

Force Coordination in Object Manipulation

by

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Purpose: The purpose of this review is to present our recent findings related to the studies of hand function based on the coordination of forces exerted against hand-held objects.

Basic procedures: A novel device has been developed for recording grip (GF; acting perpendicularly at the hand-object contact) and load force (LF; acting tangentially) during uni- and bimanual manipulation tasks performed under either static or dynamic conditions. Both healthy participants and neurological patients were tested. The outcome measures were obtained from the task performance (i.e., the ability to exert accurate LF profiles), GF-LF coordination and GF modulation.

Main findings: The method applied proved to not only to be both reliable and valid, but also sufficient to detect differences between the dominant and non-dominant hand, as well as between healthy participants and mildly involved neurological patients. Marked differences in most of the depended variables were also detected between unidirectional and bi-direction tasks (i.e., in the tasks where LF acts in one and in two alternating directions). The later finding could not be based neural mechanisms known for their role in manipulative actions, such as on employing ad hoc muscle synergies or on the afferent activity of skin mechanoreceptors.

Conclusions: The employed methodological approach can be applied not only to explore various manipulation activities, but also to serve as a basis for future development of specific clinical tests for populations that demonstrate impaired hand function.

Keywords: hand, function, grasp, grip, load, test

Introduction

The manner in which primates, and especially humans, use their hands to interact with objects is one of the characteristics that differentiate them from other animals. Due to the essential importance of object manipulation in daily living, a large number of studies have investigated qualitative and quantitative aspects of hand function. Various quantitative methods of analysis have been employed to explore the mechanical and neural aspects involved in different types of manipulation tasks. Similarly to all other motor functions, the hand function has been studied from different aspects, including behavioral, kinematic, kinetic, electromyographic, and neural one. The kinetic approach has been frequently used because of (1) the availability of a relatively simple model that can explain manipulation kinetics through the interaction of two force components and the coefficient of friction between the skin and the object, (2) the validity of the selected kinetic variables since they can reveal essential mechanical and control characteristics of hand function, and

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(3) the property of these dependent variables to detect differences in hand function between healthy individuals and those known for impaired hand function (e.g., neurological patients or elderly). The aim of the present paper is to review basic findings regarding force coordination in manipulation task, to present a method for studying manipulation activities using a novel device developed in our lab, as well as to present our recent finding regarding force coordination in various populations and performing different manipulation tasks.

Neuromechanical characteristics of force interaction in manipulation tasks

In order to either manipulate a free-moving object or to use a fixed object as external support, individuals have to apply a certain amount of force at the digits-object contact area. In a simple mechanical model (see figure 1), the normal force component acting upon both sides of the object is usually referred to as grip force (GF), while the tangential component has usually been referred to as load force (LF) (Jaric et al. 2005; Johansson and Westling 1984; Westling and Johansson 1984).



Figure 1

A simple model of forces acting at the digitsobject contact area when holding a free-moving object (rectangle) using precision grip. The ellipses indicate the digits in contact with the object represented by the large rectangle. While load force (LF) generated by the weight of the object acts tangentially and tends to cause slippage of the object, the grip force (GF) acts orthogonally to the object surface increasing friction force (Fr) and, consequently, prevents slippage.

Mechanically, the object manipulation can be simply modeled by using GF, LF and coefficient of friction (µ) between the skin and object surface. To prevent slippage of a grasped object, the amount of GF exerted by the fingers and the thumb against the opposite sides of the object surface has to be at least equal to the ratio of LF and the coefficient of friction (GF=LF/µ). However, individuals inevitably tend to exert a stronger GF than necessary to prevent the slippage. The excess of the applied GF has been referred to as safety margin (equals GF - GFmin). In most of the previous studies the safety margin proved to be relatively low and stable (Johansson and Westling 1984; Westling and Johansson 1984).

To maintain GF-to-LF ratio low when LF changes, GF should change in parallel to LF. Inevitably, this must be achieved by presumably complex neural coordination of muscles responsible for generating LF and GF. Note that the muscle groups associated with LF exertion are those that either maintain the position of the arm segments while an object is held still, or move them from one position to another. On the other hand, the muscle groups associated with GF are those associated with prehension (i.e., extrinsic and intrinsic forearm and hand muscles). Hence, how are the actions of GF and LF muscles coordinated during manipulation tasks?

It has been consistently demonstrated that when the mechanical characteristics of the manipulated objects (e.g., weight, size, shape, or surface friction) and the self-induced changes in LF are known in advance, the CNS coordinates the actions of muscle groups responsible for exerting LF and GF in a predictive way (i.e., 'feedforward control'). Specifically, the CNS is able to anticipate the effects of the applied LF and, therefore, maintains a relatively stable relationship between GF and LF (Johansson and Westling 1984; Flanagan and Wing 1995; Flanagan and Wing 1993; Blakemore et al. 1998). Moreover, it has been shown that the sensory feedback information (presumably provided primarily by skin mechanoreceptors that detect 'micro-slips' occurring at the contact area (Johansson and Westling 1984; Johanson and Westling 1988; Johanson and Westling 1987)) are utilized by the CNS for coordinating GF and LF (Danion 2007).

In summary, the CNS anticipates the changes in LF and applies appropriate GF scaling of to avoid either the object slippage (due to insufficient GF) or 'over-gripping' due to excessive GF (Jaric et al. 2005; Johansson and Westling 1984; Westling and Johansson 1984). When the CNS cannot anticipate the changes in LF (e.g., due to unexpected external perturbations), an adaptation period is needed to adequately use feedback information and provide necessary changes of GF (Blakemore et al. 1998; Johanson and Westling 1988; Flanagan and Wing 1997).

Assessment of GF-LF coordination

The relationship between GF and LF has been investigated in various discrete and continuous manipulation tasks typically using freemoving objects. These objects have been instrumented by multi-axis force transducers and accelerometers that enable the calculation of GF and LF throughout the task execution. The most often studied tasks have been lifting, holding, and replacing instrumented objects (Johansson and Westling 1984; Westling and Johansson 1984; Flanagan et al. 1993; Zatziorsky et al. 2005; Jenmalm et al.1998). Objects of different weights, textures, and shapes have been utilized to explore the effect of objects' physical proprieties on GF and LF coordination. Nevertheless, the most often applied continuous manipulation task has been 'shaking' (i.e., cyclically moving the arm up and down while holding an instrumented object) (Flanagan and Wing 1995; Blakemore et al.1998; Zatsiorsky et al. 2005; Gao et al. 2007).

A considerable number of dependent variables have been utilized to assess different aspects of GF and LF coordination in both discrete and continuous tasks. For example, the ability to scale GF with respect to LF has been assessed by GF to LF ratio (GF/LF). It can be calculated either as the ratio of GF and LF at a specific time point of the task (e.g., maximum LF during lifting task), or as the ratio of their averaged values. A low GF/LF (i.e. low safety margin) has been interpreted as an index of higher force coordination (Jaric et al. 2005; Flanagan and Wing 1995; Flanagan et al. 1993; Zatsiorsky et al. 2005;

Jaric et al. 2006; Jaric et al.2005). Furthermore, spatial and temporal force coupling have been often assessed by the maximum cross-correlation coefficient and the corresponding time lag between GF and LF (Rost et al. 2005; Hermsdorfer et al. 2003). A high level of GF and LF coupling is expected to be revealed by maximum cross-correlation coefficients close to 1 and the corresponding time lags close to zero (Flanagan and Wing 1995; Gysin et al. 2003). Another frequently used index of GF and LF coordination has been GF modulation revealing how much GF changes with respect to the changes in LF. GF modulation has been assessed by GF gain and offset obtained from the slope and intercept, respectively, of the regression line obtained from diagrams of GF and the absolute LF values (Jaric et al. 2005; Flanagan and Wing 1995; Flanagan et al. 1993; Zatsiorsky et al. 2005; Jaric et al. 2006; Jaric et al. 2005). A high value of GF gain combined with a low value of GF offset have been interpreted as an index of high GF and LF coordination.

Note that all above mentioned variables could have a property of face validity because low but sufficient GF can only be provided by low GF/LF ratio, high GF and LF coupling and a high GF modulation. Not surprisingly, populations known for impaired hand function (e.g., neurological patients) consistently reveal deteriorated values of the same variables. For example, individuals with Parkinson's disease (PD) need a longer time to initiate lifting of a hand-held object and, also, they generate slow changing and unstable GF (Invarsson et al. 1997; Wenzelburger 2002; Benice et al. 2007). Regarding the indices of GF and LF coordination, individuals with PD are able to control and coordinate GF and LF in an anticipatory fashion, adjusting GF with respect to changes in LF, as well as with changes in object coefficient of friction. However, it has been observed that the same patients in early (Fellows et al. 2003) and advanced stages (Fellows et all. 1998; Nowak and Hermsdorfer 2006) of disease apply excessive GF when lifting and holding an object. Likewise, individuals with Huntington Disease generate a higher amount of GF during lifting and holding tasks (Gordon et al. 2000; Schwarz et al. 2001), take a longer time to both generate the maximum of GF and lift the object from the

table. Individuals with cerebellar dysfunction generate a large amount of GF during lifting and holding tasks (Nowak et al. 2005; Nowak et al. 2002; Babin-Ratte et al. 1999), as well as during vertical point to point movements (Nowak et al. 2002; Babin-Ratte et al. 1999). Rost and collaborators (Rost et al. 2005) also investigated the GF and LF coordination in cerebellar patients during vertical cyclic arm movements (amplitude \approx 30 cm) performed at low and moderate frequencies (<1.7 Hz). The patients were able to modulate GF with continuous change in LF, but they also showed problems in scaling GF (i.e., elevated GF/LF ratio) and coupling GF and LF (i.e., a low maximum crosscorrelation coefficient and variable time lag) relative to healthy controls. Hermsdorfer and colleagues (Hermsdorfer et al. 2003) assessed GF and LF coordination in stroke patients during three different manipulation tasks: holding, transporting and performing vertical cyclic arm movements (30 cm at 1.5 Hz). They observed alteration in GF and LF coordination that was more or less related to the severity of the stroke and the brain region where it occurred. In general, most of the stroke patients were able to adjust their GF with the LF demanded by the task. However, the amount of GF and, consequently, the safety margin adopted by stroke patients were considerably higher than in healthy individuals during all three manipulation tasks.

A novel device for testing hand function

Despite 25 years of applying the discussed method in studies of hand function, a number of important aspects have been mainly neglected. For example, although being a very important variable in motor control, the task performance of various manipulation tasks has been often ignored. In particular, the ability to perform a smooth and accurate manipulation action could be of essential importance for hand function in general and, therefore, performance measures based on the recorded forces could be candidates for outcome variables in the discussed area of research. In addition, studies of static manipulations, such as those mimicking using external support, have been rarely performed. Note that static tasks could allow for better control of experimental conditions than



Figure 2

Schematic version of the experimental device. The circles illustrate the positions of the fingers and thumbs applying a precision grip against two handles of the device. The single-axis force transducers recording compression force (Fc), as well as the multi-axis force transducers recording vertical and horizontal forces are depicted with gray filled squares and gray filled rectangles, respectively. The direction of the recorded Fc, Fx, Fy and Fz are indicated by arrows. The equations used to calculate GF and LF are also presented.

the tasks based on free hand movements, particularly those involving complex bimanual actions (Jaric et al. 2005; Jaric et al. 2006; Jaric et al. 2005).

To fill this gap we developed a novel device for hand function evaluation. Based on the earlier simpler versions (Jaric et al. 2005; Jaric et al.2006; Jaric et al. 2005), the latest one consists of two instrumented handles. It allows for the evaluation of both static and dynamic manipulation tasks performed with either one or both hands, as well as for accurate recording the exerted LF and GF (Figure 2). It consists of two externally fixed parallel handles covered by rubber and contains built-in two single-axis (WMC-50, Interface Inc., USA) and two multi-axis force transducers (Mini40, ATI, Apex, NC, USA). Each single-axis force transducer records the compression force (Fc) exerted against the handle laterally by the tip of the thumb. Each multiaxis force transducer (positioned beneath the handle) records all three force components applied against the handle. The horizontal force component acting perpendicularly to the handle's contact area (Fy) records the force exerted by the tips of the fingers and, thus, enables calculation of GF as the average orthogonal force applied against two sides of each handle. The remaining two components (Fz and Fx) serve for calculation of the LF (see equation in Figure2). Note that due to the direction of the recorded forces, GF acts normally, while LF acts tangentially to the contact area.

The device allows for testing a large variety of tasks based on various hand actions. For instance, the handle can be oriented both vertically and horizontal, the participants can perform the tasks in sitting and standing position, actions can be either static or dynamic, and both uni- and bimanual. The participants can be tested either with (i.e., to match force targets showed on a computer screen) or without visual feedback, while various force profiles can be performed (e.g., static, ramp-and-hold, simple lifting, or sinusoidal profiles paced with a metronome).

Evaluation of the experimental method

Several studies have been performed in our lab to evaluate the reliability and validity of the data recorded from the device. In the first one, eight healthy individual and three patients with neurological dysfunction (2 moderatly impaired individuals with multiple sclerosis and one individual with transient radial neuropathy) where tested on three static manipulation tasks: constant, ramp LF and oscillatory LF exertions over three consecutive sessions (Jaric et al. 2005). High intraclass correlation coefficients and no systematic bias among the sessions suggested moderate to high reliability of the most of the calculated variables related to task performance and force coordination (see previous text for details). When the data from healthy individuals were compared with the data obtained from the neurological patients, prominent differences occurred between the evaluated variables. Therefore, we concluded that the experimental approach based on the evaluated device could provide reliable and valid measures of task performance and force coordination and, consequently, can be used for evaluation of hand function in both healthy and neurologically disabled individuals. We also concluded that the applied methodological approach could be employed in studies of the neural control



Figure 3

GF (dashed lines) and LF (continuous lines) profiles obtained from the right (thin lines) and left (thick lines) hands of a representative MS patents and healthy control (HC). Reprinted with permission from Krishnan et al.

mechanisms involved in manipulation tasks in general [1].

We also explored GF and LF coordination in individuals with multiple sclerosis (MS) under static and dynamic conditions (Marwaha et al. 2006; Krishnan et al. 2008). Under the static conditions, participants were asked to exert LF against one or two fixed handles using different profiles and magnitudes of LF. In the first study (Marwaha et al. 2006), mildly affected individuals with MS and age-matched healthy individuals were tested at the constant, ramp and oscillation LF profiles tasks performed with available visual feedback. Interestingly, most of the patients claimed that they had no problems with hand function in daily life. The profiles were generally designed to mimic daily living tasks, such as holding or moving external objects or using external supports. The results showed that although MS patients was able to maintain a high GF-LF coupling (e.g., high correlation coefficient and time lag close to zero in oscillation task), they revealed deteriorated task performance (deteriorated ability to produce required LF profiles), as well as 'over-gripping' (higher safety margin revealed through a higher GF/LF ratio).

These results were confirmed by the following study (Krishnan et al. 2008) based on oscillation and ramp-and-hold tasks, and on a simple dynamic conditions task. Regarding the later one, the participants were instructed to lift one or both handles disassembled from the device simultaneously and, thereafter, hold them steadily. The experiment was performed on another group of mildly involved MS patients and healthy controls. The results showed that the



Figure 4

GF and LF recorded in a representative subject under two tasks and two frequency conditions. Note high correspondence among two grip and two load forces obtained from the unidirectional tasks. Bidirectional tasks, however, demonstrate a higher overall level and of grip forces, as well as a lower and more irregular grip force modulation. Reprinted with permission from Jaric et al.

patients applied an unnecessary larger amount of GF in order to lift the object. While holding the object, the smoothness was lower in the patients than in healthy individuals (Figure 3). Note that the obtained findings related to task performance and GF scaling observed in mildly impaired MS patients during both static and dynamic manipulation tasks could be detrimental for controlling object manipulation, and also could generate premature muscle fatigue (Marwaha et al. 2006; Krishnan et al. 2008).

Besides evaluating hand function in individuals with multiple sclerosis, we also investigated other aspects of the control of manipulative activities. For example, the effect of handedness in various manipulation tasks was studied (Ferrand and Jaric 2006; de Freitas et al.

2007). Having in mind recent finding regarding hand specialization (Bagesteiro and Sainburg 2002; Bagesteiro and Sainburg 2003; Sainburg 2005), it should not be surprising that the results of both studies showed some advantages of the non-dominant hand. While Ferrand and Jaric (Ferrand and Jaric 2006) reported a lower GF/LF ratio in the non-dominant than in dominant hand, de Freitas and collaborators (de Freitas et al. 2007) reported not only a higher GF modulation, but also a directionally more accurate exertion of LF of the non-dominant hand. These results also suggest a high sensitivity of the outcome measures since a presumably weak effect of handedness on hand-arm control was detected (Bagesteiro and Sainburg 200 Bagesteiro and Sainburg 2002; Bagesteiro and Sainburg 2003; Sainburg 2005).

In addition to the studies of hand function in neurological patients and the effect of handedness, we also found a potentially important effect LF direction change. A more careful examination of this phenomenon could be potentially useful in understanding of how human movement is planned, as well as how sensory information can be utilized in planning and controlling of the studied motor actions. The next session will provide more details regarding that phenomenon.

Effects of change of LF direction on GF-LF coordination

Consecutive exertion of LF in two opposite directions is an important component of manipulations performed during daily living. Examples of such tasks are shaking vigorously an object, performing consecutive strokes using hand-held tools (e.g. handsaw, or hammer) or using external support to provide reaction forces in different directions in order to preserve balance in a turbulent bus ride. However, until recently the GF and LF coordination associated with this type of manipulation tasks has not been explored.

In our first study (Jaric et al. 2005) the participants were instructed to exert sinusoidal pattern of LF either by only pushing in (LF is exerted in only one direction - unidirectional task) or by pushing in and pulling out consecutively (bidirectional task) the handles of an old version of the experimental device. The applied frequencies were 1.33 and 2.67 Hz. Figure 4 shows a clear distinction between uni- and bidirectional task regarding the relationship of GF and LF. In unidirectional tasks GF and LF varied in parallel providing, therefore, a low and stable GF/LF ratio, whereas in bidirectional tasks GF and LF seem poorly related and GF/LF ratio appears to be higher and more variable over time. In general, the results of the study showed a prominent deterioration in GF and LF coordination associated with switching from unidirectional to bidirectional tasks, which was revealed by an increase in GF/LF ratio, as well as by a decrease in both GF-LF coupling and GF modulation. The findings also suggested that the changes in force coordination did not origi-



Figure 5

Schematic representation of the index of bidirectionality (IB) obtained from the intervals of load force exertion relative to the zero force.

The values -25 and 0% IB are considered as unidirectional trials, whereas 25, 50, 75 and 100% are considered as bidirectional trials.

nate from the requirement for a doubled LF exertion (corresponding to the upward and downward of the bidirectional task) and, consequently, for a doubled GF frequency during bidirectional tasks as compared to unidirectional ones. Specifically, unidirectional trials performed at 2.67 Hz demonstrated a higher GF and LF coordination than the bidirectional trials performed at 1.33 Hz. Therefore, the results revealed a potentially important phenomenon relevant not only for bidirectional tasks, but also for understanding some basic mechanisms and phenomena regarding force coordination in manipulation activities.

In the subsequent study (de Freitas et al. 2007) we tested a similar tasks that gradually changed from uni-directional to bi-directional one. Our aim was to investigate whether uniand bidirectional could be either controlled by a single control mechanism or, alternatively, by two distinctive ones. In particular, we manipulated the "index of bidirectionality" (IB) of the task that was calculated from the magnitude and duration of the vertical component of LF (Fz) exerted in the opposite directions (Figure 5). Two unidirectional trails were performed and the Fz minima were set either at zero (0% bidirectional) or at 25% of the Fz maxima (-25% bidirectional). In addition, four bidirectional trials were performed and the Fz minima were set either at 25%, 50%, 75% and 100% in the opposite direction of the Fz maxima.

We hypothesized that if GF-LF coordination were a part of a single control mechanism, a gradual reduction in the indices of GF-LF coordination would be observed as the task gradually becomes bidirectional. Conversely, if GF-LF coordination is controlled by two distinct neural control mechanism, we would expect an abrupt change in GF and LF coordination as soon as LF changes direction, regardless of how low and brief LF exerted in opposite direction is. Figure 6 illustrates GF and LF profiles and GF-LF diagrams exerted by the dominant and non-dominant hand during -25%, 50% and 100% IBs. As depicted, the results showed an abrupt reduction in the indices of GF-LF coordination no matter how low and brief LF exertion was in the opposite direction, which supported the hypothesis of the existence of two partly distinctive neural control mechanism being responsible for coordinating GF and LF in uni- and bidirectional LF exertions.

In spite of identifying the existence two partly distinctive neural control mechanisms driving the coordination of GF and LF in uniand bidirectional tasks, the nature of the mechanisms remained unclear. Based on both the recent experimental findings and the current motor control theories and models, we assumed that the likely candidates could be either the switches among muscle synergies when changing LF direction, or changes in the activation patterns of the digital and non-digital mechanoreceptors, or a combination of both. A motor synergy can be defined as a neural organization of a multi-element system that is designed to improve task performance and shares a common input or neural drive, which leads to a stable relationship among these multi-elements over time (Latash et al. 2002). Based on both the concept of synergy and the results of studies that have shown an elaborate coordination of GF and LF, we could presume that during most of manipulation tasks the muscle groups responsible for controlling or exerting LF form a synergy with the muscles responsible for exerting GF. For example, very close spatial and temporal GF and LF relationships and a relatively stable GF to LF ratio indicate that muscle groups associated with exertion of LF and GF might share the same common neural drive. If this were the neural mechanism that the CNS uses to coordinate the exertion of LF and GF, a question would be how this concept of GF and LF muscle synergy can be applied to explain the differences in GF and LF coordination between uni- and bidirectional LF exertions. Jaric and collaborators (Jaric et al. 2005) suggested that when a participant exerts LF in one direction (unidirectional task), a strong synergy could be formed between the muscles re-



Figure 6

The data obtained from a representative subject under three indices of bidirectionality (IB). Left-hand panels show GF and LF of the dominant (D) and non-dominant (ND). Right-hand panels illustrate the corresponding GF-LF diagrams with the corresponding regression lines, equations and correlation coefficients for each hand separately. Reprinted with permission from de Freitas and collaborators.

sponsible for exerting LF and GF. However, in bidirectional tasks (i.e. when LF is consecutively exerted in two opposite directions) switching between two synergies (i.e., antagonistic muscles exerting LF in opposing directions create synergies with the same GF muscles) could be needed. This switching could force the CNS to set another pattern of GF and LF coordination which could be based on an increased safety margin and reduced GF modulation.

Another factor that could contribute to the deterioration of GF and LF coordination is related to the activation pattern of the skin mechanoreceptors located at the tip of the digits. The main function of these receptors is to provide a quick and accurate sensory information to the CNS regarding spatial and temporal characteristics of skin deformation during manipulation and tactile exploration tasks (Jonansson and Wallbo 1983; Johansson and Westling 1987). The activation of skin digital mechanoreceptors could have a important role in GF and LF coordination (Johansson and Westling 1984; Johansson and Westling 1987; Nowak et al. 2002; Nowak et al. 2001; Westling and Johansson 1987). Several studies have shown that the activation of the these mechanoreceptors has an excitatory effect on the muscles responsible for generating GF (Gandevia and McCloskey 1977; Gandevia and McCloskey 1977; Marsden et al. 1979; Garnett and Stephens 1980; Garnett and Stephens 1981). Others have shown that the individuals with a loss of sensation in the tip of the digits either due to anesthesia (Johansson and Westling 1984; Nowak et al. 2001; Dun et al. 2007; Nowak and Hermsdorfer 2003; Monzee et al. 2003; Johansson et al. 1992; Cole and Abbs 1988; Augurelle et al. 2003) or due to some neurological diseases (Nowak et al. 2004; Nowak et al. 2003; Nowak and Hermsdorfer 2003; Thonnard et al. 1997) demonstrate partly impaired ability to manipulate objects. It has been also shown that, due to the activity of these receptors, the CNS is able to distinguish changes in GF and LF occurring simultaneously by distinct modes of activation of their mechanoreceptors (Srinivasan et al. 1990; Birznieks et al. 2001; Pare et al. 2002; Wheat et al. 2004). Information about the magnitude of GF applied to the object surface is mostly triggered by the size of the skin contact area with the object (Westling and Johansson 1987). However, the information about changes in both LF magnitude and direction could be triggered by changes in the rate of activation of neighboring mechanoreceptors, as well as by the changes in direction of skin deformation (Srinivasan et al. 1990; Birznieks et al. 2001; Pare et al. 2002; Wheat et al. 2004). In addition, bending of the skin caused by the change in LF direction could cause the consecutive changes in activation of the mechanoreceptors located at different sites of the digital pads. Those changes together could be interpreted as micro-slips and, as a result, the CNS could tend to prevent slipping by elevating the safety margin (i.e., by increasing GF/LF ratio) and reducing the GF modulation. The finding that the first impulses elicited by sensory afferents that trigger a highly coordinated muscle manipulation action could distinguish among different tangential force directions (Johansson and Birznieks 2004) seems to speak in favor of this assumption. Nevertheless, experiments performed with and without anaesthetized skin as well as performed by skin parts with different density of mechanoreceptors could provide additional elucidation of the neural mechanisms responsible not only for the studied phenomenon, but also for the neural basis of the force coordination in manipulation tasks in general.

In order to distinguish between the possible role of the synergy of the hand grip and arm muscle (exerting GF and LF, respectively) and the role of sensory information provided by digital and non-digital mechanoreceptors in the



Stick figures representing the four grasping techniques utilized by the participants during oscillatory Fz exertion. (A) Precision grip, (B) palm grip, (C) wrist grip, and (D) fist grip.



Schematic representation of the task. Reprinted with permission from Freitas and collaborators

reduction of GF-LF coordination (see previous paragraph) we performed another study (de Freitas et al. 2008). Similarly to the previous study (de Freitas et al. 2007), we tested sinusoidal LF pattern exerted in vertical direction against an externally fixed device in trials that gradually changed from uni- to fully bidirectional. In addition, the participants performed the tasks having their wrists either unsupported, or supported by rubber bands pulling their hands and forearms with a force equal to the one or two weights of their hand-forearm segments. This manipulation intended to decouple LF measured by the device (and, therefore, recorded by the cutaneous receptors) from the action of arm muscles exerting LF. Figure 7 depict a schematic representation of the task and participant's configuration.

We hypothesized that, if the differences in GF-LF coordination seen between uni- and bidirectional task would be caused by the switching of muscle synergies, the manipulation of external support would affect the indices of GF-LF coordination. Alternatively, a lack of the effect of the external support would suggest an important role of the digital mechanoreceptors (that are not affected by the external support) in the studied phenomenon. Similar to the previous studies (Jaric et al. 2005; de Freitas et al. 2007), the results revealed that switching from uni- to bidirectional tasks, no matter how low and brief LF exertion was in the opposite direction, was associated with an abrupt decrease in GF and LF coordination. However, of utmost importance was that the studied GF-LF coordination remained unaffected by the manipulation of external support. This finding strongly suggested that the discussed difference in GF and LF coordination between the uni- and bidirectional tasks could be based on the afferent sensory input, rather than on the switching of synergies of the muscles exerting GF and LF (de Freitas et al. 2008).

In order to evaluate the role of afferent cutaneous input in the studied control mechanisms, we performed another study (de Freitas and Jaric in preparation) based on two distinctive manipulations. In the first experiment the participants exerted LF using four different bimanual grasping techniques (precision, palm, fist and wrist; Figure 8), which intended to manipulate both the density and sensibility of the skin mechanoreceptors due to the manipulation of skin areas in direct contact with the handles. In the second experiment, LF was exerted by the tips of the digits (precision grip) of the participant's dominant hand both at the normal body temperature and after cooling the digits which intended to reduce the sensibility of the skin mechanoreceptors.

Once again, the results revealed that, independently of grasping technique and the skin temperature, the indices of GF-LF coordination were considerably higher in uni- than in bidirectional tasks. However, the cooling of the skin revealed no effect whatsoever on the studied force coordination. Moreover, the manipulation of the hand skin area in contact with the device also revealed a week and inconclusive effect of the studied GF and LF coordination (see de Freitas et al. 2007) for similar findings). As a result, based on the findings of our three studies aimed towards the distinction between the uniand bidirectional tasks (Jaric et al. 2005; de Freitas et al. 2007; de Freitas el al. 2007; de Freitas et al. 2008), the role of both the muscle synergies and skin mechanoreceptors in the studied phenomenon could be ruled out. Therefore, we believe that further exploration not only of the studied phenomenon, but also of the control of hand function in general, should be mainly focused to the various supraspinal control mechanisms.

Summary

An elaborate coordination of forces applied against hand-held objects is essential for successful manipulation activities. Our newly developed device allowed for force recordings under the conditions that have been partly neglected in the literature. This device proved to provide both reliable and valid data that could be used in various motor control areas. In particular, the data seems to be sufficiently sensitive to detect mild levels of hand impairment in neurological patients. Therefore, a standard clinical test could be derived from both the developed device and the applied experimental protocols. In addition, the device allows for a variety of manipulation tasks to be studied which could be applied in studies of various phenomena associated with manipulation activities and their underlying neural control mechanisms.

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