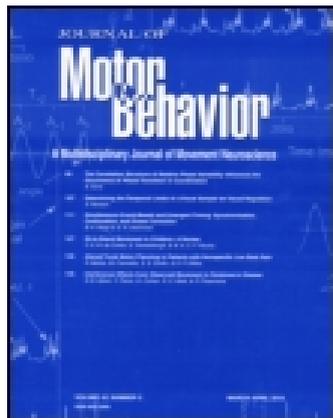


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Dependence of Finger Flexion Force on the Posture of the Nonperforming Fingers During Key Pressing Tasks

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ABSTRACT. The influence of different positions of the nonperforming (idle) fingers on the maximal force contraction of flexion (master) fingers during key pressing tasks was investigated. Ten participants performed maximal voluntary flexion contractions with various combinations of the index, middle, ring, and little fingers while the idle fingers rested on or were lifted away from the supporting surface. The effect of idle finger posture on total finger force production of master fingers was dependent on finger combination. In general, force production by master fingers was higher when the idle fingers were lifted away from the supporting surface than when they rested on it. The average increase in total force production by master fingers caused by the lifting of idle fingers was +12.4% (from -8.3% to +30.2%). Force-production capability of individual master fingers can be facilitated (as high as 34.1%), unchanged, or depressed (as high as -29.0%) by lifting the idle fingers. The effect of idle finger posture on finger force production of master fingers led to changes in force deficit. Neural, anatomical, and mechanical factors might account for the dependence of finger flexion force of master fingers on the posture of the idle fingers.

Key words: biomechanics, hand, isometric contraction

Investigators frequently study human fingers to understand the way in which the motor system controls its action (movement). A few finger coordination principles have been reported, including force sharing (Amis, 1987; Kinoshita, Kawai, & Ikuta, 1995; Li, Latash, & Zatsiorsky, 1998), force deficit (Li et al., 1998; Ohtsuki, 1981a), enslaving effects (Zatsiorsky, Li, & Latash, 1998), and error compensation (Cole & Abbs, 1986; Darling, Cole, & Abbs, 1988; Latash, Li, & Zatsiorsky, 1998).

During maximal voluntary force production by several fingers acting in parallel, the total force is shared among involved fingers in a specific manner (Latash, Gelfand, Li, & Zatsiorsky, 1998; Li et al., 1998). The force produced by a given finger in a multifinger task is lower than the force generated by that finger in a single-finger task; that is, there

is a force deficit (Li et al., 1998; Ohtsuki, 1981a). Investigators have used the ceiling hypothesis to explain the force deficit for fingers (Li et al., 1998); that is, the total neural drive to all the fingers is limited, and, as a result, the activation of a given finger reduces the drive to other fingers. It can be generally observed that voluntary extension–flexion of one finger can induce accompanying involuntary flexion–extension of other fingers. The interdependence among fingers has been reported for motion tasks (Kimura & Vanderwolf, 1970; Schieber, 1995) and for force-production tasks (Zatsiorsky et al., 1998). When a participant is asked to press maximally with one, two, or three fingers without lifting the idle fingers, the idle fingers are involuntarily activated and produce flexion force, which is termed *force enslaving* (Zatsiorsky et al., 1998).

In many daily activities that involve flexion of various combinations of fingers (e.g., pinching, grasping, typing, or piano playing), the nonperforming (idle) fingers can rest on (e.g., during typing) or be extended away from (e.g., piano playing) the contact surface. Previous studies (Li et al., 1998; Zatsiorsky et al., 1998) in which finger flexion force has been measured have indicated that participants prefer to position the idle fingers in different ways, depending on which fingers are used to produce flexion force. Results of cadaver, biomechanical, and electromyographic studies (An, Chao, Cooney, & Linscheid, 1985; Close & Kidd, 1969; Long, Conrad, Hall, & Furler, 1970; Valero-Cuevas, Towles, & Hentz, 2000) have shown that some extensor activation of a finger is needed so that the flexion

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force itself can be optimized, that is, intrafinger interaction. When an idle finger is extended together with flexion of other fingers in a multifinger task, the extension activation of the idle finger might have potential effects on the flexor activities of the flexion (master) fingers, that is, interfinger interaction. It is unclear, however, how the force-production capability of master fingers is affected by the posture of idle fingers.

Our purpose in the current study was to investigate the influence of different postures of the idle fingers on the flexion maximal force contraction of master fingers. We hypothesized that finger forces would be different depending on whether the idle fingers remained on or were lifted away from the support surface.

Method

Participants

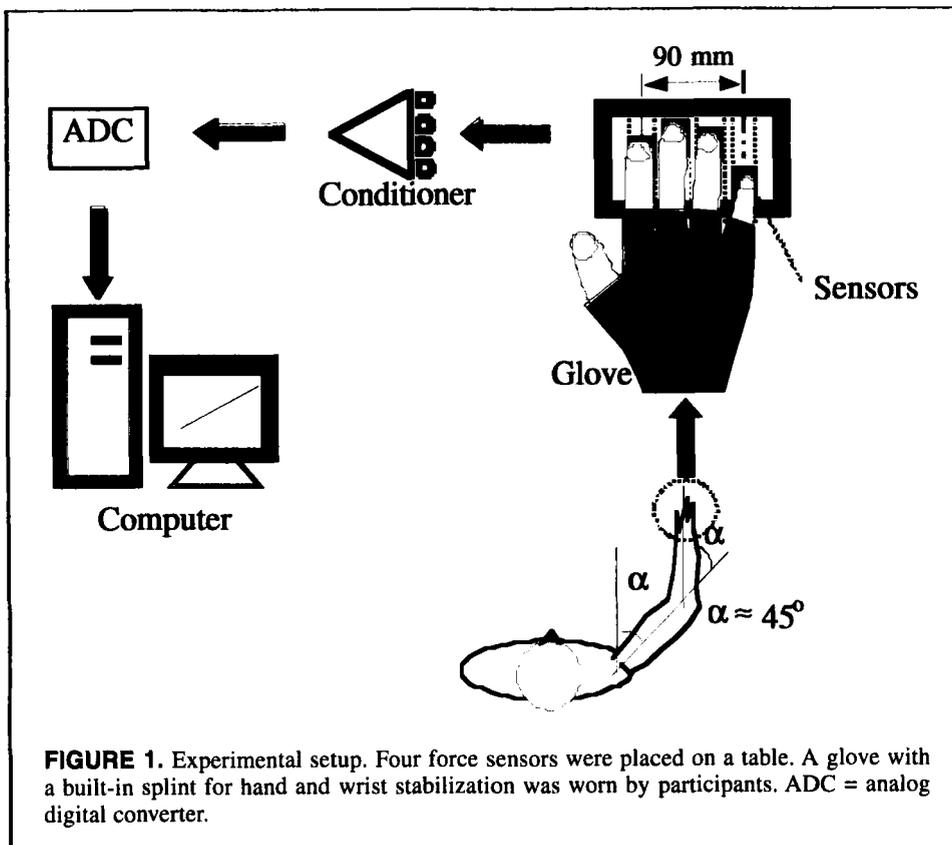
Ten male college students volunteered to participate in this study. Their mean (\pm SD) age, height, and body weight were 24.7 ± 3.1 years, 178.4 ± 5.3 cm, and 72.8 ± 12.1 kg, respectively. Their hand size (defined from the tip of the middle finger to the wrist delineation line) averaged 19.96 ± 1.94 cm. All participants were right-handed and had no previous history of neuromuscular disorders. Informed consent was obtained from each participant before testing, according to the procedures approved by the Institutional Review Board of Walsh University.

Apparatus

We used four piezoelectric force sensors (M208A03, PCB Piezotronics, Inc., Depew, NY) to measure flexion force of the individual fingers. Each analog output from the force sensor was connected to a signal conditioner (M482M66, PCB Piezotronics, Inc.) from which the signals were then analog-to-digital converted (PCI-6031E, National Instruments, Austin, TX). See Li et al. (1998) for a detailed description of hardware specifications. The digitized force signals were stored in a personal computer. The sensors were fixed on a tabletop 30 mm apart mediolaterally but could be moved in the longitudinal direction of the fingers to accommodate different hand sizes (Figure 1). Each participant wore a glove (IMAK Products Corporation, San Diego, CA) that had a small built-in uniform splint that ensured a consistent and comfortable hand position during task performance (see Figure 1). A LabVIEW program (National Instruments, Austin, TX) was designed for data collection and processing.

Procedure

Participants were seated comfortably, facing the testing table and leaning slightly backward against the chair. The individual fingers were positioned on the sensors, with the right arm positioned at approximately 45° of abduction in the frontal plane, 45° of flexion in the sagittal plane, and with the elbow at approximately 45° of flexion (Figure 1).



The participants were asked to perform maximal voluntary contractions (MVCs) with various combinations of the index (I), middle (M), ring (R), and little (L) fingers. The finger combinations used were as follows: (a) one-finger tasks, I, M, R, and L; (b) two-finger tasks, IM, IR, IL, MR, ML, and RL; (c) three-finger tasks, IMR, IML, IRL, and MRL; and (d) a four-finger task, IMRL.

For convenience, the fingers that we asked participants to use to produce flexion force are referred to herein as master fingers, and the remaining nonperforming fingers are called idle fingers. Each participant took part in two experimental sessions on 2 consecutive days, one session on each day. In the first session, the participant was instructed to maintain the idle fingers on the sensors all the time during the pressing tasks (the on condition). The idle fingers were allowed to produce forces naturally whenever the participant felt involuntary flexion of idle fingers (Zatsiorsky et al., 1998). Five randomly selected combinations were used for five practice trials before the experiment began. In the second session, the participant was instructed to lift the idle fingers from the sensor surface while the master fingers pressed (the off condition). Note that because there was no idle finger for Task IMRL, that task was performed in the first session only. In both sessions, the order of finger combinations used in the experiment was randomized. Participants were asked to perform each MVC within a 5-s period after a beep signal. In general, it took about 2 s to reach MVC after force initiation. A 15-s rest was given between trials. After one set of combinations (15 trials for the first session, 14 trials for the second session) was completed, a 30-s break was given before starting the next set. The participant was asked to perform each of the different finger combinations three separate times. Therefore, each participant performed 45 trials in the first session and 42 trials in the second session. The data were collected at 1,000 samples per second.

Data Analysis

The force data were digitally low-pass filtered with a second-order Butterworth filter. The cutoff low frequency was set at 5 Hz. The value of each finger's flexion force at the instant when the maximal total force occurred was determined from each trial. That step allowed us to gather both individual finger force and total force produced from each trial. The following parameters were defined:

1. *Total force (T)*. The total force in a combination task j is the sum of the forces produced by the master fingers; that is,

$$T_{j,k} = \sum_i F_{i,j,k},$$

where F represents force; i represents a finger that is involved in a task, that is, a master finger ($i = I, M, R, \text{ or } L$); j represents a finger combination ($j = I, M, R, L, IM, IR, \dots, \text{ or } IMRL$); k represents an experimental condition ($k = \text{on or off}$). Note that in the on condition, the idle fingers produced a certain amount of force (force enslaving phenomenon; Zatsiorsky et al., 1998); however, the enslaving force gen-

erated by the idle fingers was not included in the total force calculations.

2. *Force actualization (FA, f)*. The force actualization of a finger i in a task j was defined as the ratio of the maximal force produced by finger i in task j to the maximal force generated by the same finger in the single-finger task, expressed as a percentage value. That is,

$$f_{i,j,k} = \frac{F_{i,j,k}}{F_{i,i,k}} \times 100\%,$$

where i, j , and k have the same notations as in Equation 1. Note that the data were calculated separately for the on and off conditions.

3. *Force deficit (d)*. The force deficit of a task was defined as the difference between the total force in a multi-finger task and the sum of the maximal forces of the same fingers in the single-finger task expressed as percentage of the latter value. That is,

$$d_{j,k} = \left(1 - \frac{\sum_i F_{i,j,k}}{\sum_i F_{i,i,k}} \right) \times 100\%,$$

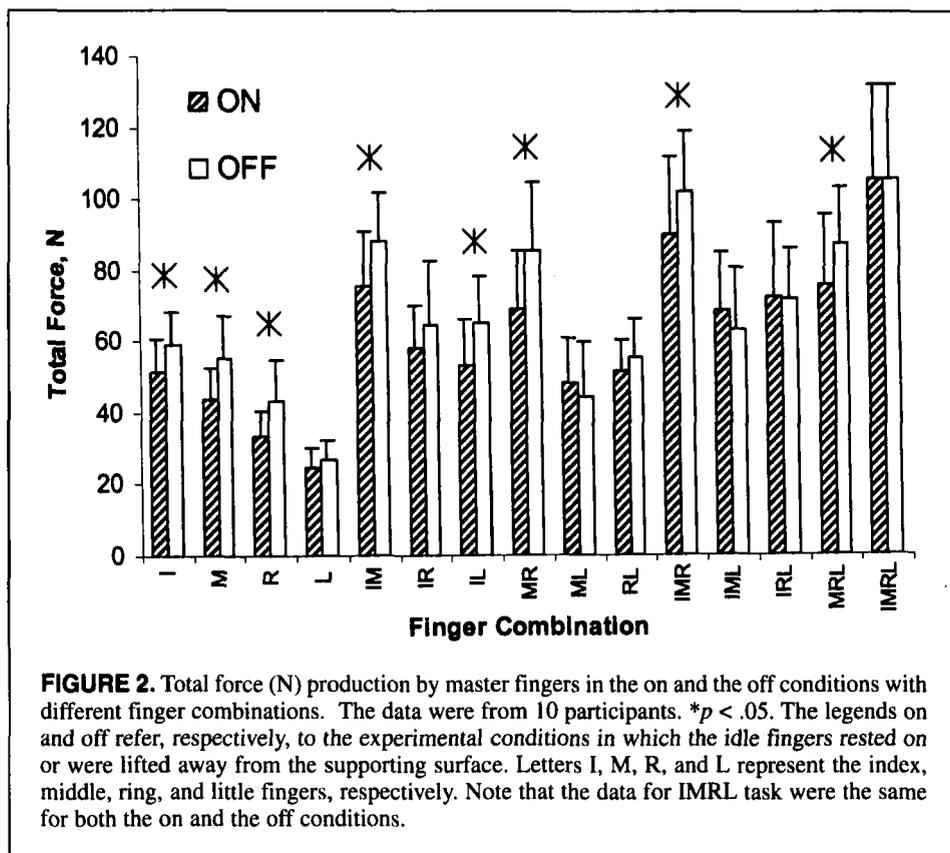
where i, j , and k have the same notations as in Equation 1.

The above parameters, which were determined for each trial and were then averaged across the three trials of each finger combination, served as representative scores. To determine whether there was an effect of finger combination or finger position on finger force production, we conducted a two-way analysis of variance (finger combination and position of idle fingers), with finger positions treated as repeated measures (SPSS for Windows Version 10.1, SPSS Inc., Chicago). The data for the IMRL task were not included in the statistical analysis because there was no idle finger in that task. For total force and force deficit analysis, 14 levels of finger combinations were used; for individual finger forces and force actualizations, 7 out of 14 finger combinations were included. For example, the index finger was a master finger that produced force in combinations I, IM, IR, IL, IMR, IML, and IRL but was an idle finger in the other 7 combinations. If significance was demonstrated, then we performed Tukey's tests to determine which finger combination was different. The statistical significance level was at $\alpha = .05$.

Results

Total Force Produced by Master Fingers

Total maximal force production was dependent on the experimental condition, on or off, $F(1, 126) = 31.69, p < .001$. The total force, on average, ranged from 24.5 N (L finger, on condition) to 103.3 N (IMRL fingers). In the single-finger tasks for both the on and the off conditions, the index finger produced the largest force, followed by the middle, ring, and little fingers, respectively (Figure 2). In the two-finger tasks, the IM and the MR fingers produced the high-



est total forces, whereas the ML fingers generated the least amount of force for both conditions. For both conditions, the IMR fingers produced the largest total force among the four three-finger tasks, followed by the MRL, IRL, and IML finger combinations, respectively. In the off condition, the IML fingers produced less total force than two of the two-finger tasks, IM and MR. In three-finger combination tasks, adjacent fingers (IMR or MRL) produced higher total forces than the total force produced by nonadjacent fingers.

The total forces produced by the master fingers differed in the two conditions (on and off). Eleven combinations showed an increasing trend in total force when the idle fingers were lifted away from the sensor (off) as compared with the on condition. In 8 combinations (I, M, R, IM, IL, MR, IMR, and MRL), a significant difference was found ($p < .05$; Figure 2). For those 8 combinations, the average total force produced in the off condition was 18.4% greater than the force produced in the on condition; the percentage increase ranged from 13.5% (IMR) to 30.2% (R). See also Figure 3 for the percentage difference in total force by master fingers, as indicated by the open circles. Three combinations (ML, IML, and IRL) showed slight but nonsignificant decreases in total force in the off condition as compared with the on condition (Figures 2 and 3).

Individual Finger Forces

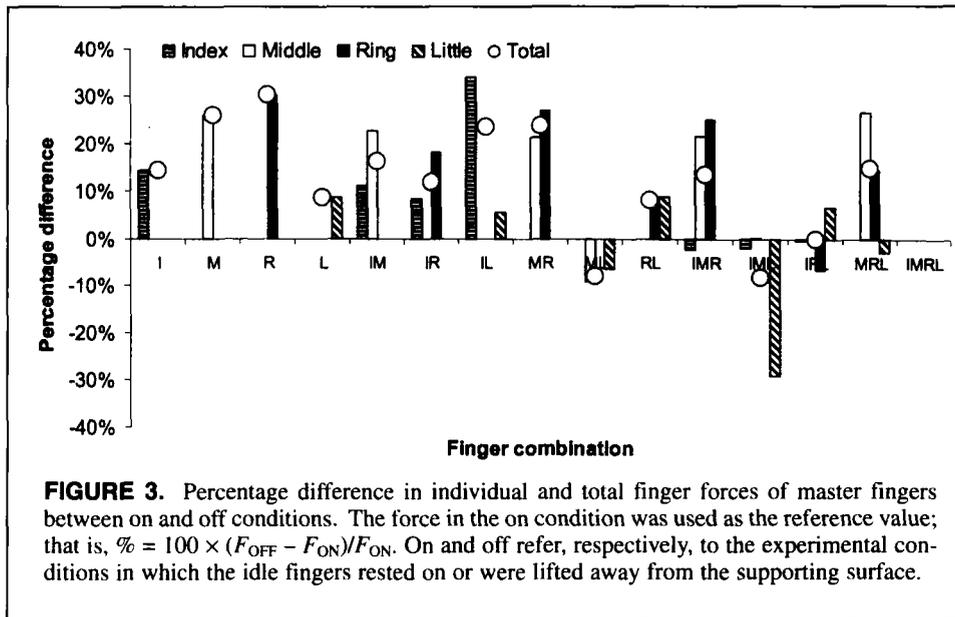
Table 1 shows the force data of the master fingers in the on and off conditions for all combinations. Individual fingers,

except the little finger, produced different forces, depending on whether the idle fingers were on or were lifted away from the sensor surface: index, $F(1, 63) = 10.4$, $p = .02$; middle, $F(1, 63) = 20.9$, $p < .001$; ring, $F(1, 63) = 20.8$, $p < .001$; little, $F(1, 63) = 0.01$, $p = .092$.

When a finger was explicitly involved as a master finger, its force-production capability could be facilitated, unchanged, or depressed by lifting the idle fingers (Table 1 and Figure 3). The index finger produced significantly higher forces in the off than in the on condition in combinations I and IL ($p < .05$). The percentage differences were 14.3% and 34.1% for I and IL, respectively. The middle finger generated higher force in the off than in the on condition in combinations of M, IM, MR, IMR, and MRL out of seven comparisons ($p < .05$); the percentage increases ranged from 21.3% to 26.8%. Lifting the IR fingers (ML combination) did not lead to a significant increase in middle finger force production, nor did R finger lifting in the IML combination. The ring finger produced greater forces in R, IR, MR, and IMR combinations in the off condition ($p < .05$). The largest increase occurred when IML fingers were lifted. The little finger did not show a significant increase in force production when the idle fingers were lifted. On the contrary, the little finger showed a 29.0% decrease when the ring finger was lifted (i.e., IML combination).

Force Actualization (FA) of Individual Fingers

Each finger produced its highest force when it acted



alone (single-finger task) in both the on and the off conditions (Tables 1 and 2). The FA values of individual fingers in multifinger tasks were less than 100% of the maximal single-finger task force. Note that FA values were calculated separately for the on and the off conditions (Equation 2). In the off condition, for example, the overall FA of the master fingers ranged from 36.0% to 89.7%. That finding means that the maximal amount of force produced by any finger in a multifinger combination was at best 89.7% of the maximum force generated by the finger in the single-finger task. In general, as the number of fingers increased in a combination, the FA value decreased. For example, in the chain of the tasks $M \rightarrow MR \rightarrow MRL \rightarrow IMRL$ in the off condition, the corresponding FA values for the middle finger were 100% \rightarrow 89.7% \rightarrow 65.6% \rightarrow 54.6%, respectively. Furthermore, the FA for a finger could differ for different finger combinations even though the number of fingers was the same in each combination. For example, the FAs of the ring finger in IR and MR tasks were 56.4% and 85.2%, respectively—a difference of 28.8%. Likewise, in the three-finger tasks, the FA values for the little finger were 48.4% and 73.9% in IML and IRL combinations, respectively. FA values were dependent on finger combinations—index, $F(6, 63) = 2.23, p = .043$; middle, $F(6, 63) = 9.07, p < .001$; ring, $F(6, 63) = 2.95, p = .013$; little, $F(6, 63) = 3.55, p = .004$ —but not on position of idle fingers—index, $F(1, 63) = 0.87, p = .354$; middle, $F(1, 63) = 1.96, p = .167$; ring, $F(1, 63) = 1.09, p = .300$; little, $F(1, 63) = 2.18, p = .145$.

Force Deficit

Although force actualization defines the relative force of an individual finger in multifinger tasks as compared with the maximal force generated in its single-finger task, force deficit offers insight into the decreased capability in total force production of two or more fingers acting together as

opposed to individually (Equation 3). Force deficit was strongly dependent on finger combination, $F(13, 126) = 32.5, p < .001$, and on finger position of idle fingers, $F(1, 126) = 16.8, p < .001$. Because each individual finger produced the greatest force in its single-finger task, and on the basis of Equation 3, no force deficit (i.e., 0%) should be measured for the single-finger tasks. For multiple finger combinations, force deficit ranged from 9.6% to 46.8% for the on condition and from 12.7% to 55.1% for the off condition (Figure 4). The least force deficit occurred in the MR task (10% and 13% for the on and the off conditions, respectively); thus, the total force produced simultaneously by the middle and ring fingers was about 90% (for on) and 87% (for off) of the maximal potential for those two fingers acting individually. In general, force deficit increased with an increased number of fingers in a combination. For instance, in the off condition, in chain tasks of $I \rightarrow IM \rightarrow IMR \rightarrow IMRL$, the corresponding force deficit values were 0% \rightarrow 23.0% \rightarrow 35.5% \rightarrow 42.8%, respectively. As for the force actualization of individual fingers, the force deficit of multiple fingers differed with different finger combinations even though the number of fingers involved was the same. For example, in the two-finger combinations, the largest force deficit occurred in the ML (45.9%) and the least occurred in the MR (12.7%) combination for the off condition.

The force deficit between the on and off conditions was greater in the off than in the on condition in ML, RL, IML, and IMRL combinations (Figure 4; $p < .05$). Note that the force deficit for the IMRL combination was different, even though the tasks were the same, because the single-finger forces used for the calculation were different between the on and off conditions. Because the sum of single-finger forces was smaller in the on (51.6 + 43.7 + 33.3 + 24.5 = 153.1 N) than in the off (59.0 + 55.1 + 43.3 + 26.6 = 184.0 N) condition, the force deficit of the IMRL task, which was

TABLE 1
Mean and Standard Deviation of Flexion Force (N) Produced by Individual Fingers
With Various Finger Combinations for On and Off Conditions

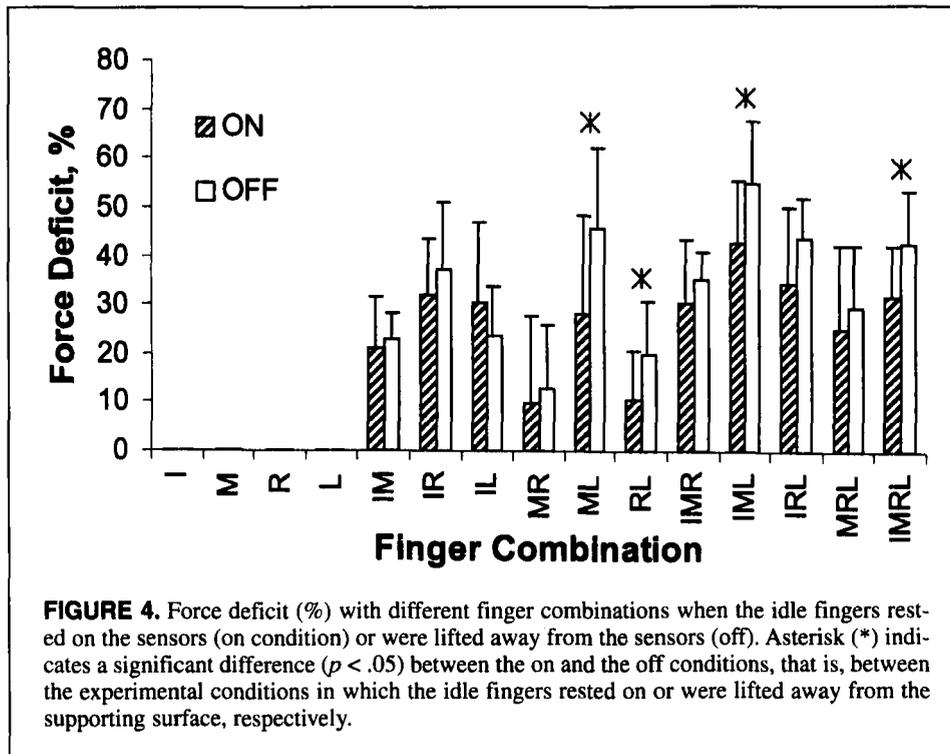
Index		On				Off									
		Middle		Ring		Little		Index		Middle		Ring		Little	
<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
<i>Index finger</i>															
51.6	8.9							59.0 [↑]	9.5						
<i>Middle finger</i>															
		43.7	8.6							55.1 [↑]	12.4				
<i>Ring finger</i>															
				33.3	7.3							43.3 [↑]	11.5		
<i>Little finger</i>															
						24.5	5.4							26.6	5.8
<i>Index-middle fingers combination</i>															
42.3	9.6	33.4	8.7					46.9	7.8	40.9 [↑]	11.2				
<i>Index-ring fingers combination</i>															
36.2	9.2			21.6	5.7			39.2	6.4			25.4	13.4		
<i>Index-little fingers combination</i>															
33.1	11.3					19.7	5.1	44.5 [↑]	9.1					20.8	5.1
<i>Middle-ring fingers combination</i>															
		39.6	9.9	29.2	8.4					48.0 [↑]	11.1	37.1 [↑]	11.4		
<i>Middle-little fingers combination</i>															
		30.3	9.4			18.0	4.9			27.6	10.5			16.9	5.3
<i>Ring-little fingers combination</i>															
				28.9	7.2	22.4	3.5					30.9	7.7	24.4	5.6
<i>Index-middle-ring fingers combination</i>															
33.6	10.5	33.7	9.1	22.1	3.9			32.8	6.5	40.9 [↑]	7.9	27.7 [↑]	8.4		
<i>Index-middle-little fingers combination</i>															
31.5	11.6	19.2	6.3			17.7	6.5	30.9	12.9	19.3	6.2			12.6	7.0
<i>Index-ring-little fingers combination</i>															
34.4	11.6			19.2	7.8	18.5	4.8	34.2	8.0			17.9	7.9	19.7	4.9
<i>Middle-ring-little fingers combination</i>															
		27.7	10.8	29.2	8.6	18.7	5.1			35.1 [↑]	7.7	33.4 [↑]	8.4	18.2	5.3
<i>Index-middle-ring-little fingers combination</i>															
32.8	8.1	29.3	11.1	25.1	7.6	17.9	6.4	32.8	8.1	29.3	11.1	25.1	7.6	17.9	6.4

Note. The arrow (↑) indicates that master finger force was higher in the off condition than in the on condition.

TABLE 2
Mean and Standard Deviation of Force Actualization (%) of Master and Idle Fingers

		On						Off									
Index		Middle		Ring		Little		Index		Middle		Ring		Little			
<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>		
<i>Index finger</i>																	
100.0	0.0	24.8	16.4	15.5	11.8	9.8	9.3	100.0	0.0								
<i>Middle finger</i>																	
26.6	9.3	100.0	0.0	38.9	23.5	16.1	11.60			100.0	0.0						
<i>Ring finger</i>																	
15.1	20.4	34.8	19.2	100.0	0.0	40.7	14.5					100.0	0.0				
<i>Little finger</i>																	
12.7	10.8	16.4	15.0	44.4	27.9	100.0	0.0							100.0	0.0		
<i>Index-middle fingers combination</i>																	
81.7	9.0	77.3	20.0	26.7	13.0	12.0	9.6	81.1	10.0	74.7	13.7						
<i>Index-ring fingers combination</i>																	
70.4	14.2	32.3	13.1	65.5	13.2	33.5	17.9	67.4	12.6			56.5	26.2				
<i>Index-little fingers combination</i>																	
65.1	24.3	18.5	9.1	30.5	15.4	80.7	11.7	75.9	12.6							79.3	14.9
<i>Middle-ring fingers combination</i>																	
22.7	13.7	93.2	26.1	89.2	21.9	31.1	19.2			89.7	22.9	85.2	19.1				
<i>Middle-little fingers combination</i>																	
21.1	13.9	72.2	26.6	71.2	51.3	74.1	15.8			50.2	17.1			64.6	19.1		
<i>Ring-little fingers combination</i>																	
13.1	11.1	41.4	23.3	88.7	20.1	94.1	20.8					72.4	12.0	92.7	14.3		
<i>Index-middle-ring fingers combination</i>																	
64.5	13.2	79.5	22.9	68.7	15.9	27.7	21.3	56.2	10.2	75.9	14.8	63.9	10.1				
<i>Index-middle-little fingers combination</i>																	
61.3	20.8	47.0	21.4	32.2	19.3	73.0	24.8	53.0	22.2	36.0	13.5			48.4	25.5		
<i>Index-ring-little fingers combination</i>																	
66.1	19.1	24.0	15.9	59.2	21.7	76.9	19.3	58.8	13.4			40.2	12.0	73.9	11.5		
<i>Middle-ring-little fingers combination</i>																	
20.8	13.3	67.0	30.8	89.7	24.9	77.5	20.0			65.6	16.8	78.8	15.7	68.8	17.8		
<i>Index-middle-ring-little fingers combination</i>																	
63.8	11.8	68.4	24.8	76.7	20.7	75.9	34.0	56.2	13.2	54.6	19.3	59.7	16.0	67.6	20.8		

Note. Enslaving forces of idle fingers were recorded for the on condition.



calculated on the basis of the on condition reference, was smaller than the deficit calculated on the basis of the off condition reference (see also Equation 3).

Discussion

We have reported that the force production of the master fingers was affected by the position of the idle fingers. In a majority of finger combinations (8 out of 14), the flexion forces increased significantly when the idle fingers were lifted away from the sensors. For example, the middle finger task produced a 26% higher force when the index, ring, and little fingers were lifted than when they remained on the supporting surface. Other three-finger combinations showed a trend of increasing the flexion force when the idle fingers were held off the keys, but the increase did not reach the significance level.

The finding that the flexion force of a set of fingers is increased by lifting the idle fingers is consistent with previous observations by Latash, Li, & Zatsiorsky, (1998). In their study, participants generated a level of finger flexion force and then self-initiated a series of tapping movements with one of the pressing fingers. During index or middle finger tapping, the nontapping fingers showed increases in the flexion force in a feed-forward manner. Latash and his colleagues attributed the simultaneous force increase accompanied by the sudden removal of a finger to error compensation, a proposition that is in line with the idea that human digits are not controlled independently but rather behave synergistically as a single unit (Cole & Abbs, 1986; Darling et al., 1988). In the current study, however, the finger position was preset, and therefore participants did not

need to correct errors such as those caused by tapping the finger; yet, an increase in force was still observed.

One possible explanation for the improvement in the master fingers flexion force caused by lifting the idle fingers is that the flexor muscles are stretched when the idle fingers are lifted because the lifting involves a certain degree of finger extension. The stretching of the flexor muscle compartments of the idle fingers would increase the excitatory input from the muscle spindles to the motoneuron pool of the flexor muscle compartments of the master fingers.

Some biomechanically related motor control strategies, particularly the so-called minimization of secondary moment, might play a role in the enhancement of finger flexion force by the lifting of the idle fingers. When a participant produces a steadily increasing ramp force with a set of fingers, the force sharing among fingers is established at the beginning of the trial and remains constant throughout the ramp (Amis, 1987; Kinoshita et al., 1995; Li et al., 1998). The secondary moment hypothesis was proposed as an explanation for that simple force-sharing strategy (Danion, Latash, Li, & Zatsiorsky, 2000; Li et al., 1998), although it has been found that this principle might be violated in certain situations (Danion, Latash, Li, & Zatsiorsky, 2001). According to the hypothesis, finger forces are coordinated in such a way that the total moment generated by all fingers with respect to the longitudinal neutral axis of the hand is minimized. That proposal might partially explain the increase in the flexion force production in the off condition. When pressing fingers in the off condition, the hand tended to rotate about the longitudinal axis that was opposite to the idle fingers. As a result, the longi-

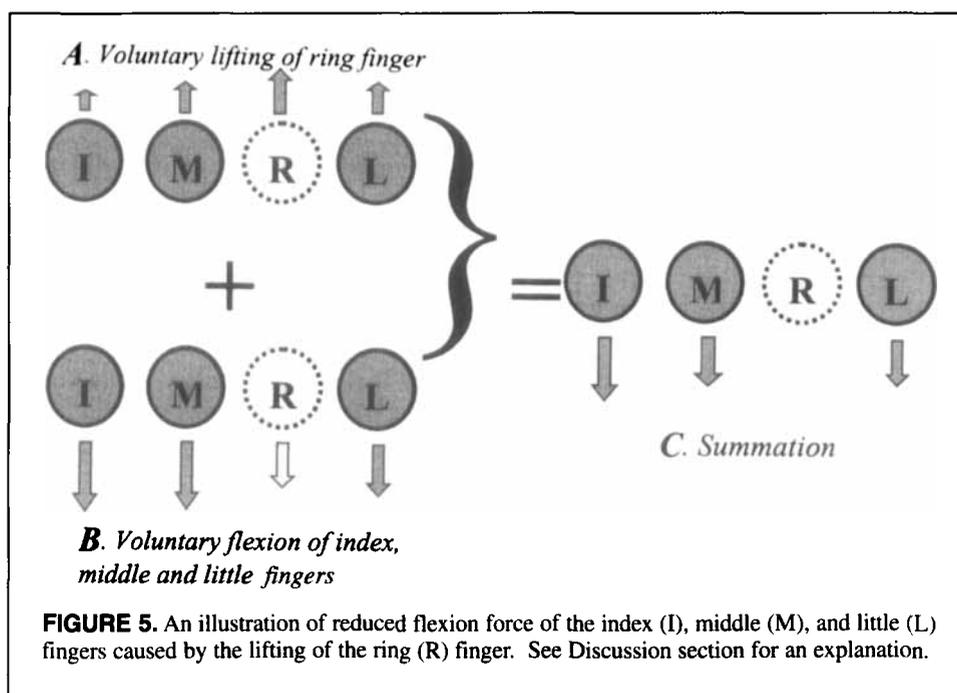
tudinal neutral axis was aligned closer to the point of resultant force application by the master fingers. For example, when the index finger produced flexion force, the resultant force application was at the tip of the index finger, which would tend to produce a supination moment while all other fingers remained on the supporting surface. If the middle, ring, and little fingers were lifted up, the lifting would pronate the hand and shift the longitudinal axis of the hand closer to the index finger, thus avoiding the exertion of other muscular effort in the hand or forearm to balance the secondary moment.

The rotational effect was further supported by the results from the multifinger combinations. In three-finger combinations, for example, an adjacent finger combination (IMR or MRL) produced higher total force when the idle finger was allowed to be lifted up (off condition) than when the idle finger was kept on the support surface (on condition), whereas force produced by a nonadjacent finger combination (IML or IRL) in the off condition was not greater, or was even smaller, than the force produced in the on condition. The reason for that finding might be that in nonadjacent finger combinations, the lifting of the idle finger does not allow the desired rotation of the hand because the hand position is constrained by master fingers adjacent to the idle finger in both radial and ulnar sides.

In most of the combinations, lifting the idle fingers enhanced the force-production capability of the master fingers. In certain finger combinations, however, the flexion force might also be reduced by lifting the idle fingers (e.g., IML task; Table 1). Interdependence among fingers might help explain the decreased maximal force contraction in certain finger combinations. Interdependence among fingers within a hand has been reported in motion tasks (Flan-

ders & Soechting, 1992; Schieber, 1995), finger force production (Zatsiorsky et al., 1998), and muscle activities (Kilbreath & Gandevia, 1994). Studies of finger kinematics have shown that voluntary extension–flexion of one finger can induce accompanying involuntary flexion–extension of other fingers (Flanders & Soechting, 1992; Schieber, 1995). In multifinger isometric flexion tasks, Zatsiorsky et al. (1998) demonstrated the effect of force enslaving among fingers; that is, when a participant was asked to press maximally with one, two, or three fingers without lifting the other fingers, the other fingers also produced certain forces. The interaction among fingers might be explained by peripheral mechanical interconnections (von Schroeder, Botte, & Gellman, 1990), co-activation of muscle bellies or branches (Kilbreath & Gandevia, 1994; Leijnse, 1997), or central convergence–divergence mechanisms (Lemon, Mantel, & Muir, 1986; Schieber & Hibbard, 1993), alone or in combination.

A hypothesis as to how the interdependence among fingers might affect force production is illustrated in Figure 5 for the IML combination in the off condition as an example. When the ring finger is lifted, the index, middle, and little fingers tend to be lifted as well (Figure 5A). When the index, middle, and little fingers produce flexion force, the ring finger also flexes involuntarily (Figure 5B), and that enslaving force can be as high as 30% of its single-finger maximal force (Zatsiorsky et al., 1998). To keep the ring finger away from the supporting surface (by instruction), the large enslaving force on the ring finger must be negated by a large extension force on that finger, which tends to produce extension of all the other fingers. As a result, the flexion forces for the index, middle, and little fingers are counteracted by the extensor enslaving forces that are caused by



the voluntary extension of the ring finger (Figure 5C). That is what we observed in the experiment—a significant force drop of the little finger in the IML combination when the ring finger was lifted (Table 1). The functional dependency among muscle compartments can also help explain the relatively large force deficit in tasks such as ML, IML, and IRL, in which the lifted finger or fingers are functionally connected with the flexion (intended) fingers.

In the current study, we confirmed previous findings regarding multifinger force deficit (Li et al., 1998; Ohtsuki, 1981a) and probed that phenomenon to a greater extent. Ohtsuki (1981b) studied the multifinger pulling exertion with six different finger combinations: IM, MR, RL, IMR, MRL, and IMRL. The magnitude of force generation by finger pulling in Ohtsuki's study was much higher than the press force (105 N) of the current study; the force actualization (i.e., percentage value), however, was similar. For example, the participants in Ohtsuki's experiment produced a total of 430 N for four-finger pulling, whereas a total of 105-N four-finger pressing force was obtained in the present study. For force actualization, the pulling forces of the index and middle finger acting together were 84.6% and 86.5% of their single-finger strength in Ohtsuki's study. The corresponding values in the current study were 80.1% and 74.7%. Ohtsuki (1981a) proposed the hypotheses of synergistic inhibition, and Li et al. (1998) proposed the central ceiling hypothesis to explain the force deficit phenomenon.

One limitation in the current study is that the tasks of the two experimental conditions were performed on 2 consecutive days in a fixed order. There might have been a practice effect of first-session performance on the second-session test. However, we believe that because the finger control mechanisms under investigation are formed by extensive use of the hand for years (> 20), dozens of pressing tasks on 1 day are unlikely to change the observed phenomena.

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