Human Movement Science 33 (2014) 185–193

Contents lists available at ScienceDirect

Human Movement Science

journal homepage: www.elsevier.com/locate/humov

Finger enslaving in the dominant and non-dominant hand

Luke A. Wilhelm [a,*], Joel R. Martin [b], Mark L. Latash [a], Vladimir M. Zatsiorsky [a]

[a] The Biomechanics Laboratory, Department of Kinesiology, The Pennsylvania State University, University Park, PA 16802, USA
[b] School of Recreation, Health, and Tourism, George Mason University, 10900 University Blvd, Manassas, VA 20110, USA

ARTICLE INFO

Article history:
Available online 18 December 2013

Keywords:
Laterality
Isometric force production
Finger interaction
Neural network

ABSTRACT

During single-finger force production, the non-instructed fingers unintentionally produce force (finger enslaving). In this study, enslaving effects were compared between the dominant and non-dominant hands. The test consisted of a series of maximum voluntary contractions with different finger combinations. Enslaving matrices were calculated by means of training an artificial neural network. The dominant hand was found to be stronger, but there was found to be no difference between the overall enslaving effects in the dominant and non-dominant hands. There was no correlation between the magnitude of finger enslaving and the performance in such tests as the Edinburgh Handedness Inventory, the Grooved Pegboard test, and the Jebsen-Taylor Hand Function test. Each one of those three tests showed a significant difference between the dominant and non-dominant hand performances. Eleven subjects were retested after two months, and it was found that enslaving effects did not fluctuate significantly between the two testing sessions. While the dominant and non-dominant hands are involved differently in everyday tasks, e.g. in writing or eating, this practice does not cause significant differences in enslaving between the hands.

1. Introduction

Studies of multi-finger tasks have revealed several aspects of finger interactions, such as force deficit and enslaving (Kim, Shim, Zatsiorsky, & Latash, 2008; Li, Danion, Latash, Li, & Zatsiorsky, 2000a;

* Corresponding author. Tel.: +1 (717) 808 1733.
E-mail addresses: law326@psu.edu (L.A. Wilhelm), joel.r.martin@gmail.com (J.R. Martin), mll11@psu.edu (M.L. Latash), vxz1@psu.edu (V.M. Zatsiorsky).

0167-9457/$ - see front matter
http://dx.doi.org/10.1016/j.humov.2013.10.001

Ohtsuki, 1981; Schieber & Santello, 2004; Slobounov, Chiang, Johnston, & Ray, 2002a; Slobounov, Johnston, Chiang, & Ray, 2002b; Zatsiorsky, Li, & Latash, 1998; Zatsiorsky, Li, & Latash, 2000; Zhang, Sainburg, Zatsiorsky, & Latash, 2006). Force deficit describes the tendency of individual fingers during multi-finger pressing tasks to produce less maximal force than during single-finger tasks. Enslaving is the unintentional force production by non-instructed fingers when one or more fingers of the same hand produce force intentionally. These interactions have been shown to persist over the whole range of finger forces and have been modeled using neural networks (Danion et al., 2003; Gao, Li, Li, Latash, & Zatsiorsky, 2003; Zatsiorsky et al., 1998). Enslaving has been considered an indirect measure of dexterity, as smaller enslaving effects (EEs) would imply a greater ability to move fingers independently (Li, Danion, Latash, Li, & Zatsiorsky, 2000b).

Neural network models have been used to relate neural commands to forces produced by fingers (Zatsiorsky et al., 1998). Previous neural network models consisted of: (1) an input layer that models a central neural drive; (2) a hidden layer that accounts for finger interactions; and (3) an output layer that models the force output of fingers and receives inputs both from the input and middle layers. These models included the input from the middle layer scaled by the inverse of the number of the fingers explicitly involved in the task.

The method of neural networks, as opposed to multiple linear regression, has been used to estimate finger interactions because neural networks are more accurately able to model force deficit. Most regression methods completely neglect force deficit, or else become an approximation of the neural network (Danion et al., 2003). A comparison of neural networks with regression methods has shown that the neural network more accurately describes the force production of the fingers for all finger combinations (Martin, Terekhov, Latash, & Zatsiorsky, 2013).

Studies conducted on dominant (D) and non-dominant (ND) arm movements have led to the dynamic-dominance theory of brain lateralization. This theory states that the brain lateralization associated with handedness is a form of motor control specialization, with the D side better suited to dynamic tasks and the ND side better suited to stabilizing tasks (Sainburg, 2002; Sainburg, 2005; Zhang et al., 2006). However, there is no clear evidence from the literature that D and ND hands show differences in finger independence. Several studies have suggested that there is no significant difference between indices of independence of finger actions of the two hands (Häger-Ross & Schieber, 2000; Kimura & Vanderwolf, 1970; Reilly & Hammond, 2004). Li et al. (2000a),Li et al. (2000b) indicated that there are some differences in enslaving effects between the hands. Though no difference was found between the hands when all four finger were compared, when the little finger was neglected, the ND hand was reported to have slightly higher enslaving effects than the D hand (Li et al., 2000a). Zhang et al. (2006) applied the dynamic-dominance theory to four-finger force production. It was hypothesized that the D hand would show advantages in controlling the production of quick force pulses, while the ND would show advantages for controlling steady force production. The results showed that the D hand showed better control for force pulses, but no similar advantage was found for the ND hand. Such an advantage has been documented in a later study (Park, Wu, Lewis, Huang, & Latash, 2012).

The purpose of this study was to analyze the EEs in the D and ND hands of right-handed subjects using a neural network approach. Based on the dynamic-dominance theory, we hypothesized that fingers of the D hand would be more independent and show smaller EEs than the fingers of the ND hand. The second hypothesis was that the magnitude of EEs in both hands would correlate with functional test measures reflecting handedness.

2. Methods

Twenty-two volunteers took part in the study. All subjects were right-handed males (age: 26.9 ± 1.6 years, height: 176.8 ± 1.7 cm, mass: 74.8 ± 2.7 kg). The subjects' right hand length and width were 18.7 ± 0.2 cm and 8.4 ± 0.1 cm, respectively, and the left hand length and width were 19.0 ± 0.2 cm and 8.4 ± 0.1 cm, respectively. Hand length was measured from the distal crease of the wrist to the tip of the middle finger. Hand width was measured across the metacarpophalangeal joints of digits two through five. All subjects were healthy and had no history of hand injury. All subjects gave informed consent according to the procedures approved by the Office for Research Protection of the Pennsylvania State University.

2.1. Equipment

Four unidirectional piezoelectric force transducers (208C02, PCB Piezotronics, Depew, NY) were used to measure the subjects' finger pressing forces. Each sensor could be moved independently along a groove in the longitudinal direction to accommodate different sized hands (Fig. 1). The distance between adjacent grooves was 3 cm.

Signals from the piezoelectric sensors were sent through an AC/DC conditioner (5134B, Kistler, Amherst NY, USA) and then converted by a 16-bit analog-to-digital converter (CA-1000, National Instruments, Austin, TX, USA). LabView (LabVIEW version 8.0, National Instruments, Austin, TX, USA) was used to collect the data and provide visual feedback to the subjects. Data were collected at 200 Hz. Data filtering and neural network analysis was done in Matlab (Matlab 7.11.0, Mathworks, Inc, Natick, MA, USA). Statistical analysis was performed in SAS (SAS 9.3, SAS Institute, Inc, Cary, NC, USA) and Matlab.

2.2. Experimental procedure

Handedness was assessed by the Edinburgh Handedness Inventory. In addition, the subjects performed the Grooved Pegboard test and the Jebsen-Taylor Hand Function test. The standard 10-question format of the Edinburgh Handedness Inventory was used (Oldfield, 1971). Each subject performed the Grooved Pegboard test with the left hand followed by the right hand, and performance times were recorded for both hands. The seven different tasks of the Jebsen-Taylor test were performed by the left hand followed by the right hand, and performance times were recorded for both hands. The functional handedness tests were conducted in this order (left hand followed by right hand) in order to be comparable to other standardized handedness tests.

Subjects performed maximum voluntary contractions (MVCs) with 15 different finger combinations (I, M, R, L, IM, IR, IL, MR, ML, RL, IMR, IML, IRL, MRL, IMRL, where I designates the index finger, M – the middle finger, R – the ring finger, and L – the little finger). During the pressing tasks, the subject's arm rested at approximately 45° of abduction in the frontal plane, 45° of shoulder flexion in the sagittal plane, and 45° of elbow flexion in the sagittal plane (Fig. 1). The palm was supported by a block of foam such that the hand formed a natural arch. For each finger combination, subjects were given a five-second window and were instructed to produce a maximal force with the involved fingers for one

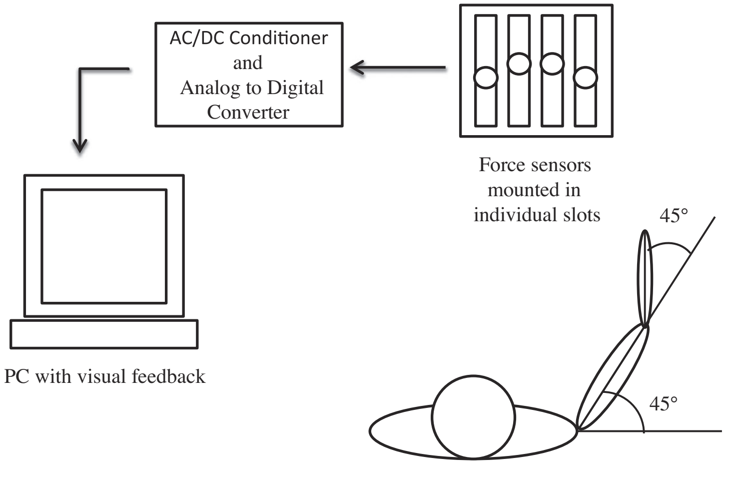

Fig. 1. The experimental setup. ADC is the analog to digital converter.

to two seconds. Subjects were instructed to keep all four fingers on the sensors during a given task, but were instructed to pay no attention to the force produced by the non-instructed fingers. The order of the finger combinations was randomized. The subjects performed the MVC task twice in a row with each finger combination. Several breaks were taken during the test to avoid fatigue.

2.3. Data processing

For each subject, the performance times for the Grooved Pegboard test were converted into a handedness score:

$$\text{Handedness score} = \frac{t_{LH} - t_{RH}}{t_{LH} - t_{RH}} \times 100\% \tag{1}$$

where t_{LH} and t_{RH} are the times for the left and right hands, respectively. The times for the seven tasks in the Jebsen–Taylor Test were also converted into a score using Eq. (1). These scores were then averaged to obtain an overall handedness score for the Jebsen–Taylor test.

Enslaving matrices were calculated from the MVC data by means of training an artificial neural network (Li, Zatsiorsky, Latash, & Bose, 2002; Zatsiorsky et al., 1998). The network consisted of three layers: the input layer, hidden layer, and output layer. This resulted in a matrix equation of the form:

$$\begin{bmatrix} F_I \\ F_M \\ F_R \\ F_L \end{bmatrix} = \frac{1}{n}\begin{bmatrix} W_{11} & W_{12} & W_{13} & W_{14} \\ W_{21} & W_{22} & W_{23} & W_{24} \\ W_{31} & W_{32} & W_{33} & W_{34} \\ W_{41} & W_{42} & W_{43} & W_{44} \end{bmatrix}\begin{bmatrix} X_I \\ X_M \\ X_R \\ X_L \end{bmatrix} + \begin{bmatrix} v_1 & 0 & 0 & 0 \\ 0 & v_M & 0 & 0 \\ 0 & 0 & v_R & 0 \\ 0 & 0 & 0 & v_L \end{bmatrix}\begin{bmatrix} X_I \\ X_M \\ X_R \\ X_L \end{bmatrix} \tag{2}$$

where $F_I \ldots F_L$ are the finger forces for the individual fingers; n is the number of fingers explicitly involved in the task; $w_{11} \ldots w_{44}$ are the finger connection weights; $x_I \ldots x_L$ represent the neural commands sent to each finger, and $v_I \ldots v_L$ are referred to as the gain vector. The neural commands can range from zero (not explicitly involved) to one (maximally involved). The network was trained in MATLAB according to the method described in Zatsiorsky et al. 1998 and Li et al. 2002. A 4×4 interfinger connection matrix (IFC) was created for the IMRL task, changing the form of Eq. (2) to:

$$[\mathbf{F}] = [IFC][\mathbf{X}] \tag{3}$$

where $[\mathbf{F}]$ is the 4×1 vector of finger forces, and $[\mathbf{X}]$ is the 4×1 vector of neural commands (all ones for the IMRL task). Because this IFC was calculated for the IMRL task, the sum of the elements of the IFC represents the total four-finger force for the subject. The IFCs were normalized by dividing the elements of the matrix by the total four-finger force. The trace, i.e. the sum of the diagonal elements, of the normalized IFC matrix represents the percentage of the total force produced due to direct neural commands to each of the four fingers. The off-diagonal elements represent the percentage of the total force produced due to EEs. The twelve off-diagonal elements were summed to create a total EE index for each hand.

2.4. Statistics

The MVC and EE data from the right and left hand were compared using Student's *t*-tests. The EEs of individual fingers were compared using a 2-way ANOVA (*hand* × *finger*). The *hand* factor had two levels (right and left), while the *finger* factor had four levels (I, M, R, and L). Correlations between EEs and handedness scores were calculated using Pearson's *r*.

Reliability of EEs was assessed by retesting 11 subjects approximately two months after the original testing. The EE values were compared using intra-class correlation coefficients (ICC) and the standard error of the mean (SEM) (McGraw, 1996; Shrout & Fleiss, 1979; Weir, 2005). The ICC was given by:

$$\text{ICC} = \frac{MS_s - MS_E}{MS_s + MS_E + \frac{2(MS_T - MS_E)}{n}} \tag{4}$$

Where MS_S, MS_E, and MS_T are the mean squared errors from the ANOVA model for between subjects, error, and between trials, respectively, and n represents the number of subjects. The SEM was given by:

$$\mathrm{SEM} = \sqrt{\frac{SS_{TOTAL}(1 - ICC)}{(n-1)}} \tag{5}$$

where SS_{TOTAL} is the total sum of squares from the ANOVA analysis. As described in Weir (2005), the SEM can be used to calculate a minimum difference:

$$\mathrm{MD} = \mathrm{SEM} \times 1.96\sqrt{2} \tag{6}$$

If the differences between a subject's performances on two different trials is greater than the minimum difference, than the change is considered to be a "real" change in performance that is not due to random variability or systematic error.

3. Results

All the subjects showed force production by both instructed and non-instructed fingers in all the tasks. The four-finger MVC of the left hand (70.6 ± 3.6 N) was, on average, 13.4% less than the MVC for the right hand (81.5 ± 4.2 N) ($t_{21} = -4.57$, $p < .001$).

Results of the IFC matrices, averaged across the 22 subjects, are presented in Table 1. Averaged results of the normalized IFC matrices, normalized by the four-finger MVC force values, are presented in Table 2. The enslaving (EE) indices for each finger were computed by summing the off-diagonal elements of each column of the IFC (Fig. 2). The overall EE indices for the right hand (19.7 ± 1.9%) and the left hand (21.0 ± 2.0%) were not statistically different ($p = .229$). The EE indices for individual fingers were analyzed using the two-way ANOVA (*hand* × *finger*), which showed a significant *finger* effect ($F_{1,168} = 5.93$, $p < .001$) but no significant *hand* effect ($p = .454$) and no significant interaction.

The handedness scores for each subject (Table 3) were compared with EE indices. The average time for the Grooved Pegboard test was 61.04 ± 1.67 s for the right hand and 68.15 ± 1.58 s for the left hand, while the average time for the Jebsen-Taylor test was 5.56 ± 0.13 s for the right hand and 8.99 ± 0.22 s for the left hand. The handedness scores were 79.62 ± 3.89, 0.056 ± 0.012, and 0.135 ± 0.006 for the Edinburgh handedness inventory, the Grooved Pegboard, and the Jebsen–Taylor test, respectively. All three scores were significantly above zero ($t_{21} > 4.6$, $p < 0.001$). The EE indices for individual subjects were compared with the three handedness scores using Pearson's correlation coefficients (Table 3). None of the correlations were significant. As a further test, the subjects were separated into two groups, those with higher left hand EE indices and those with higher right hand EE indices. The EE indices in the two groups were then separately compared with the handedness scores. No systematic correlations were found.

Table 1
Average interfinger connection matrices.[1]

Task/finger	Right hand				Left hand			
	I	*M*	*R*	*L*	*I*	*M*	*R*	*L*
I	**20.47**	2.10	0.88	0.94	**17.29**	1.83	0.67	0.59
	5.72	*1.34*	*0.91*	*0.87*	*5.08*	*1.15*	*0.73*	*0.61*
M	2.01	**18.79**	3.06	0.90	1.70	**16.35**	2.51	0.72
	1.44	*5.14*	*1.69*	*1.20*	*1.03*	*4.24*	*1.25*	*1.07*
R	0.62	1.53	**13.05**	2.14	0.92	1.99	**11.12**	1.87
	0.72	*1.07*	*4.58*	*1.20*	*0.74*	*1.44*	*3.37*	*1.22*
L	0.58	0.36	1.45	**12.62**	0.52	0.32	1.63	**10.56**
	0.47	*0.73*	*1.27*	*4.69*	*0.39*	*0.65*	*1.07*	*2.98*

[1] Values in bold are the trace of the matrix. Values in italics are standard deviations. I – index finger, M – middle finger, R – ring finger, L – little finger.

Table 2
Interfinger connection matrices normalized by four-finger MVC force.[1]

Task/finger	Right hand				Left hand			
	I	*M*	*R*	*L*	*I*	*M*	*R*	*L*
I	**0.237**	0.022	0.007	0.006	**0.229**	0.027	0.015	0.008
	0.029	*0.012*	*0.007*	*0.004*	*0.037*	*0.011*	*0.009*	*0.006*
M	0.029	**0.234**	0.020	0.004	0.028	**0.239**	0.034	0.006
	0.012	*0.052*	*0.012*	*0.009*	*0.011*	*0.044*	*0.016*	*0.009*
R	0.014	0.039	**0.161**	0.021	0.011	0.040	**0.160**	0.028
	0.012	*0.018*	*0.046*	*0.013*	*0.010*	*0.014*	*0.038*	*0.011*
L	0.012	0.012	0.030	**0.152**	0.008	0.009	0.024	**0.134**
	0.007	*0.013*	*0.011*	*0.051*	*0.009*	*0.010*	*0.014*	*0.031*

[1] Values in bold are the trace of the matrix. Values in italics are standard deviations. I – index finger, M – middle finger, R – ring finger, L – little finger.

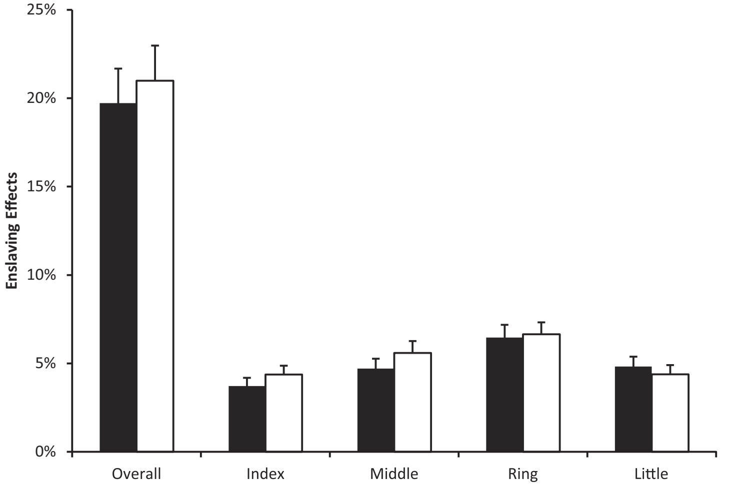

Fig. 2. Enslaving effect (EE) values (means and standard error bars) for all four fingers and each individual finger. Black bars show the right hand data, and white bars show the left hand data.

Table 3
Results from handedness tests and correlations with enslaving indices.[1]

	Edinburg	Grooved Pegboard		Jebsen–Taylor	
		RH	LH	RH	LH
Time (s)		61.04	68.15	5.56	8.99
Handedness score	76.58	0.056		0.135	
Correlation with EE for right hand	0.244	0.335		0.050	
	p = 0.274	*p = 0.128*		*p = 0.827*	
Correlation with EE for left hand	0.104	0.154		−0.129	
	p = 0.645	*p = 0.494*		*p = 0.568*	

[1] LH: Left Hand, RH: Right Hand, EE: Enslaving Effects.

To estimate reliability of the EE indices, the values of the ICC, SEM, and minimum difference were calculated for the 11 subjects who were tested twice (Table 4). The absolute values of the average changes in EE indices for the right hand (0.005 ± 0.007) and the left hand (0.028 ± 0.019) were smaller than the minimum difference for each hand (0.087 and 0.184 for the right and left hands,

Table 4
Indices of reliability.[1]

	ICC	SEM	MD	Average change
Right hand	0.918	0.031	0.087	−0.005
Left hand	0.548	0.066	0.184	−0.028

[1] Intraclass correlations (ICC), standard error of the mean (SEM), minimum difference (MD), and average change in enslaving effects (EEs) for the subjects who were tested twice ($n = 11$).

respectively). Since the differences were smaller than the minimum difference, the variability was attributed to random error and not to an actual change in EE indices for the subjects.

4. Discussion

Overall, this study suggests that there is no significant difference between enslaving effects (EEs) in the dominant (D) and non-dominant (ND) hands. The EEs showed no correlation with any of the three measures of handedness, while each of the three measures distinguished between the D and ND hands. So, both hypotheses presented in the introduction were shown to be false.

Previous studies that found significant differences in EEs between the D and ND hands reported small difference values, on the order of 2% (Li et al., 2000a). However, there are important differences between the methodologies of the study conducted by Li et al. (2000a) and the present study. Li et al. (2000a) computed EEs as a percentage of a given finger's MVC when the finger produced enslaving forces. In the present study, enslaving indices were computed from a neural network. Recent studies have indicated that neural network models are more accurate and comprehensive than models based on single finger MVCs (Martin et al. 2013). Furthermore, the significant differences found by Li et al. (2000a) were only found when examining tasks where the L finger was neglected. When all four fingers were included in the analysis, the difference in EEs between the two hands was no longer significant (Li et al. 2000a). In the present analysis, the enslaving indices were based on the combined actions of all four fingers and on each finger individually. Thus, our finding of non-significant differences between the hands does not contradict the previous literature.

The EEs have been hypothesized to be a consequence of peripheral mechanical coupling, multi-digit extrinsic muscles, and central nervous system command coupling (Lang & Schieber, 2004; Zatsiorsky et al., 1998; Zatsiorsky et al., 2000). Furthermore, the magnitude of EEs has been found to decrease for populations that practice tasks that require a high level of individual finger movement, such as piano players (Slobounov et al., 2002b). Theoretically the modifications could be due to changes in (1) the peripheral structures, (2) the neural descending signals, or a combination of 1 and 2. Several studies presented evidence for the strong effects of neural factors on enslaving. These include the demonstration of practically the same EEs during pressing tasks that involved primarily intrinsic hand muscles and those that involved primarily extrinsic hand muscles (Latash, Li, Danion, & Zatsiorsky, 2002). In addition, significant changes in EEs have been demonstrated over relatively short practice, from one hour to three days, when changes in peripheral structures were highly unlikely (Kang, Shinohara, Zatsiorsky, & Latash, 2004; Wu, Pazin, Zatsiorsky, & Latash, 2012).

Given the importance of neural factors in EEs and the focus of the dynamic dominance hypothesis on cortical mechanisms (Sainburg, 2005), we expected EEs to show differences between the D and ND hands similar to those reflected in the performance of functional hand tasks. While the two hands differed in the MVC force magnitudes and in the indices of functional task performance, there were no similar differences between the EEs. This is not the first counter-intuitive finding in studies of EEs. In particular, lower EEs (better finger individuation) have been reported in studies of older persons (Kapur, Zatsiorsky, & Latash, 2012; Shinohara, Li, Kang, Zatsiorsky, & Latash, 2002), while this population is characterized by a marked decline in the hand function (Francis & Spirduso, 2000; Hackel, Wolfe, Bang, & Canfield, 1992; Hughes et al., 1997). These observations suggest that a certain amount of EEs may be optimal for the typical range of everyday tasks, while very low EEs (as in the cited studies of older persons), as well as very high EEs (as in some studies of neurological patients) (Park, Lewis, Huang, & Latash, 2013; Park et al., 2012) may both be detrimental to the hand function.

While the D and ND hands differ in their sharing of everyday tasks, both are much more likely to be involved in tasks that require coordinated multiple finger action (grasping, object manipulating, using tools and utensils, handwriting, etc.), not individual finger action. We hypothesize that the predominance of such tasks leads to the elaboration of similar EE patterns in the two hands.

The retesting of a subgroup of our subjects after two months showed that under normal conditions, EEs do not change significantly. Given the mentioned studies demonstrating quick changes in EEs under specialized practice (Kang et al., 2004; Wu et al., 2012), one could expect the EEs to be highly variable and changing on a day-to-day or even hour-to-hour basis depending on the tasks the person performs. Our results suggest that typical everyday tasks do not affect EEs significantly, and this index is a reliable measure of finger individuation in both D and ND hands.

Acknowledgments

The study was in part supported by NIH grants NS-035032, and AR-048563.

References

Danion, F., Schöner, G., Latash, M., Li, S., Scholz, J., & Zatsiorsky, V. (2003). A mode hypothesis for finger interaction during multi-finger force production tasks. *Biological Cybernetics*, 91–98.

Francis, K., & Spirduso, W. (2000). Age differences in the expression of manual asymmetry. *Experimental Aging Research*, 169–180.

Gao, F., Li, S., Li, Z., Latash, M., & Zatsiorsky, V. (2003). Matrix analyses of interaction among fingers in static force production tasks. *Biological Cybernetics*, 407–414.

Hackel, M., Wolfe, G., Bang, S., & Canfield, J. (1992). Changes in hand function in the aging adult as determined by the Jebsen Test of Hand Function. *Physical Therapy*, 373–377.

Häger-Ross, C., & Schieber, M. (2000). Quantifying the independence of human finger movements: comparisons of digits, hands, and movement frequencies. *The Journal of Neuroscience*, 8542–8550.

Hughes, S., Gibbs, J., Dunlop, D., Edelman, P., Singer, R., & Chang, R. (1997). Predictors of decline in manual performance in older adults. *Journal of the American Geriatrics Society*, 905–910.

Kang, N., Shinohara, M., Zatsiorsky, V., & Latash, M. (2004). Learning multi-finger synergies: an uncontrolled manifold analysis. *Experimental Brain Research*, 336–350.

Kapur, S., Zatsiorsky, V., & Latash, M. (2012). Age-related changes in the control of finger force vectors. *Journal of Applied Physiology*, 1827–1841.

Kim, S., Shim, J., Zatsiorsky, V., & Latash, M. (2008). Finger inter-dependence: Linking the kinetic and kinematic variables. *Human Movement Science*, 408–422.

Kimura, D., & Vanderwolf, C. (1970). The relation between hand preference and the performance of individual finger movements by left and right hands. *Brain: A Journal of Neurology*, 769–774.

Lang, C., & Schieber, M. (2004). Human finger independence: limitations due to passive mechanical coupling versus active neuromuscular control. *Journal of Neurophysiology*, 2802–2810.

Latash, M., Li, S., Danion, F., & Zatsiorsky, V. (2002). Central mechanisms of finger interaction during one- and two-hand force production at distal and proximal phalanges. *Brain Research*, 198–208.

Li, S., Danion, F., Latash, M., Li, Z., & Zatsiorsky, V. (2000a). Characteristics of finger force production during one- and two-hand tasks. *Human Movement Science*, 897–923.

Li, S., Danion, F., Latash, M., Li, Z., & Zatsiorsky, V. (2000b). Finger coordination and bilateral deficit during two-hand force production tasks performed by right-handed subjects. *Journal of Applied Biomechanics*, 379–391.

Li, Z., Zatsiorsky, V., Latash, M., & Bose, N. (2002). Anatomically and experimentally based neural networks modeling force coordination in static mult-finger tasks. *Neurocomputing*, 259–275.

Martin, J., Terekhov, A., Latash, M., & Zatsiorsky, V. (2013). Comparison of inter-finger connection matrix computation yechniques. *Journal of Applied Biomechanics*, 525–534.

McGraw, K. (1996). Forming inferences about some intraclass correlation coefficients. *Psychological Methods*, 30–46.

Ohtsuki, T. (1981). Inhibition of individual fingers during grip strength exertion. *Ergonomics*, 21–36.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neurophyschologica*, 97–113.

Park, J., Lewis, M., Huang, X., & Latash, M. (2013). Effects of olivo-ponto-cerebellar atrophy (OPCA) on finger interaction and coordination. *Clinical Neurophysiology*, 991–998.

Park, J., Wu, Y., Lewis, M., Huang, X., & Latash, M. (2012). Changes in multi-finger interaction and coordination in Parkinson's disease. *Journal of Neurophysiology*, 915–924.

Reilly, K., & Hammond, G. (2004). Human handedness: is there a difference in the independence of the digits on the preferred and non-preferred hands? *Experimental Brain Research*, 255–262.

Sainburg, R. (2002). Evidence for a dynamic-dominance hypothesis of handedness. *Experimental Brain Research*, 241–258.

Sainburg, R. (2005). Handedness: differential specializations for control of trajectory and position. *Exercise and Sport Sciences Reviews*, 206–213.

Schieber, M., & Santello, M. (2004). Hand function: peripheral and central constraints on performance. *Journal of Applied Physiology*, 2293–2300.

Shinohara, M., Li, S., Kang, N., Zatsiorsky, V., & Latash, M. (2002). Effects of age and gender on finger coordination in MVC and submaximal force-matching tasks. *Journal of Applied Physiology*, 259–270.

Shrout, P., & Fleiss, J. (1979). Intraclass correlations: uses in assessing rater reliability. *Psychological Bulletin*, 420–428.
Slobounov, S., Chiang, H., Johnston, J., & Ray, W. (2002a). Modulated cortical control of individual fingers in experienced musicians: an EEG study. *Clinical Neurophysiology*, 2013–2024.
Slobounov, S., Johnston, J., Chiang, H., & Ray, W. (2002b). Motor-related cortical potentials accompanying enslaving effect in single versus combination of fingers force production tasks. *Clinical Neurophysiology*, 1444–1453.
Weir, J. (2005). Quantifying test-retest reliability using the intraclass correlation coefficient and the SEM. *Journal of Strength and Conditioning Research*, 231–240.
Wu, Y., Pazin, N., Zatsiorsky, V., & Latash, M. (2012). Practicing elements versus pracicing coordination: changes in the structure of variance. *Journal of Motor Behavior*, 471–478.
Zatsiorsky, V., Li, Z., & Latash, M. (1998). Coordinated force production in multi-finger tasks: finger interaction and neural network modeling. *Biological Cybernetics*, 139–150.
Zatsiorsky, V., Li, Z., & Latash, M. (2000). Enslaving effects in multi-finger force production. *Experimental Brain Research*, 187–195.
Zhang, W., Sainburg, R., Zatsiorsky, V., & Latash, M. (2006). Hand dominance and multi-finger synergies. *Neuroscience Letters*, 200–204.