumb position* x *digit* interaction ($F_{[4,44]} = 41.28$; $p < 0.001$). Pairwise contrasts confirmed the significant differences between the two thumb positions for all the digits ($p < 0.05$) except the little finger.

Force Deficit

In Fig. 3, one can see that when the thumb acted in opposition to the fingers (filled symbols), its peak force was higher in the five-digit task (panel B) as compared to its single-digit task (panel A). According to our definition of force deficit (see the Methods), the force deficit of the thumb in this condition was negative. This was not the case when the thumb acted in parallel to the fingers. Its force deficit was positive, i.e. it showed a smaller peak force in the five-digit test as compared to the single-digit test (open symbols in Fig. 3). Other digits showed similar behaviors, i.e. smaller force deficit values when the thumb acted in opposition to the fingers, although, on average, finger force deficit was always positive. These results are illustrated in Figure 4.

A three-way *thumb position* x *thumb* x *number of digits* repeated-measures ANOVA showed main effects of *thumb position* ($F_{[1,11]} = 95.84$; $p < 0.001$) and *number of digits* ($F_{[2,22]} = 26.97$; $p < 0.001$) but not of *thumb*. This finding shows that the amount of force deficit quantified over a group of digits did not depend on whether this group involved or did not involve the thumb. There was also a significant *thumb position* x *number of digits* interaction ($F_{[3,33]} = 3.06$; $p < 0.05$). Paired comparisons confirmed the significant difference between the two thumb positions for all sets of digits ($p < 0.05$) as well as between different sets of digits for both thumb positions ($p < 0.05$), except between 3- and 4-digit tasks when the thumb acted in opposition to the fingers.

Enslaving

In single-digit tasks, the middle and ring fingers had the strongest enslaving effects on other digits. Thumb position had, in general, little effect on enslaving. The average amount of enslaving during index, middle, and little finger MVC tests was independent of the position of the thumb. However, enslaving changed considerably for the ring finger and thumb MVC tests. When acting in opposition to the fingers, the thumb enslaved the fingers 2.1-times more than when acting in parallel. The ring finger, on the other hand, showed a 42% more enslaving when then thumb acted in parallel to the fingers.

Figure 5A illustrates these results with the data averaged across the subjects. A two way *thumb position* x *digit* ANOVA showed a main effect of *digit* ($F_{[4,44]} = 4.57$; $p < 0.05$) and a significant *thumb position* x *digit* interaction ($F_{[4,44]} = 4.66$; $p < 0.05$). Tukey HSD test showed a significant difference between the index and middle finger ($p < 0.05$); index and ring finger ($p < 0.05$), and between the middle finger and the thumb ($p < 0.05$). Planned comparison confirmed significant effects of thumb positions on enslaving produced by the ring finger ($p < 0.05$) and close to significant effects on enslaving produced by the thumb ($p < 0.08$).

For multi-digit tasks, positioning the thumb in opposition to the other fingers caused, on average, 90% higher enslaving. This effect was seen in 2,3 and 4 digit tasks regardless of whether the thumb was a master finger or not (see Figure 5B). Statistical analysis was done using a three-way repeated measures *thumb position* x *thumb* x *number of digits* ANOVA. It showed a main effect of *thumb position* ($F_{[1,11]} = 19.92$; $p < 0.05$) and no other significant

effects. Note that inclusion or non-inclusion of the thumb into a group of master fingers did not have an effect on the amount of enslaving the group produced.

Proximity hypothesis

Earlier studies of enslaving (Z.-M. Li et al. 1998; Zatsiorsky et al. 2000) suggested a hypothesis that the magnitude of enslaving effects in one-finger MVC tasks is larger in fingers that are closer to the master finger. For example, during a little finger MVC test, the enslaving is supposed to be the largest in the ring finger, smaller in the middle finger, and smallest in the index finger. We will refer to this hypothesis as a “proximity hypothesis”. To test this hypothesis for sets of digits that include the thumb, we ranked each slave digit according to its position with respect to the master digit (anatomical ranking). The closest slave digits (for example, the index and middle fingers or the index finger and the thumb) are ranked one, the next closest fingers (for example, the middle finger and the thumb) are ranked two, and so forth up to the proximity of the thumb and the little finger that is ranked four. The slave digits were also ranked according to their forces (force ranking). The digit that produced the largest enslaved force in a one-digit MVC test (in percents of its MVC force) was ranked one, the next – two, and so forth. Then the force rank values were averaged across finger pairs with the same anatomical ranking. This was done separately for the two thumb positions.

Figure 6 illustrates average ranks (across subjects) for the two thumb positions. For the anatomical rank of unity, the force rank is the smallest, as predicted by the proximity hypothesis. However, there are only small differences in the average force rank for anatomical ranks 2, 3, and 4. This general trend was true for the both thumb positions.

A two-way repeated measures ANOVA with factors *thumb position* and *rank* showed significant effect of both *thumb position* ($F_{[1,11]} = 5.85$; $p < 0.05$) and *rank* ($F_{[3,33]} = 51.55$; $p < 0.001$). Planned comparisons revealed differences between the thumb positions only for anatomical rank of one ($p < 0.05$). Tukey's HSD post-hoc test showed significant differences between all ranks ($p < 0.05$) except between ranks 3 and 4.

Sharing

In the five-digit task, the digits shared the total force differently depending on the thumb position. When the thumb acted in parallel to the other digits, the index finger had the largest force share, followed by the middle finger, the thumb, the ring finger and the little finger. However when the thumb acted in opposition to the fingers, it was the strongest digit without a change in the order of force shares of the other four digits.

These results are illustrated in Figure 7A, which shows averaged across the subjects data. For the five digit MVC task, a MANOVA using four shares (those of the thumb, middle, ring, and little fingers) showed a significant main effect of *thumb position* (Rao's $R_{[4,8]} = 29.86$; $p < 0.001$); post-hoc analyses confirmed different shares for each of the four digits ($p < 0.05$).

For the five digit MVC task, a *thumb position* $\times$ *digit* MANOVA using four shares (those of the thumb, middle, ring, and little fingers) showed a significant main effect of *thumb position* (Rao's $R_{[4,8]} = 29.86$; $p < 0.001$). Post-hoc analyses confirmed different shares for each of the four digits ($p < 0.05$).

Panel B of Figure 7 shows individual finger shares during the four-finger task (IMRL), averaged across subjects. For this task, there are no major changes in the sharing pattern between the two thumb positions. The index and middle finger had the largest shares of the total force, while the little finger has the smallest share. A *thumb position* $\times$ *digit* MANOVA showed a significant effect of *digit* (Rao's $R_{[4,8]} = 7.79$; $p < 0.05$) but no significant effect of the *thumb position* ($R_{[3,9]} = 0.37$; $p = 0.78$).

Modeling finger-thumb interactions

A computational approach has been suggested (Danion et al. 2003) that models the four-dimensional vector of finger forces $\mathbf{f} = [F_I, F_M, F_R, F_L]$ as a product of a 4x4 inter-finger matrix $[\mathbf{E}]$ obtained in single-finger MVC tests and a four-dimensional input vector of force modes $\mathbf{m} = [m_I, m_M, m_R, m_L]^T$, where subscripts refer to individual fingers and the superscript T means transpose. The result is attenuated by an empirically defined factor, k , reflecting the force deficit and dependent on the number of explicitly involved (master) fingers, n :

$$\mathbf{f} = k(n) [\mathbf{E}] \mathbf{m} \quad (1)$$

For MVC tasks, the vector of force modes consists of zeroes (for slave fingers) and ones (for master fingers). For example, an MVC task involving the middle and ring fingers will have an input $\mathbf{m} = [0, 1, 1, 0]^T$. We have decided to use Eq. (1) generalized for five digits ($\mathbf{f}$ and $\mathbf{m}$ are five-dimensional vectors while $[\mathbf{E}]$ is a 5x5 matrix) to model force patterns observed during the multi-digit MVC tests. This attempt was based on the lack of effects of thumb inclusion or exclusion into digit groups on indices of digit interaction. Data obtained in the single-digit MVC tests were used to construct the 5x5 $[\mathbf{E}]$ matrix. We assumed the same $k(n)$ function as empirically defined by Danion et al., $k(n) = 1/n^{0.712}$. The computed and actually observed digit forces across all the subjects and groups of multi-digit tests with equal numbers of master digits (equal n) were compared. This was done for the two thumb positions separately (Table 1).

For the finger forces obtained when the thumb acted in parallel to the fingers, the average absolute error of the model prediction was 2.05 N. When the thumb acted in opposition to the fingers, the fit was not as good with the average error of 5.38 N. For the thumb force, the average absolute error was 2.09 N when the thumb acted in parallel to the fingers, and it was much higher (12.56 N) when the thumb acted in opposition.

Discussion

Historically, the thumb has always been viewed as a special digit. Thumbs-up or -down defined the fate of defeated gladiators. Thumb amputation was used as a punishment for criminals and enemy soldiers to make sure that they would never be able to handle weapons again. This attitude found support in the famous brain maps of Penfield and Rasmussen (1950), which showed disproportionally large areas occupied by the thumb of the homunculus – a drawing of a distorted human body on different brain areas including the primary motor area.

More recently, separation of the thumb from other digits of the human hand has received support in a number of neurophysiological and behavioral studies. In particular, Lang and Schieber (2003) studied effects of damage to the motor cortex or corticospinal tract on the individual control of digits. They found little changes in the thumb independent control in contrast to larger changes in the control of fingers and concluded that the spared components of the neuromuscular system possessed a greater ability to control the thumb independently compared to the four fingers. Rearick and Santello (2002) showed that normal forces exerted by pairs of digits during a static grasp task tended to change in synchrony: Out-of-phase force changes were seen between pairs of fingers, while in-phase changes were observed between forces produced by the thumb and one of the fingers. The sensorimotor processing differs for the thumb and middle finger in the human primary motor and somatosensory cortices (Tanosaki et al. 2001; Jarvelainen and Schuurman 2002). Differences in patterns of cortical activation during movements of the thumb and the index finger have also been reported (Hamada et al. 2000).

A special role for the thumb has been implicitly recognized in an idea that control of the human hand may be hierarchical with the upper level defining the forces produced by the thumb and the so-called virtual finger (MacKenzie and Iberall 1994; Baud-Bovy and Soechting 2001). Virtual finger is an imaginable digit whose mechanical action is equivalent to the combined action of a set of fingers. At the lower level the action of the virtual finger is assumed to be distributed among the actual fingers. The idea of such hierarchical control has been supported recently in several studies (Gentilucci et al. 2003; Shim et al. 2003).

On the other hand, more detailed recent studies of cortical representations have cast doubt on the idea of a Penfield-type homunculus, particularly for the primary motor area M1 (reviewed in Schieber 2001). The representations seem to be much more mosaic, without clear borders between cortical areas that were traditionally thought to represent different body parts. This is true, in particular, for the thumb and finger representations. In a recent study, Waberski et al. (2003) have shown no functional border between the cortical representations of the thumb and the index finger in a particular task.

In the current study, we asked a specific question: Do indices of digit interaction depend on whether the thumb is one of the explicitly involved digits? An affirmative answer would suggest that the thumb is indeed special in a sense that the central nervous system treats it differently from the fingers in multi-digit tasks. However, our results suggest that the answer to this question is no.

The thumb is a fifth finger

In everyday motor actions, the thumb can play different roles, as a fifth digit producing force in parallel to the other four digits of the hand (as during pushing against a large object) and as a digit opposing the other four digits (as during grasping and manipulating relatively small objects). These two thumb actions involve different muscles. The focal force generators during pressing in parallel to the fingers are abductor pollicis brevis and abductor pollicis longus, while opponens pollicis, flexor pollicis brevis and flexor pollicis longus are the focal force generator when the thumb produces flexion force in opposition to the fingers (Johanson et al. 2001). Based on these differences, we expected indices of digit interaction to differ between the two thumb positions, particularly indices that reflect the thumb involvement.

The peak forces produced by the thumb in the MVC tests were much higher when the thumb acted in opposition to the fingers and its share of the total force in the five-digit MVC test increased dramatically. There may be several factors contributing to the task dependence of the thumb MVC. The first factor is the strength difference between the main muscle groups activated during force production at the two thumb position. When the thumb acts in opposition to the fingers, stronger muscles, such as opponens pollicis and flexor pollicis longus, produce force as compared to the smaller and weaker abductor pollicis longus and brevis, which are focal force generators during pressing in parallel to the fingers. Besides, a strong grip with the thumb acting in opposition to the fingers is both familiar and comfortable, whereas its action parallel to the fingers feels more awkward. Other task-related factors might include differences in the interaction between digit action and stabilization of the wrist. We would like to emphasize, however, that the task-related differences were pronounced mainly in the MVC values for the thumb, while the fingers showed relatively similar peak forces and unchanged sharing patterns in the four-finger MVC task when the thumb acted in parallel and in opposition to the fingers.

Enslaving during one-digit tasks showed relatively mild differences between the two conditions, while the differences became large when enslaving was quantified for multi-digit tasks. Force deficit was pronounced when the thumb acted in parallel to the fingers (similar values of force deficit have been reported by others, Z.-M. Li et al. 1998; Zatsiorsky et al.

1998). However, it all but disappeared when the thumb started to act in opposition to the fingers. This task-dependent drop of the force deficit could be related to differences between the thumb action in the two configurations, in particular to the relative awkwardness of the task of pressing with the thumb alone when it acts in opposition to the fingers as compared to the much more common gripping action involving the thumb and a subset of the fingers.

These major differences stand in stark contrast to the lack of significant effects of the *thumb* factor on any of the indices of digit interaction quantified for either thumb position: Indices of digit interaction were similar for groups of digits that did or did not include the thumb. Hence, one can conclude that these indices cannot distinguish the thumb from the fingers for a given configuration of the hand, i.e. the thumb behaves as a fifth finger with respect to indices of finger interaction during MVC tasks.

Implications for the role of neural and peripheral factors in digit interaction

Indices of finger interaction have been traditionally viewed as consequences of both peripheral factors (such as multi-digit extrinsic muscles and passive connective tissue links between adjacent pairs of fingers) and central neural factors (Leijne et al. 1993; Kilbreath and Gandevia 1994; Roullier 1996; Schieber 2001). A series of recent studies have provided indirect evidence suggesting that the neural factors play a dominant role in defining these indices (Danion et al. 2001; Latash et al. 2002). The results of the current study provide thus far the most convincing evidence that indices of finger interaction are mostly defined by neural mechanisms. Indeed, the thumb does not share multi-digit muscles with the fingers and its passive mechanical links to the fingers are minimal. Nevertheless, indices of digit interaction within groups of digits that did and did not include the thumb showed no significant differences, while they changed with other factors such as the number of explicitly involved digits and the thumb position (on the roles of mechanical and neural factors in motor coordination, see recent reviews by Carson and Kelso 2004 and by Schieber and Santello 2004). Anthropological evidence suggests, however, that the flexor pollicis longus evolved from being a part of the multi-digit flexor digitorum profundus (Marzke 1992). This might be the origin of some of the similarities in indices of thumb-finger interaction as compared to indices of finger-finger interaction.

It is generally unknown what particular neurophysiological structures play important roles in finger interaction and coordination. On the one hand, the cerebellum has been implicated in the control of interactions among body segments and in the organization of multi-effector synergies in general (Thach et al. 1992; Miall et al. 1993; Houk et al. 1996; Goodkin and Thach 2003). On the other hand, the role of both motor and sensorimotor cortical areas of the large hemispheres in dexterous actions involving the hand has been supported in many studies (Roullier 1996; Ehrsson et al. 2001; Duque et al. 2003; Schieber 2001; Pascual-Leone et al. 1995; Pascual-Leone 2001).

An empirical proximity hypothesis has been suggested implying stronger enslaving effects between pairs of fingers that are closer to each other (Zatsiorsky et al. 2000). Our analysis of the relation between the strength of enslaving and anatomical proximity of the digits for the full set of five digits has provided only partial support for the hypothesis. We observed significantly higher enslaving between adjacent pairs of digits but no differences between pairs that were separated from each other by one, two, or three digits. These results are more in line with recent observations of Biermann et al. (1998) that there is an overlap of finger representations in human SI which differs between anatomically adjacent and non-adjacent digit pairs but does not seem to distinguish among non-adjacent pairs of digits based on their anatomical proximity.

Revisiting two models of finger interaction

Without specifying particular neurophysiological structures, phenomena of finger interaction have been modeled using neural networks trained on experimental data with MVC tasks performed with different finger combinations (Zatsiorsky et al. 2000); they were also analyzed analytically (Goodman et al. 2002).

An alternative computational approach has been suggested that uses the notion of force modes as independent input signals reflecting planned involvement of fingers into a task (Danion et al. 2003). Danion and his colleagues used equation 1 successfully to simulate experimental data in multi-finger MVC tests obtained in several studies of multi-finger force production by young subjects with and without fatigue and healthy elderly (S. Li et al. 2000, 2001; Danion et al. 2000).

When this approach was applied to model digit forces in multi-finger tasks based on the results of single-digit tasks, accuracy of the model prediction was different for the two thumb positions. For the data obtained when the thumb acted in parallel to the fingers, the fit between the model prediction and the actual data was even somewhat better than in the original publication by Danion et al. (2003). The average absolute error in our study was under 2.1 N while it was about 2.4 N in the study by Danion et al. When the thumb acted in opposition to the fingers, the fit was not as good with the average error of 5.38 N for the finger forces and over 12 N for the thumb force.

Earlier studies of finger interaction during MVC tasks showed an increase in the force deficit with the number of master fingers (Z.-M. Li et al. 1998). Consequently, the neural network by Zatsiorsky et al. (1998) and the model of Danion et al. (2003) both assumed an attenuating factor that was a monotonic function of the number of master fingers. Our results, however, show that this rule breaks down when all five digits are involved in an MVC task: Force deficit showed an increase when the number of master digits grew from 2 to 3 and to 4, but it dropped when it became 5. This result shows a limitation in the applicability of that particular component of the two models.

Enslaving as a compound index

Our findings on the effects of thumb position on enslaving look contradictory. Indeed, there were only minor effects of thumb position on the average index of enslaving computed over single-digit tasks (Fig. 5A). On the other hand, the two conditions differed significantly when enslaving was quantified for multi-digit tasks (Fig. 5B). The mentioned contradiction is only seeming, however. As follows from Eq. (1), digit forces are defined by both the enslaving matrix and a coefficient k reflecting the phenomenon of force deficit. This coefficient is unity for single-digit tasks. In these tasks, enslaved forces are defined only by the inter-finger matrix $[E]$. The matrix is supposed to be unchanged for multi-digit tasks. However, enslaved forces will be attenuated by k .

Force deficit is typically computed over master fingers (e.g., Z.-M. Li et al. 1998). However, it also affects the enslaved forces. There is a major difference in force deficit between the two conditions (Fig. 4). On average, force deficit was about 30% when the thumb acted in parallel to the fingers, and it was close to zero when the thumb acted in opposition. Higher force deficit is expected to lead to a drop in the forces produced by slave fingers and, hence, lead to seemingly smaller enslaving. Note that the difference in the magnitude of the force deficit between the two conditions was nearly constant for groups of master digits that involved 2, 3, or 4 digits. This finding parallels the nearly constant difference between indices of enslaving computed at the two thumb positions for 2, 3, and 4 digit groups.

Concluding Comments

It has been argued that the thumb is a special digit, and some of our data support this generally accepted view. The thumb can change its action with respect to other fingers (parallel or in opposition), and such a change has profound effects on indices of digit interaction. Such factors as the different muscle involvement and different mechanical conditions may be viewed as leading to the existence of two different multi-muscle synergies involved in multi-digit force production when the thumb acts in parallel or in opposition to the fingers. Addition of the thumb to the four fingers leads to a violation in the previously described monotonic behavior of force deficit with the number of explicitly involved fingers. However, we would like to emphasize findings that suggest that, given the hand configuration, the thumb is treated by the nervous system as a fifth finger. This conclusion is supported by the fact that indices of digit interaction were similar for groups of digits that did or did not include the thumb. It is also supported by the applicability of the previously developed formal description of finger interactions for all five digits of the human hand. These findings have been unexpected and surprising given the specificities of the muscular design and neural representations of the thumb. They suggest that these specificities may only be apparent and not dominating the neural control of the human hand.

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A

B

Figure 1.

A: The experimental setup. Subjects were instructed to rest the forearm on the armrest and the heel of the hand on the edge of the board. B: Positioning of the hand when the thumb pressed in parallel to the fingers.

Figure 2.

Typical finger force profiles in a representative subject. A: MVC-I task with the thumb acting in parallel to the fingers. B: MVC-TIM task with the thumb acting in parallel to the fingers. C: MVC-I task with the thumb acting in opposition to the fingers. D: MVC-TIM task with the thumb acting in opposition to the fingers. MVC – maximal voluntary contraction, I – index finger, M – middle finger, T – thumb.

Figure 3.

A: Peak force values for the thumb (T), index (I), middle (M), ring (R) and little (L) fingers during single digit tasks when the thumb acted in parallel to the fingers (open symbols) and in opposition to the fingers (filled symbols). B: Peak forces of the digits during the MVC-TIMRL task for both thumb positions. Average across subjects data are shown with standard error bars; * $p < 0.05$.

Figure 4. Force deficit as a function of the number of master digits for the two thumb positions, in parallel to the fingers (open symbols) and in opposition to the fingers (filled symbols). Average across subjects data are shown with standard error bars; * $p < 0.05$.

Figure 5.

A: Enslaving during single-digit tasks for the two thumb positions. For abbreviations see Fig. 2. B: Average enslaving during multi-digit tasks for the two thumb positions. Average across subjects data are shown with standard error bars; * $p < 0.05$.

Figure 6.

The dependence of the force rank on the anatomical rank during single digit MVC tasks for the two thumb positions. Average across subjects data are shown with standard error bars; * $p < 0.05$.

Figure 7.

A: Individual digit shares during the five-digit MVC task when the thumb acted in parallel and in opposition to the fingers. B: Individual digit shares during the four-digit (IMRL) MVC task when the thumb acted in parallel and in opposition to the fingers. Average across subjects data are shown with standard error bars; * $p < 0.05$.

Table 1

Mean absolute errors of the model

	Number of digits (N)	Thumb in parallel	Thumb in opposition
Fingers	2	1.57 ± 0.38	3.98 ± 0.81
Fingers	3	2.40 ± 0.55	4.24 ± 0.87
Fingers	4	1.81 ± 0.45	4.51 ± 0.88
Fingers	5	2.43 ± 0.5	8.79 ± 1.44
Thumb	all	2.09 ± 0.52	12.5 ± 2.1

For fingers, mean values are shown with standard errors across fingers and tasks with equal numbers (N) of explicitly involved digits. For the thumb, the data are pooled over all multi-digit tasks.