

## Force coordination in static manipulation: Discerning the contribution of muscle synergies and cutaneous afferents

Paulo Barbosa de Freitas<sup>a</sup>, Goran Markovic<sup>b</sup>, Vennila Krishnan<sup>a</sup>, Slobodan Jaric<sup>a,\*</sup>

<sup>a</sup> Department of Health, Nutrition, and Exercise Sciences, University of Delaware, 547 South College Avenue, Newark, DE 19711, USA

<sup>b</sup> School of Kinesiology, University of Zagreb, Horvacanski zavoj 15, 10000 Zagreb, Croatia

Received 18 October 2007; received in revised form 24 January 2008; accepted 30 January 2008

### Abstract

Both an elaborate coordination of the hand grip force ( $G$ ; normal component of force acting at the digits–object contact area) and load force ( $L$ ; tangential component), and the role of cutaneous afferents in  $G$ – $L$  coordination have been well documented in a variety of manipulation tasks. However, our recent studies revealed that  $G$ – $L$  coordination deteriorates when  $L$  consecutively changes direction (bidirectional tasks; e.g., when vigorously shaking objects or using tools). The aim of the study was to distinguish between the possible role of the synergy of hand grip and arm muscles (exerting  $G$  and  $L$ , respectively) and the role of cutaneous afferent input in the observed phenomenon. Subjects ( $N=14$ ) exerted sinusoidal  $L$  pattern in vertical direction against an externally fixed device in trials that gradually changed from uni- to fully bidirectional. In addition, a manipulation of an external arm support decoupled  $L$  measured by the device (and, therefore, recorded by the cutaneous receptors) from the action of arm muscles exerting  $L$ . The results revealed that switching from uni- to bidirectional tasks, no matter how low and brief  $L$  exertion was in the opposite direction, was associated with an abrupt decrease in  $G$ – $L$  coordination. This coordination remained unaffected by the manipulation of external support. The first result corroborates our previous conclusion that the force coordination in uni- and bidirectional manipulation tasks could be based on partly different neural control mechanisms. However, the second finding suggests that the studied control mechanisms could depend more on the cutaneous afferent input, rather than on the synergy of the muscles exerting  $G$  and  $L$ .

© 2008 Elsevier Ireland Ltd. All rights reserved.

**Keywords:** Unidirectional; Bidirectional; Grip; Load; Force; Neural control

Holding and manipulating objects are important motor activities of daily living. Two distinct force components act upon an object when it is manipulated. The load force ( $L$ ) that acts in parallel to the digits–object contact surface(s) is exerted by both the proximal and distal upper limb muscles either to counteract the object's weight and inertia or to produce a reaction force from external support to preserve the posture. The grip force ( $G$ ) is exerted by both the intrinsic and extrinsic hand muscles and acts perpendicularly to the longitudinal axis of the object.  $G$  needs not only to be sufficiently high to prevent slippage caused by  $L$ , but also to be low enough to avoid crushing the object or preclude fine coordination of the ongoing manipulation task. During the digits–object interaction, a high level of coordination of  $G$  and  $L$  (see further text for the specific methods of

assessment) accounts for the simultaneous modulation of  $G$  to the changing  $L$ , which is responsible for keeping a stable and low (relative to the minimum required to prevent the slippage) grip-to-load ( $G/L$ ) ratio [16]. The relationship between  $G$  and  $L$  is planned in advance by the central nervous system (CNS) and the feedback information from mechanoreceptors located both at the tip of the digits [16,18,23] and at the muscles responsible for  $G$  and  $L$  exertion [2,6] are used by the CNS to trigger necessary adjustments in this relationship. However, this elaborate coordination between  $G$  and  $L$  can deteriorate either with an underlying pathology within the sensorimotor system [24], with cutaneous receptors anaesthetized [1,25], or in increasingly complex tasks [28].

Most of the previous studies of hand function have investigated the  $G$ – $L$  coordination in manipulation tasks where  $L$  is exerted in only one direction (unidirectional tasks). Consequently, the differences in the  $G$ – $L$  force coordination between the manipulation tasks that require exerting  $L$  in one and two directions (bidirectional tasks) have been neglected. A number

\* Corresponding author at: Rust Ice Arena, 547 South College Avenue, Newark, DE 19716, USA. Tel.: +1 302 8316174.

E-mail address: [jaric@udel.edu](mailto:jaric@udel.edu) (S. Jaric).

of daily activities involve bidirectional tasks, such as operating tools, shaking vigorously an object, or using external support under dynamical conditions. Only recently we compared the uni- and bidirectional static manipulation tasks [4,12] and observed an abrupt deterioration in the indices of *G–L* coordination whenever the subjects switched from uni- to bidirectional tasks. We interpreted the findings using the concept of muscle synergies. The current view of synergies operationally defines them as neural organizations of elements aimed towards improvement in task performance. In addition, the synergies typically share a common neural drive that leads to both stable and flexible relationships among the elements over time [21,22]. Within the aforementioned studies we referred to the joint action of *G* and *L* muscles that could (according to the aforementioned definition) create a synergy when performing the tested manipulation tasks. In particular, a unidirectional task would involve a single synergy of *G* muscles and *L* muscles exerting force in a single direction. In a bidirectional task, however, the synergy would need to be re-established every time when *L* changes the direction and it has been generally recognized that such process is likely to require certain transient time to be conducted [5,10]. The possible role of muscle synergies in the observed deterioration of force coordination in bidirectional tasks has been also corroborated by findings that the feedforward control mechanisms of manipulation activities keep *G* largely subordinate to ongoing arm actions [3]. Alternatively, one could speculate on the well-documented role of cutaneous and other sensory afferents in *G* and *L* coordination. The information regarding either the direction and relative velocity of micro-slips of the object [29] or about the magnitude of the exerted *L* independently of the magnitude of the exerted *G* [26] can be provided by the mechanoreceptors located within the tip of the digits. This information can be thereafter used by the CNS to perform necessary adjustments of *G* exerted throughout a continuous manipulation task [13,17,18]. However, some recent evidence also suggest that the role of the cutaneous afferents can change with altered mechanical conditions [9], as well as that other sensory afferents could also play a role in the discussed *G* and *L* coordination [2].

The aim of our study was to explore the neural mechanisms responsible for reduced indices of *G–L* coordination observed in bidirectional tasks. The subjects exerted a static sinusoidal *L* pattern in vertical direction against an instrumented device in trials that gradually changed from uni- to fully bidirectional, while manipulation of external support decoupled the load (*L*) exerted against the object (and, therefore, recorded by the cutaneous sensory afferents) from the action of muscles exerting *L*. We hypothesized that, if the switching of muscle synergies is responsible for the differences in force coordination between the uni- and bidirectional tasks, the manipulation of external support would affect the indices of *G–L* coordination. Alternatively, a lack of the effect of external support on *G–L* coordination would suggest an important role of the cutaneous afferents in the studied phenomenon. The findings were expected to be important not only for understanding control mechanisms of until recently neglected bidirectional manipulation tasks, but potentially also for discriminating the role of muscle synergies and sensory information in manipulation activities in general.

Fourteen volunteers (seven males and seven females) aged  $29.1 \pm 5.4$  (mean  $\pm$  S.D.) participated in the study. The experiment was approved by the Human Subject Review Board of the University of Delaware and conducted in accordance with the declaration of Helsinki. The participants were tested on unimanual manipulation tasks performed with their dominant hand under isometric conditions. The experimental device is illustrated schematically in Fig. 1A. A single-axis force sensor (WMC-50, Interface Inc., USA) measured the compression force ( $F_C$ ) exerted against the handle by the tip of the thumb. A multi-axis force transducer (Mini40, ATI, USA) positioned below the handle recorded all three components of the force applied against the handle. The component orthogonal to the

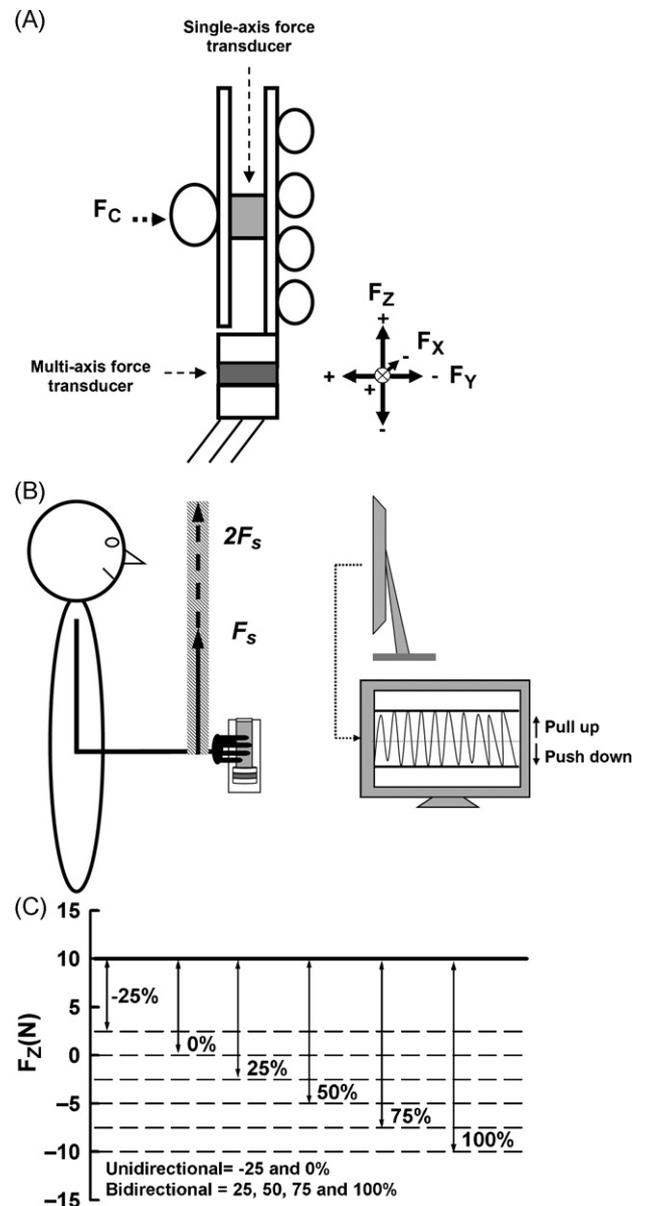


Fig. 1. (A) Schematic representation of the device. Force transducers (shaded rectangles) record grip force (*G*) and load force (*L*). (B) Illustration of the experimental conditions: subject exerts vertical *L* with the feedback depicted at computer monitor. (C) Illustration of the prescribed indices of bidirectionality (B) depicted on the computer screen.

contact area ( $F_Y$ ) was used to calculate the force exerted by the tips of the fingers medially as  $|F_C + F_Y|$  and, thus, enabled calculation of the grip force ( $G$ ) as the average of the forces applied against two opposing sides of the handle. Both sides of the handle were covered by rubber. The remaining two components acting tangentially (vertical  $F_Z$  and horizontal  $F_X$ ) were used to calculate the load force ( $L$ ) that tended to cause slippage [4]. When  $F_Z$  acted upward and downward,  $L$  was considered positive and negative, respectively. Note that despite the fact that there was no load originating from the weight of the externally fixed device, due to the generally accepted terminology in the area we decided to refer to the tangential force acting at the digit–handle contact area as ‘load force’.

The subjects were instructed to exert a sinusoidal pattern of  $L$  by pulling up and pushing down the handle using their dominant hand, paced by a metronome set at 1.33 Hz. According to our previous studies, this frequency proved to be within a ‘comfortable range’ since it was neither too low to allow for the feedback based corrections, nor too high to be close to the physical limit [10,11]. Placed in front of the subject (Fig. 1B), a computer monitor displayed two horizontal lines for the upper and lower boundary ( $F_{Zmax}$  and  $F_{Zmin}$ ) along with the current  $F_Z$  exerted by the subjects. The prescribed  $F_{Zmax}$  and  $F_{Zmin}$  served as a feedback to the subjects to target their sinusoidal patterns within those lines. The individual  $F_{Zmax}$  ranged between 6 and 13 N. It was determined by means of the Dempster’s model [31] to correspond to the weight of the lower arm and hand acting upon the device.

To manipulate the extent to which  $F_Z$  was exerted in one with respect to the opposite direction, we manipulated the *index of bidirectionality* (IB) by gradually lowering  $F_{Zmin}$  [4]. Specifi-

cally, we calculated the *prescribed* IB as:

$$IB = \left[ 100 - \left( \frac{100 * (F_{Zmax} + F_{Zmin})}{F_{Zmax}} \right) \right] \% \quad (1)$$

IB ranged from  $-25\%$  to  $100\%$ , where  $-25\%$  and  $0\%$  were expected to provide unidirectional tasks, while the  $25\%$ ,  $50\%$ ,  $75\%$  and  $100\%$  were expected to provide bidirectional tasks (see Fig. 1C).

The second independent variable was expected to alter the activity of muscle groups responsible for producing upward and downward  $L$  while maintaining the same cutaneous afferent activation pattern from the mechanoreceptors responsible for detecting changes in  $L$ . In particular, an external support was manipulated by providing the *no-support*, *single-support*, and *double-support* conditions, where the wrist was either unsupported, or supported by a single or double rubber band, respectively, positioned to pull the forearm and hand vertically upward (Fig. 1B). The pulling force was adjusted in a way that the *single-support* canceled the effect of gravity acting upon the forearm–hand segment, while the *double-support* provided double pulling force that, inevitably, created a net force upward equal to twice the weight of the forearm–hand segment. Since the prescribed  $L$  peak ( $F_{Zmax}$ ) corresponded to the weight of the forearm–hand system acting upon the handle, both the uni- and bidirectional tasks performed either under no-support or double-support conditions required muscle groups to act only in one direction producing force upward or downward, respectively. Only the bidirectional tasks performed under the single-support condition required the antagonistic arm muscle groups to exert force in both directions. However, the external support did not affect the force acting at the digits–handle contact area.

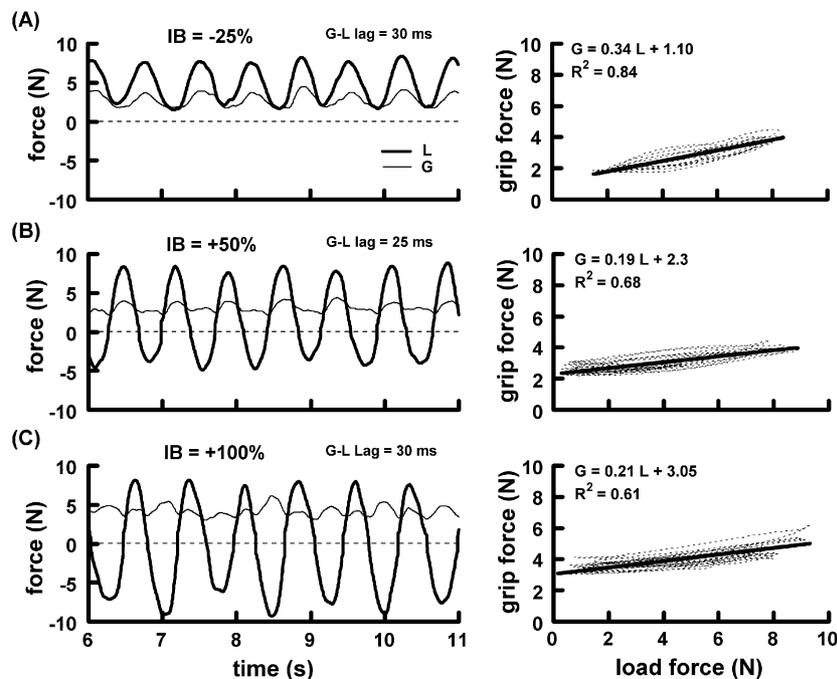


Fig. 2. The data obtained from a representative subject under three indices of bidirectionality (IB). Right-hand panels illustrate the corresponding  $G$ – $L$  diagrams and the regression lines.

The subjects were given 15 min for familiarization with the tasks and, thereafter, the experimental trials were recorded. A total of 18 trials (12 s each) were recorded including each of the 6 IBs performed under 3 external supports in random sequence.  $G$  was never mentioned to the subjects. The first 6 s of each trial were considered as a time period needed to adjust to both the prescribed frequency and the prescribed force peaks, while the last second could be affected by preparation for the trial termination. As a result, only the data between the 6th and 11th s were analyzed. The signals were recorded at a sampling frequency of 200 Hz, and digitally low pass filtered at 10 Hz with a fourth order Butterworth filter. Since slippage (and, therefore, a need for a sufficient  $G$  to prevent it) does not depend on the direction of tangential force,  $L$  was rectified prior to data analysis [10–12].

In general, the data suggest that subjects were fairly accurate regarding exerting the prescribed  $F_z$ . Specifically, virtually all subjects revealed both constant and variable errors [27] below 1 N suggesting the exerted force profiles closely corresponded to the prescribed IB. Neither the effect of IB nor of external support was revealed.

Fig. 2 shows the force profiles obtained under three out of six IBs and no-support condition from a representative subject. A prominent difference regarding both the coordination of  $G$  and  $L$  and the amount of  $G$  modulation appeared between the unidirectional task (IB = -25%; Fig. 2A) and two-bidirectional ones (IB = 50% and IB = 100%; Fig. 2B and C). When depicted by  $G$ - $L$  diagrams (right-hand panels of Fig. 2), the unidirectional trial reveals a higher slope and lower intercept (correspond to the gain and offset of  $G$  modulation, respectively [32]) of the regression lines, as well as a higher  $G$ - $L$  correlation coefficients (interpreted as  $G$ - $L$  coupling) than either of the two-bidirectional tasks.

In line with both our and other authors' studies, we assessed the coordination of  $G$  and  $L$  by calculating  $G/L$  ratio, the maximum cross correlation coefficient between  $G$  and  $L$  and their respective time lags, as well as the  $G$  modulation through  $G$  gain and offset [4,7,11,12,32]. Fig. 3 depicts the indices of  $G$  and  $L$  coordination averaged across the subjects. Note a prominent difference observed between the uni- and bidirectional tasks. In particular, when compared with all bidirectional tasks, the unidirectional tasks depict higher force coordination through a lower  $G/L$  ratio and higher  $G$ - $L$  correlation coefficient, as well as through higher gain and lower offset (correspond to higher slope and lower intercepts of the  $G$ - $L$  regression lines, respectively). A two-way repeated measures MANOVA was employed to assess the main effects of IB and external support on  $G/L$  ratio,  $Z$ -transformed correlation coefficients of  $G$  and  $L$ , the corresponding time lags, and the  $G$  gain and offset. The results revealed a significant main effect of IB [Willks' Lambda = 0.03,  $F(25,228) = 16.3$ ,  $p < 0.001$ ,  $\eta^2 = 0.49$ ], but no main effect of external support [Willks' Lambda = 2.01,  $F(10,44) = 1.89$ ,  $p > 0.05$ ,  $\eta^2 = 0.30$ ] and no interaction [Willk's Lambda = 0.47,  $F(50,578) = 0.86$ ,  $p > 0.05$ ,  $\eta^2 = 0.06$ ]. The univariate analyses revealed the effect of IB on all five dependent variables [ $G/L$  ratio ( $F(5,65) = 28$ ,  $p < 0.001$ );  $Z$ -transformed correlation coefficients ( $F(2,30) = 113$ ,  $p < 0.001$ ); time lags ( $F(5,65) = 2.42$ ,  $p < 0.05$ ); gain ( $F(3,37) = 30$ ,  $p < 0.001$ ); and

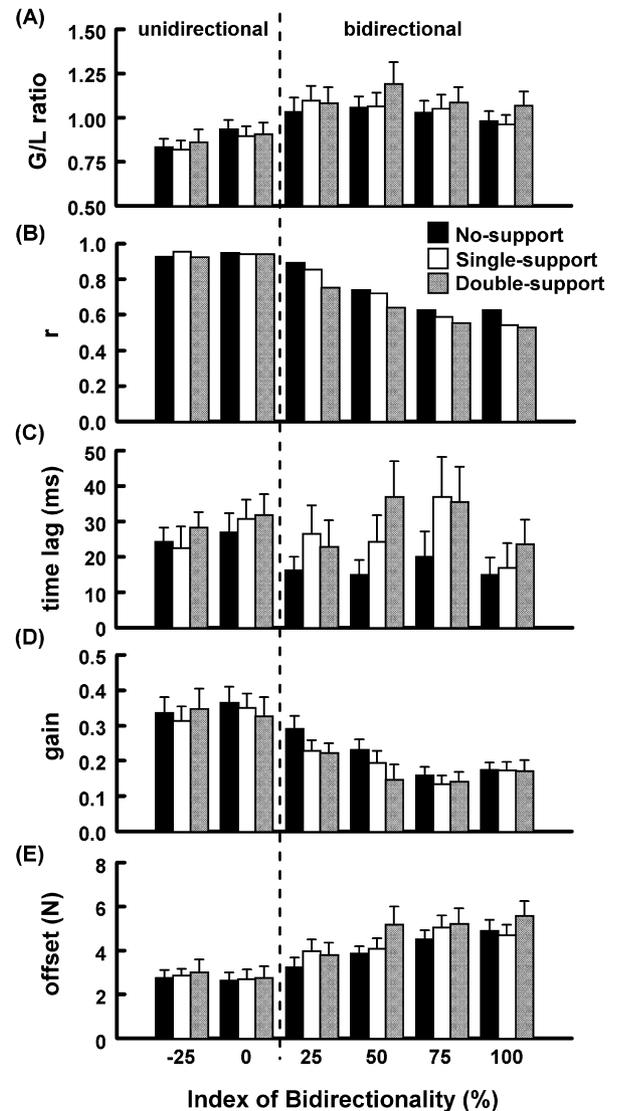


Fig. 3. Indices of force coordination averaged across the subjects (error bars depict standard errors).

offset ( $F(2,26) = 36$ ,  $p < 0.001$ ]). The post hoc analysis with Bonferroni correction revealed lower  $G/L$  ratio, higher correlation coefficient, higher gain and lower offset in unidirectional than in bidirectional tasks. The only exceptions were that both the gain and offset obtained from IB = 25% trials that were different from other bidirectional trials, but not from the unidirectional ones. Regarding the time lags, the post hoc analysis revealed no significant differences among individual IBs.

Within the present study we tested two alternative hypotheses regarding the cause of deterioration of  $G$  and  $L$  coordination in bidirectional, as compared with unidirectional static manipulation tasks. The observed effect of the change in  $L$  direction on the  $G$ - $L$  coordination *per se* (i.e., the effect of IB; see previous paragraphs) was similar to the results of our previous studies [4,12]. In particular, when switching from uni- to bidirectional tasks, no matter how short and brief the exertion of  $L$  in the opposite direction was, the indices of coordination demonstrated a marked decrease. As already suggested in our previous study,

this finding suggests that the control of uni- and bidirectional manipulation tasks could be based on partly different neural mechanisms [4]. However, the main aim of the present study was to distinguish between two neural mechanisms that could be responsible for the observed differences in force coordination between the uni- and bidirectional tasks. Therefore, the most of the further discussion will be based on the lack of effect of external support designed to alter the action of muscle groups responsible for *L* generation, while keeping the digital cutaneous afferent input unaffected.

As explained in detail in the above text, no matter how high or low IB was, all tasks performed under the no-support and double-support conditions required the *L* exerting muscles to act in only one direction (upward and downward, respectively). Consequently, no switches between the hypothesized two distinctive *G–L* synergies were required. As a result, one could expect a deterioration of *G–L* coordination only in bidirectional tasks performed under *single-support* condition that required switching *L* exerting muscle groups acting consecutively in two opposite directions. However, the results revealed no effect of the external support on any index of force coordination. Therefore, the discussed findings contradict the hypothesized role of muscle synergies in *G* and *L* coordination in the tested task.

While refuting the muscle synergies hypothesis, our findings seem to support the alternative hypothesis based on the role of the cutaneous afferents in the studied *G* and *L* coordination. Namely, the prescribed IB accurately reflected not the action of the arm muscles exerting force against the forearm–hand segment, but the tangential force (i.e., *L*) acting at the digits–handle contact area independently of the external support. As a result, the switching in *L* direction detected by digital skin mechanoreceptors, rather than the switching between *G* and *L* muscle synergies, could be a more plausible explanation for the recorded deterioration of the *G–L* coordination in bidirectional manipulation tasks.

Although the important role of cutaneous sensory afferents in elaborate *G* and *L* coordination during performing discrete manipulation tasks (e.g. lifting and holding task) has been documented [1,25], we could not find a single study aimed towards the role of the same afferents in manipulation tasks where *L* changes direction. Here we can only speculate on the role of the cutaneous afferent signals in the studied neural control mechanisms. Among a number of partly specialized receptors, those with small receptive fields (e.g. Meissner corpuscles and Merkel disks) could particularly be sensitive to the change in direction of the acting tangential force and, therefore, be able to discriminate between the uni- and bidirectional tasks [15,30]. As a result, bending of the skin caused by the change in *L* direction could cause the consecutive changes in activation of the receptive fields from neighboring sites of the digit pads [14]. Those changes could be interpreted as slips and, consequently, the CNS could tend to prevent slipping by elevating the “safety margin” (i.e., increasing *G/L* ratio [16,20]), as well as by reducing both the *G–L* coupling and *G* modulation. A certain transient time well known to be required to establish highly coordinated motor actions (c.f., of individual fingers [5,33], or postural muscles, [19]) could explain why switches in activity between two

opposite sites of sensory afferents could be associated with deterioration of *G* and *L* coordination.

To conclude, the obtained results suggest that the cutaneous afferent input, rather than synergetic activity of *G* and *L* muscles, could be responsible for a marked deterioration of force coordination recently observed in bidirectional manipulative tasks [4,12]. Since the neural control mechanisms of static and dynamic manipulation tasks could be different [9,11,32], the current research could be extended to free movement (i.e., dynamic) tasks, as well as to a variety of uni- and bimanual grasping techniques [8]. Finally, a similar experiment performed with and without anaesthetized skin could discern between the roles of cutaneous afferents and other sensory mechanisms in the studied effects of *L* direction.

### Acknowledgments

The study was supported in part by grant HD-48481 from the National Institute of Health to S. Jaric. P.B. de Freitas has been partly supported by Fulbright Program (15053184) and Brazilian Government (CAPES #2051-04/4).

### References

- [1] A.S. Augurelle, A.M. Smith, T. Lejeune, J.L. Thonnard, Importance of cutaneous feedback in maintaining a secure grip during manipulation of hand-held objects, *J. Neurophysiol.* 89 (2003) 665–671.
- [2] F. Danion, The contribution of non-digital afferent signals to grip force adjustments evoked by brisk unloading of the arm or the held object, *Clin. Neurophysiol.* 118 (2007) 146–154.
- [3] F. Danion, How dependent are grip force and arm actions during holding an object? *Exp. Brain Res.* 158 (2004) 109–119.
- [4] P.B. de Freitas, V. Krishnan, S. Jaric, Force coordination in static manipulation tasks: effects of the change in direction and handedness, *Exp. Brain Res.* 183 (2007) 487–497.
- [5] D. Domkin, J. Laczko, S. Jaric, H. Johansson, M.L. Latash, Structure of joint variability in bimanual pointing tasks, *Exp. Brain Res.* 143 (2002) 11–23.
- [6] J.R. Flanagan, J. Tresilian, A.M. Wing, Coupling of grip force and load force during arm movements with grasped objects, *Neurosci. Lett.* 152 (1993) 53–56.
- [7] J.R. Flanagan, A.M. Wing, The stability of precision grip forces during cyclic arm movements with a hand-held load, *Exp. Brain Res.* 105 (1995) 455–464.
- [8] P.B. de Freitas Jr., V. Krishnan, S. Jaric, Elaborate force coordination of precision grip could be generalized to bimanual grasping techniques, *Neurosci. Lett.* 412 (2007) 179–184.
- [9] F. Gao, M.L. Latash, V.M. Zatsiorsky, Similar motion of a hand-held object may trigger nonsimilar grip force adjustments, *J. Hand Ther.* 20 (2007) 300–307.
- [10] S.L. Gorniak, V.M. Zatsiorsky, M.L. Latash, Emerging and disappearing synergies in a hierarchically controlled system, *Exp. Brain Res.* 183 (2007) 259–270.
- [11] S. Jaric, J.J. Collins, R. Marwaha, E. Russell, Interlimb and within limb force coordination in static bimanual manipulation task, *Exp. Brain Res.* 168 (2006) 88–97.
- [12] S. Jaric, E.M. Russell, J.J. Collins, R. Marwaha, Coordination of hand grip and load forces in uni- and bidirectional static force production tasks, *Neurosci. Lett.* 381 (2005) 51–56.
- [13] R.S. Johansson, Sensory input and control of grip, *Novartis Found. Symp.* 218 (1998) 45–63.
- [14] R.S. Johansson, I. Birznieks, First spikes in ensembles of human tactile afferents code complex spatial fingertip events, *Nat. Neurosci.* 7 (2004) 170–177.

- [15] R.S. Johansson, A.B. Vallbo, Tactile sensory coding in the glabrous skin of the human hand, *Trends Neurosci.* 6 (1983) 27–32.
- [16] R.S. Johansson, G. Westling, Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects, *Exp. Brain Res.* 56 (1984) 550–564.
- [17] R.S. Johansson, G. Westling, Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip, *Exp. Brain Res.* 66 (1987) 141–154.
- [18] R.S. Johansson, G. Westling, Significance of cutaneous input for precise hand movements, *Electroencephalogr. Clin. Neurophysiol. Suppl.* 39 (1987) 53–57.
- [19] V. Krishnamoorthy, M.L. Latash, J.P. Scholz, V.M. Zatsiorsky, Muscle synergies during shifts of the center of pressure by standing persons, *Exp. Brain Res.* 152 (2003) 281–292.
- [20] V. Krishnan, P.B. de Freitas, S. Jaric, Impaired object manipulation in mildly involved individuals with multiple sclerosis, *Motor Control* 12 (2008) 3–20.
- [21] M.L. Latash, J.P. Scholz, G. Schoner, Toward a new theory of motor synergies, *Motor Control* 11 (2007) 276–308.
- [22] Z.M. Li, M.L. Latash, V.M. Zatsiorsky, Force sharing among fingers as a model of the redundancy problem, *Exp. Brain Res.* 119 (1998) 276–286.
- [23] D.A. Nowak, S. Glasauer, L. Meyer, N. Mait, J. Hermsdorfer, The role of cutaneous feedback for anticipatory grip force adjustments during object movements and externally imposed variation of the direction of gravity, *Somatosens. Motor Res.* 19 (2002) 49–60.
- [24] D.A. Nowak, J. Hermsdorfer, Grip force behavior during object manipulation in neurological disorders: toward an objective evaluation of manual performance deficits, *Movement Disord.* 20 (2005) 11–25.
- [25] D.A. Nowak, J. Hermsdorfer, S. Glasauer, J. Philipp, L. Meyer, N. Mai, The effects of digital anaesthesia on predictive grip force adjustments during vertical movements of a grasped object, *Eur. J. Neurosci.* 14 (2001) 756–762.
- [26] M. Pare, H. Carnahan, A.M. Smith, Magnitude estimation of tangential force applied to the fingerpad, *Exp. Brain Res.* 142 (2002) 342–348.
- [27] R.A. Schmidt, T.D. Lee, *Motor control and learning: a behavioral emphasis*, in: *Human Kinetics*, 4th edn., 2005, 535 pp.
- [28] D.J. Serrien, M. Wiesendanger, A higher-order mechanism overrules the automatic grip-load force constraint during bimanual asymmetrical movements, *Behav. Brain Res.* 118 (2001) 153–160.
- [29] M.A. Srinivasan, J.M. Whitehouse, R.H. LaMotte, Tactile detection of slip: surface microgeometry and peripheral neural codes, *J. Neurophysiol.* 63 (1990) 1323–1332.
- [30] A.B. Vallbo, R.S. Johansson, Properties of cutaneous mechanoreceptors in the human hand related to touch sensation, *Hum. Neurobiol.* 3 (1984) 3–14.
- [31] D.A. Winter, *Biomechanics and Motor Control of Human Movement*, 3rd edn., John Wiley & Sons, Inc, 2005.
- [32] V.M. Zatsiorsky, F. Gao, M.L. Latash, Motor control goes beyond physics: differential effects of gravity and inertia on finger forces during manipulation of hand-held objects, *Exp. Brain Res.* 162 (2005) 300–308.
- [33] V.M. Zatsiorsky, M.L. Latash, Prehension synergies, *Exerc. Sport Sci. Rev.* 32 (2004) 75–80.