RESEARCH NOTE

Finger force enslaving and surplus in spinal cord injury patients

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Abstract This study investigated the phenomena of finger enslaving, involuntary finger actions by non-intended fingers, and force deficit, smaller maximum force by all four fingers than the sum of individual finger maximum forces in individuals with cervical spinal cord injuries (SCI). A total of 16 subjects participated in this study: 8 with a cervical spinal cord injury and 8 controls. Each of the injured subjects had one paralyzed finger. The results showed that the efforts to produce force using any individual finger induced force production in all other fingers, suggesting finger force enslaving. The maximum force during the four-finger task was greater than the sum of the individual finger forces during single-finger tasks in the SCI group, which was reflected by positive force deficit, "force surplus". One may utilize these findings for rehabilitation of paralyzed fingers caused by cervical spinal injuries.

Keywords Spinal cord injury · Finger independence · Force surplus · Finger enslaving · Force deficit

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J. K. Shim Fischell Department of Bioengineering, University of Maryland, College Park, MD 20742, USA Impaired hand strength and dexterity severely limits daily living activities of individuals with cervical spinal injuries (Colver and Kappelman 1981; Beekhuizen 2005). One of the critical factors affecting hand dexterity is the ability to move fingers individually (Schieber and Santello 2004). When the central nervous system (CNS) tries to move a single finger or produce force using a single finger, other non-intended fingers also move or produce forces. This coupling phenomenon has been known as finger enslaving or finger inter-dependency (Zatsiorsky et al. 1998; Shim et al. 2006). Finger enslaving is caused by various constraints such as biomechanical, neural and task constraints. Biomechanical constraints include musculotendinous connections in the forearm and hand. For example, the flexor digitorum profundus, an extrinsic muscle located in the forearm, is connected to each of the fingers by tendons that run along the arm and into the hand; it enables flexion of the fingers (Malerich et al. 1987; Kilbreath and Gandevia 1994). There are usually several finger movers involved even in a single finger action while multiple fingers often share common muscles. Kilbreath and Gandevia (1994) recorded motor unit firing of the flexors of distal phalanges of fingers, flexor pllicis longus and digital portions of flexor digitorum profundus, and showed that there existed varied coactivation of these muscles. They also demonstrated that it was not possible to deliver independent neural signals to thumb and finger muscles.

Other neural constraints also cause interdependent finger actions. Schieber et al. showed that individual fingers do not occupy segregated areas in the motor cortex (M1) (Schieber and Hibbard 1993). Motor tasks can cause fingers to be interdependent as well. When a person holding a glass of water with all five digits tries to increase thumb force, other finger forces will also increase in order to satisfy static mechanics. For example, the sum of digit forces should be equal to zero for static grasping (Shim et al. 2004, 2005b). Previous studies have shown that the independent actions of fingers constrained by biomechanical and neural factors change with practice, resistance training, child development and aging (Shinohara et al. 2003; Shim et al. 2007, 2008a; Oliveira et al. 2008). Previous studies on multi-finger actions in healthy populations also showed that the maximum force of all four fingers together is often smaller than the sum of maximum individual finger forces. This phenomenon has been known as finger force deficits (Zatsiorsky et al. 1998).

Individuals with a cervical spinal cord injury (SCI) often have limited functions in hands and upper extremities causing difficulties in even simple daily manipulation activities such as grasping a spoon and handwriting (Beekhuizen 2005). Due to the disruption and reorganization of the neural network after SCI, we suspected that the independent finger actions and force deficit might change. The overall goal of this study is to describe finger interactions, such as force enslaving and force deficit, during maximum finger force production tasks in persons with selective finger paralysis after cervical SCI. We hypothesized that (1) paralyzed fingers will produce involuntary forces during maximum force production by other functioning fingers in individuals with SCI and (2) the maximum force during four fingers will be greater than the sum of individual finger maximum forces during individual finger tasks (i.e., force surplus).

A total of 16 right-handed subjects were recruited for the study. The SCI group consisted of eight males with traumatic spinal cord injuries at the cervical level (C6–C8) (age: 35.9 ± 14.0 years; history of SCI: 11.8 ± 10.4 years; American Spinal Injury Association Motor Score: 47.5 \pm 12.2). Each SCI subject, identified from pre-tests of individuals with spinal cord injuries, had paralysis in only one of the four fingers on the right hand. This paralysis was determined by assessing the maximum pressing or flexion finger force at the fingertips. When a finger produced a pressing force less than 0.5 N in magnitude, the finger was considered "paralyzed". Some subjects produced lifting force, causing negative forces. The average force produced by the paralyzed fingers was 0.11 ± 0.21 N and was not statistically different from zero. Among the eight SCI subjects, the paralyzed fingers were two index fingers, two middle fingers, two ring fingers and two little fingers. Eight age-matched control (CTR) subjects $(35.7 \pm 9.9 \text{ years})$ without a history of anatomical or neurological disorders participated in this study as the CTR group. All subjects gave informed consent based on the procedures approved by the university's internal review board (IRB).

The experimental setup (Fig. 1a) included four force sensors with amplifiers, one for each finger (i.e., second to fifth digits) (Models 208 M182 and 484B, Piezotronics, Inc.). The sensors were mounted on a customized aluminum frame $(14.0 \times 9.0 \times 1.0 \text{ cm})$ along four slits, which allowed for adjustments of the sensor positions along the long axis of fingers, taking into consideration the different individual hand and finger sizes of the subjects (Fig. 1b). Adjacent slits were separated medio-laterally by 20 mm. The frame was attached to a large aluminum panel $(21.0 \times 16.0 \times 2.0 \text{ cm})$ with a vertical slit (14.0 cm), which allowed the frame 2 degrees-of-freedom: vertical translation and rotation about the Z-axis. C-shaped aluminum thimbles were attached at the bottom of each sensor. The frame was tilted at 25° with respect to the anteroposterior axis (X-axis) such that all finger joints (distal inter-phalangeal, proximal inter-phalangeal and metacarpophalangeal) were slightly flexed when the distal phalanges were positioned inside the thimbles. After the position adjustment, the frame was mechanically fixed to the panel using a nut-bolt structure. Detailed descriptions of the experimental setup can found in previous publications (Shim et al. 2008a, b).

All subjects sat in a chair facing a computer screen with their shoulder abducted to 35° in the frontal plane and their elbow flexed to 45° in the sagittal plane such that the forearm was parallel to the frame. The forearm rested on the customized wrist–forearm brace, composed of a piece of foam that was attached to a semi-circular plastic cylinder and fixed to a wooden panel (29.8 × 8.8 × 3.6 cm). Velcro straps were used to avoid forearm, wrist and hand movements.

The subjects were asked to rest the distal phalange of each finger in a thimble such that all joints were slightly flexed and formed a dome shape with the hand (Fig. 1b). In order to remove the gravitational effects of the fingers and any possible favor to finger flexion or extension due to passive stretching of the intrinsic and extrinsic muscles of the finger, the force signals for the initial 0.5 s before voluntary force production by subjects were averaged for each finger and subtracted from the later force signals for each trial. Thus, only the force signals after subtraction were shown on the computer monitor as real-time feedback.

Subjects performed five conditions of the maximum voluntary force (MVF) task for isometric fingertip pressing: I, M, R and L individually for single-finger tasks and IMRL together for a four-finger task. Only one trial was performed for each condition because SCI subjects tend to fatigue easily. The order of the conditions was balanced across subjects. During each trial, all fingers were in the thimbles. Subjects were asked to produce maximum isometric force with the task finger(s) in flexion over a 3-s interval while watching the force feedback of the task finger(s) on the computer screen. The experimenter watched the subjects' right hand carefully for any joint

Fig. 1 Experimental setting: a The wrists and the forearms of the subject were rested in a wrist-forearm brace and held by Velcro straps. The subject sat in a chair and watched the computer screen to perform a task. b The experimental settings for the right hand: the force sensors were attached to an aluminum frame and the C-shaped thimbles were attached to the bottom of the sensors



movements. Trials with visible finger or wrist joint movements were rejected and performed again by the subjects. The subjects were instructed to concentrate on the task finger and to ignore the non-task finger actions. The force produced by the task finger was displayed in realtime on the computer screen in front of the subject. At the beginning of each trial, the computer generated a 'get ready' sound, which reminded subjects to relax their hand and fingers.

Signals from the force sensors were conditioned, amplified and digitized at 1,000 Hz with a 16-bit A/D board (PCI 6034E, National Instruments Corp.) and a custom software program made in LabVIEW (LabVIEW 7.1, National Instruments Corp.).

The peak magnitudes of the individual finger forces and the four-finger force were used to estimate MVF of fingers as finger strength. For each MVF trial of single-finger force production, however, the non-task fingers produced forces as well. When a task finger, for example the index finger, produces force, other non-task fingers, the middle, ring and little fingers, also produce forces. The forces produced by the non-task fingers, referred to as enslaving forces, were expressed as a percentage of the maximum force of the four-finger task. The average of the non-task finger forces was quantified as finger force enslaving of the task finger *i* (EN_{*i*}; Eq. 1):

$$EN_{i} = \sum_{j=1}^{n} \left(F_{ij} / F_{IMRL} \right) / (n-1)100\%, \quad i \neq j$$
(1)

where *i* is the task finger, *j* enumerates all other functioning fingers and the paralyzed finger during functioning finger *i* task (EN of functioning fingers) or every functioning fingers during paralyzed finger task (EN of paralyzed finger); n = 4.

When task fingers, the middle, ring and little fingers, produce forces during single-finger tasks, a non-task finger, the index finger, produces forces. The average of the non-task finger forces during the tasks of the other fingers was quantified as finger force enslaved (ED_u; Eq. 2):</sub>

$$ED_{u} = \sum_{v=1}^{n} (F_{vu}/F_{IMRL})/(n-1)100\%, \quad u \neq v$$
 (2)

where u is the non-task finger, v enumerates all other functioning fingers and paralyzed finger if u finger is a functioning finger (EDs of functioning fingers) or all functioning fingers if u finger is the paralyzed finger (ED of paralyzed fingers); n = 4.

Note that Eqs. 1 and 2 are different from the EN and ED calculations used in previous studies (Zatsiorsky et al. 1998; Shim et al. 2006). The enslaving values were normalized by individual finger MVF values in the previous studies, while the enslaving forces were normalized by the four-finger MVF values in this study. It was necessary because the enslaving forces could not be normalized by zero forces in the cases of the paralyzed fingers.

In the SCI group, the EN and ED values were calculated for paralyzed fingers and functioning fingers separately. In the CTR group, two subjects were randomly selected for the calculation of EN and ED values of an individual finger. The surrogate data sets were used to calculate the EN and ED values for functioning and paralyzed fingers in the CTR group. This rearrangement of data was performed for statistical comparisons between two subject groups under two finger conditions, paralyzed and functioning.

The force deficit (FD) for each finger was calculated by taking the difference between the sum of single-finger MVF's during single-finger tasks and the four-finger MVF during the four-finger task. This value was normalized by the four-finger MVF and averaged over all fingers to calculate the overall FD (Eq. 3). In the SCI group, the FD values were calculated for paralyzed fingers and functioning fingers separately. In the CTR group, two subjects were randomly selected as a surrogate data set for the calculation of FD values of paralyzed and functioning fingers:

$$FD_i = (F_{i,IMRL} - F_{i,i})/F_{IMRL} \times 100\%$$
(3)

where $F_{i,\text{IMRL}}$ means *i* finger force during four-finger task, $F_{i,i}$ stands for *i* finger force during *i* finger task, and F_{IMRL} is four-finger maximum force.

Analysis of variance (ANOVA) was performed with the between-subject factor of GROUP (2 levels: SCI and CTR) and the within-subject factors of FINGER (4 levels: index, middle, ring and little or 2 levels: "paralyzed" fingers and "functioning" fingers). The critical value for significant difference was set at p = 0.05. Bonferonni corrections were used for multiple comparisons. Normality and homogeneity assumptions were tested before ANOVA.

The strength of the functioning fingers of the CTR group, assessed by MVF during individual finger tasks, was about 25 times greater than those of the SCI group. In both cases, the strength of the index and middle fingers were greater than the ring and little fingers. These findings were supported by the significant effects of GROUP [F(1,7) = 237.6, p < 0.001] and finger [F(3,21) = 22.2, p < 0.001: I = M > R = L]. The interaction was not significant. The relative strengths of individual fingers were similar between the SCI and CTR groups.

When paralyzed fingers were task fingers, these fingers did not produce force. If any force was produced, it was close to zero. Non-task functioning fingers produced significant involuntary forces during paralyzed finger force production (Fig. 2a). The force enslaving (EN) of paralyzed fingers in the SCI group was smaller than the EN of functioning fingers seen both in the SCI and CTR groups. These findings were supported by the significant FINGER effect [F(1,13) = 8.6, p < 0.05] and the significant

GROUP × FINGER interactions [F(1,13) = 8.4, p < 0.05]. There was no significant GROUP effect. Conversely, when functioning fingers were task fingers and the paralyzed fingers were non-task fingers, the paralyzed fingers also produced forces (Fig. 2b). There was no significant factor effect or interaction effect in the ED values. Even though the enslaved force produced by the paralyzed fingers seemed to be higher than that of the functioning fingers, there were no significant differences between the ED values.

The sum of individual finger MVF values was greater than the four-finger MVF value in the CTR group (Fig. 2c), which was shown by positive FD in the CTR group (Fig. 2d). However, the opposite was observed with the SCI group. The sum of individual finger MVF values was smaller than the four-finger MVF value for paralyzed fingers and functioning fingers, demonstrating a "force surplus" rather than force deficit. This finding was supported by the significant factor GROUP effect on FD values [F(1,13) = 80.3, p < 0.001]. There was no FINGER effect or interaction.

The results of this study showed that the paralyzed fingers produced involuntary forces during functioning finger tasks, although they were incapable of producing voluntary force during paralyzed finger tasks. The maximum force during the four-finger task was greater than the sum of the individual finger forces during single-finger tasks in the SCI group, which was reflected by positive force deficit or force surplus.

Previous studies have shown that independent actions of fingers in a healthy population are constrained mainly by two factors: biomechanical and neurological constraints

Fig. 2 a Finger force enslaving (EN: the average force produced by the non-task fingers expressed as a percentage of the maximum force of the fourfinger task) and b finger force enslaved (ED: the average of the non-task finger forces during the tasks of the other fingers), c sum of individual finger maximum forces (sum) and four-finger maximum force (IMRL), and d finger force deficits (FD). P and F represent paralyzed fingers and functioning fingers, respectively. Mean \pm standard errors are shown. p < 0.001



(see Schieber and Santello (2004) for review). The biomechanical constraints include mechanical connections of muscles and tendons, while the neurological constraints include the CNS's control of fingers. For example, independent actions of individual fingers can decrease due to tendon insertions of the same muscle into multiple fingers (Malerich et al. 1987) and shared outputs of neurons in the primary M1 to different finger muscles (Fetz and Chenev 1980; Bremner et al. 1991; Matsumura et al. 1996). It is still unknown from this study regarding the location of neural constraints, although the force surplus and enslaving of paralyzed fingers could be caused by the shared neural outputs among individual fingers and overflow of the neural signals (Kilbreath and Gandevia 1994; Schieber 2001; Schieber and Santello 2004; Shim et al. 2008b). SCI causes neurological disruptions at the spinal cord leading to changes in the behavioral interpretations of commands from the brain. The disruptions of neural signals were reflected in our results showing dramatic decreases of finger MVF values. A surprising result was the force production by the paralyzed fingers during functioning finger tasks, and force production by the functioning fingers during paralyzed finger tasks. These findings suggest that although the neural pathway responsible for the paralyzed finger movements was disrupted due to injury of the spinal cord, biomechanical and neural connections can induce involuntary force production of paralyzed fingers. For example, when the index finger was paralyzed, the CNS could still enable movement in the middle finger by sending a signal to an extrinsic muscle in the forearm, the flexor digitorum profundus. However, since the same tendon inserts into both the index and middle fingers, activation of this shared muscle could transmit the muscle force, and therefore enable movement, in both the middle and index fingers. We also observed the involuntary force production of the functioning fingers during paralyzed fingers' MVF tasks. This could be realized by neural signals to intrinsic muscles of functioning fingers, the lumbricals, activated only by the "intention" to produce force of the paralyzed fingers. Future studies on motor neuron stimulations with electromyography recordings of intrinsic and extrinsic muscles may provide more confirmative evidence regarding this issue.

This study also showed that the paralyzed fingers could induce force production of the functioning fingers. This phenomenon can be explained by the same mechanism responsible for the functioning finger force production during paralyzed finger force production, biomechanical and neural constraints. Moreover, the smaller magnitudes of the unintended functioning finger force during paralyzed finger tasks seem to be due to the decrease in the neural activity responsible for paralyzed finger force. Previous studies on neural network models for finger enslaving suggest that the neural signal to move one finger "overflows" to other fingers (Zatsiorsky et al. 1998; Danion et al. 2003; Shim et al. 2008b). For example, when the index finger is a task finger, the neural signal that moves the index finger overflows to the middle, ring and little fingers. Thus, when an SCI is present, not only will the neural signal producing force in the index finger be reduced, but the neural overflow to other fingers will decrease as well. This claim is also supported by the differences in magnitude of unintended functioning and paralyzed fingers (see Fig. 2a, b).

Previous studies have shown that, in healthy subjects, the sum of the maximum forces produced in individual fingers during single-finger tasks is greater than the fourfinger maximum force, demonstrating finger force deficits (Zatsiorsky et al. 1998; Shim et al. 2006). The control subjects in our study showed similar trends. However, the SCI subjects showed the opposite phenomenon, a force surplus. Persons with a spinal cord injury could produce greater force during four-finger task than the sum of individual finger maximum force. This force surplus seemed to be caused by the finger enslaving effects on paralyzed fingers during functioning finger tasks as well as functioning fingers during paralyzed finger tasks (see Fig. 2c). The inability to produce force using paralyzed fingers also seemed to contribute to the phenomenon of force surplus. A reasonable step for future research may include the development of a neural network model that can explain the relationship of finger force enslaving and force deficits to the finger force outputs. This process may require force production tasks involving all finger combinations for two- and three-finger tasks (Danion et al. 2003).

Patients with cervical SCI often experience partial or complete paralysis of the upper extremities. The involuntary forces of paralyzed fingers during functioning finger tasks and the involuntary forces of functioning fingers during paralyzed finger tasks found in this study may better assist finger rehabilitation in SCI patients. In upcoming studies, we plan to investigate the possibility of the recovery of paralyzed fingers in SCI patients after training both non-paralyzed and paralyzed fingers. Based on the neural network model suggested in previous studies (Zatsiorsky et al. 1998; Danion et al. 2003), one can expect to discover increases in voluntary and involuntary strength of the paralyzed fingers from strength training. The hand and forearm have extremely large motor redundancy in terms of finger actions, because multiple muscles are activated for even a simple finger movement (Burgar et al. 1997; Valero-Cuevas et al. 1998). Previous studies have demonstrated that individuals with SCI can benefit from relatively long-term practise or training (Gregory et al. 2007; Hoffman and Field-Fote 2007; Kleim et al. 2007; Kakebeeke et al. 2008). There is also evidence that the training effect on hand dexterity can be enhanced with somatosensory stimulation (Beekhuizen and Field-Fote 2005) through neural reorganization and enhancement of the existing neural connections (Lapointe et al. 2007; Nishimura et al. 2007). The SCI individuals with partial impairments of hand and finger functions may benefit from the redundancy, because the functional improvements of functioning finger muscles may cause the secondary recovery of the paralyzed fingers.

It is still unknown if the findings of this study are due to the SCI or adaptive consequences of the neuronal systems in response to the SCI. The current study is limited in providing an evidence of cortical plasticity after SCI. Long-term monitoring of individuals with SCI may provide useful information on plastic changes of independent actions of fingers and other finger interactions such as finger force deficits and finger force sharing. Applying transcranial magnetic stimulations (TMS) on motor cortex to elicit motor outcomes, finger forces and motor evoked potentials may also provide insights into the plastic changes of neural connections of finger interactions after SCI over time (Levy et al. 1990; Shim et al. 2005a). It is also to be noted that the mechanism responsible for selective finger paralysis in SCI subjects is currently unknown.

Conflict of interest statement No conflict of interest exists.

References

- Beekhuizen KS (2005) New perspectives on improving upper extremity function after spinal cord injury. J Neurol Phys Ther 29:157–162
- Beekhuizen KS, Field-Fote EC (2005) Massed practice versus massed practice with stimulation: effects on upper extremity function and cortical plasticity in individuals with incomplete cervical spinal cord injury. Neurorehabil Neural Repair 19:34–45
- Bremner FD, Baker JR, Stephens JA (1991) Correlation between the discharges of motor units recorded from the same and from different finger muscles in man. J Physiol 432:355–380
- Burgar CG, Valero-Cuevas FJ, Hentz VR (1997) Fine-wire electromyographic recording during force generation. Application to index finger kinesiologic studies. Am J Phys Med Rehabil 76:494–501
- Colyer RA, Kappelman B (1981) Flexor pollicis longus tenodesis in tetraplegia at the sixth cervical level. A prospective evaluation of functional gain. J Bone Joint Surg Am 63:376–379
- Danion F, Schoner G, Latash ML, Li S, Scholz JP, Zatsiorsky VM (2003) A mode hypothesis for finger interaction during multifinger force-production tasks. Biol Cybern 88:91–98
- Fetz EE, Cheney PD (1980) Postspike facilitation of forelimb muscle activity by primate corticomotoneuronal cells. J Neurophysiol 44:751–772
- Gregory CM, Bowden MG, Jayaraman A, Shah P, Behrman A, Kautz SA, Vandenborne K (2007) Resistance training and locomotor recovery after incomplete spinal cord injury: a case series. Spinal Cord 45:522–530

- Hoffman LR, Field-Fote EC (2007) Cortical reorganization following bimanual training and somatosensory stimulation in cervical spinal cord injury: a case report. Phys Ther 87:208–223
- Kakebeeke TH, Hofer PJ, Frotzler A, Lechner HE, Hunt KJ, Perret C (2008) Training and detraining of a tetraplegic subject: highvolume FES cycle training. Am J Phys Med Rehabil 87:56–64
- Kilbreath SL, Gandevia SC (1994) Limited independent flexion of the thumb and fingers in human subjects. J Physiol 479(Pt 3):487– 497
- Kleim JA, Kleim ED, Cramer SC (2007) Systematic assessment of training-induced changes in corticospinal output to hand using frameless stereotaxic transcranial magnetic stimulation. Nat Protoc 2:1675–1684
- Lapointe NP, Ung RV, Guertin PA (2007) Plasticity in sublesionally located neurons following spinal cord injury. J Neurophysiol 98:2497–2500
- Levy WJ Jr, Amassian VE, Traad M, Cadwell J (1990) Focal magnetic coil stimulation reveals motor cortical system reorganized in humans after traumatic quadriplegia. Brain Res 510:130–134
- Malerich MM, Baird RA, McMaster W, Erickson JM (1987) Permissible limits of flexor digitorum profundus tendon advancement: an anatomic study. J Hand Surg [Am] 12:30–33
- Matsumura M, Chen D, Sawaguchi T, Kubota K, Fetz EE (1996) Synaptic interactions between primate precentral cortex neurons revealed by spike-triggered averaging of intracellular membrane potentials in vivo. J Neurosci 16:7757–7767
- Nishimura Y, Onoe H, Morichika Y, Perfiliev S, Tsukada H, Isa T (2007) Time-dependent central compensatory mechanisms of finger dexterity after spinal cord injury. Science 318:1150–1155
- Oliveira MA, Hsu J, Park J, Clark JE, Shim JK (2008) Age-related changes in multi-finger interactions in adults during maximum voluntary finger force production tasks. Hum Mov Sci 27:714– 727
- Schieber MH (2001) Constraints on somatotopic organization in the primary motor cortex. J Neurophysiol 86:2125–2143
- Schieber MH, Hibbard LS (1993) How somatotopic is the motor cortex hand area? Science 261:489–492
- Schieber MH, Santello M (2004) Hand function: peripheral and central constraints on performance. J Appl Physiol 96:2293– 2300
- Shim JK, Latash ML, Zatsiorsky VM (2004) Prehension synergies in three dimensions. J Neurophysiol 93:766–776
- Shim JK, Kim SW, Oh SJ, Kang N, Zatsiorsky VM, Latash ML (2005a) Plastic changes in interhemispheric inhibition with practice of a two-handforce production task: a transcranial magnetic stimulation study. Neurosci Lett 374:104–108
- Shim JK, Latash ML, Zatsiorsky VM (2005b) Prehension synergies: trial-to-trial variability and principle of superposition during static prehension in three dimensions. J Neurophysiol 93:3649– 3658
- Shim JK, Oliveira MA, Hsu J, Huang J, Park J, Clark JE (2006) Hand digit control in children: age-related changes in hand digit force interactions during maximum flexion and extension force production tasks. Exp Brain Res 176:374–386
- Shim JK, Oliveira MA, Hsu J, Huang J, Park J, Clark JE (2007) Hand digit control in children: age-related changes in hand digit force interactions during maximum flexion and extension force production tasks. Exp Brain Res 176:374–386
- Shim JK, Hsu J, Karol S, Hurley BF (2008a) Strength training increases training-specific multifinger coordination in humans. Mot Control 12:311–329
- Shim JK, Karol S, Hsu J, de Oliveira MA (2008b) Hand digit control in children: motor overflow in multi-finger pressing force vector space during maximum voluntary force production. Exp Brain Res 186:443–456

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Shinohara M, Latash ML, Zatsiorsky VM (2003) Age effects on force produced by intrinsic and extrinsic hand muscles and finger interaction during MVC tasks. J Appl Physiol 95:1361–1369

Valero-Cuevas FJ, Zajac FE, Burgar CG (1998) Large index-fingertip forces are produced by subject-independent patterns of muscle excitation. J Biomech 31:693–703 Zatsiorsky VM, Li ZM, Latash ML (1998) Coordinated force production in multi-finger tasks: finger interaction and neural network modeling. Biol Cybern 79:139–150