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## **Case Studies in Neuroscience:**

### **The central and somatosensory contributions to finger inter-dependence and coordination: Lessons from a study of a “deafferented person”**

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Abbreviated title: Finger interactions in a "deafferented person"

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## **ABSTRACT**

We tested finger force interdependence and multi-finger force-stabilizing synergies in a patient with large-fiber peripheral neuropathy ("deafferented person"). The subject performed a range of tasks involving accurate force production with one finger and with four fingers. In one-finger tasks, non-task fingers showed unintentional force production (enslaving) with an atypical pattern: Very large indices for the lateral (index and little) fingers and relatively small indices for the central (middle and ring) fingers. Indices of multi-finger synergies stabilizing total force and of anticipatory synergy adjustments in preparation to quick force pulses were similar to those in age-matched control females. During constant force production, removing visual feedback led to a slow force drift to lower values (by about 25% over 15 s). The results support the idea of a neural origin of enslaving and suggest that the patterns observed in the deafferented person were re-organized based on everyday manipulation tasks. The lack of significant changes in the synergy index shows that synergic control can be organized in the absence of somatosensory feedback. We discuss the control of the hand in deafferented persons within the alpha-model of the equilibrium-point hypothesis and suggest that force drift results from an unintentional drift of the control variables to muscles toward zero values.

## **NEW AND NOTEWORTHY**

We demonstrate atypical patterns of finger enslaving and unchanged force-stabilizing synergies in a person with large-fiber peripheral neuropathy. The results speak strongly in favor of central origin of enslaving and its reorganization based on everyday manipulation tasks. The data show that synergic control can be implemented in the absence of somatosensory feedback. We discuss the control of the hand in deafferented persons within the alpha-model of the equilibrium-point hypothesis.

## INTRODUCTION

The human hand shows the counter-intuitive combination of extraordinary dexterity and limited independence of the fingers, which has been addressed as *enslaving* (Zatsiorsky et al. 2000; reviewed in Latash and Zatsiorsky 2016). We explored the role of somatosensory feedback on finger interdependence and multi-finger synergies by studying a person with a severe case of large-fiber peripheral neuropathy, which is sometimes informally addressed as a “deafferented person” condition. There are only a few documented cases of this disorder leading to a massive somatosensory loss, no joint position and motion sense, and no muscle reflexes in the limbs and trunk (Cole and Paillard 1995). Despite the reorganization of neural control, deafferented persons present coordination deficits across a range of tasks, even under continuous visual control (Rothwell et al. 1982; Sainburg et al. 1993; Sarlegna et al. 2010).

Enslaving has been viewed as a consequence of a variety of peripheral and central mechanisms, from connective tissue links between fingers and multi-finger extrinsic hand muscles to overlapping cortical representations (Schieber and Santello 2004). Based on the idea that enslaving represents a practice-based, functional pattern of finger inter-dependence (cf. Zatsiorsky et al. 2000; Slobounov et al. 2002), we hypothesized that for the patient, adaptive reorganization would result in a changed pattern of enslaving (Hypothesis-1).

Analysis of hand actions has frequently invoked the notion of *synergy* as a neural organization stabilizing important mechanical variables, such as resultant force (Latash et al. 2007). Mechanisms of such synergies are largely unknown but have been assumed to rely on somatosensory feedback (Martin et al. 2009; Diedrichsen et al. 2010). Hence, our Hypothesis-2 was that the deafferented person would show reduced indices of stability during accurate force production tasks.

When a person is asked to generate a quick force pulse from a steady force level, a drop in the synergy index is observed about 200-400 ms prior to the force pulse initiation time (Olafsdottir et al. 2005). These anticipatory synergy adjustments (ASAs) represent a particular example of feed-forward control, which can be observed without somatosensory feedback (cf. Forget and Lamarre 1995). Hence, we expected ASAs to be preserved in the deafferented patient (Hypothesis 3).

Removing visual feedback during steady-state force production is accompanied in healthy persons by a slow force drift, typically toward lower magnitudes (Vaillancourt and Russell 2002; Ambike et al. 2015). Recently, such phenomena have been discussed within the theory of action control with referent coordinates (RCs) for the involved effectors (reviewed in Latash 2010; Feldman 2015) as consequences of an unintentional RC drift toward the effector's actual coordinate (Latash 2017). The concept of RC is tightly coupled to the mechanism of stretch reflex (for a muscle, RC is equivalent to  $\lambda$ , the threshold of the stretch reflex, Feldman 1986). Since stretch reflex was absent in the deafferented patient, we expected a different mode of control compared to normal and explored unintentional force drift.

## **METHODS**

### **Subject description**

GL, a 70-year-old right-handed woman, suffered a permanent and specific loss of the large sensory myelinated fibers that affected her whole body below the V2 cranial nerve division and left her with a massive tactile and proprioceptive deafferentation. She lost tendon reflexes and the senses of vibration, pressure, and kinesthesia from the nose down (Miall et al. 2018). Detailed clinical descriptions of GL have been provided (Forget and Lamarre 1995; Cole and Paillard 1995). Manual dexterity, with visual feedback, remained impaired: for instance, she performed the Grooved Pegboard test in 833.5 s (~14 min) compared to  $78.6 \pm 11.7$  s for controls ( $n=15$ ;  $p < 0.001$ ; see Data analysis).

### **Equipment and procedures**

The subject sat in a chair facing the testing table with her right upper arm at about  $45^\circ$  of abduction in the frontal plane,  $45^\circ$  of flexion in the sagittal plane and the elbow at approximately  $45^\circ$  of flexion. The forearm was fixed by Velcro straps; the wrist was at  $20^\circ$  of extension, and the hand formed a natural dome with the fingers slightly flexed and the four fingertips placed on the top of four unidirectional piezoelectric sensors (model 208C01, PCB Piezotronics, Depew, NY) (Fig. 1). The force data sampled at 1000 Hz. The sensors were spaced 3.0 cm center-to-center in the medial-lateral direction and adjusted in the anterior-posterior direction to match the hand anatomy. The sensors' top surface was covered with 320-grit sandpaper. A 20" monitor located 0.6 m from the subject at eye level was used to set tasks and provide visual feedback.

<Figure 1>

To measure maximal voluntary contraction (MVC) force, the subject pressed with the four fingers as hard as possible in a self-paced manner over 4 s under visual feedback on the total force ( $F_{TOT}$ ). Three trials were performed with 30-s rest periods. The highest force across the three trials and the forces of individual fingers at that time ( $MVC_i$ ,  $i$ : I – Index, M – Middle, R – Ring or L – Little) were used to normalize the following tasks.

During single-finger ramp trials, the subject pressed with one of the four fingers (task-finger) and match a template shown on the screen with the task-finger force: 5 to 40% of  $MVC_i$  over 5 s. All fingers had to stay on the force sensors at all times. The subject was asked not to pay attention to possible force production by the non-task fingers. There were three practice trials followed by three trials per finger.

In the force-pulse task, the subject produced steady  $F_{TOT}$  at 5% of MVC followed by a self-paced pulse into a target set at  $25 \pm 5\%$  of MVC. After the pulse, the subject returned to the initial steady-state force level. After about 3 min practice, the subject performed 24 trials.

During the steady force production task, the subject pressed with all the fingers to match  $F_{TOT}$  to the visual target set at 25% of MVC. After 10 s, the cursor disappeared and the subject had to continue producing the same force for 15 s more. Three trials were recorded after three practice trials.

### **Data analysis**

Data were processed offline using routines written in MATLAB R2016a (The Mathworks, Natick, MA). All data were low-pass filtered using a zero-lag 4<sup>th</sup>-order Butterworth filter with a cutoff frequency of 10 Hz.

The MVC was computed at the time where  $F_{TOT}$  reached maximum during the trial. In each single-finger ramp trial, a 3-s time interval was used, starting 1 s after the ramp initiation and 1 s before ramp termination to avoid edge effect. Within that interval, linear regression and the regression coefficients were used to create the enslaving matrix,  $\mathbf{E}$ :

$$F_{i,j} = f_i^0 + k_{i,j} \cdot F_{TOT,j} \quad (1)$$

$$\mathbf{E} = \begin{bmatrix} k_{I,I} & k_{I,M} & k_{I,R} & k_{I,L} \\ k_{M,I} & k_{M,M} & k_{M,R} & k_{M,L} \\ k_{R,I} & k_{R,M} & k_{R,R} & k_{R,L} \\ k_{L,I} & k_{L,M} & k_{L,R} & k_{L,L} \end{bmatrix}$$

where  $i, j = \{I, M, R, \text{ and } L\}$ ,  $j$  represents the task finger;  $F_{i,j}$  indicates the  $i$ -finger force when the  $j$ -finger was the task finger, and  $F_{\text{TOT},j}$  is the total force when the  $j$ -finger was the task finger. We computed an enslaving index ( $E_j$ ) as the sum of all the non-diagonal elements of  $\mathbf{E}$  for each task-finger separately, and the average of all non-diagonal elements in  $\mathbf{E}$  ( $E_{\text{AV}}$ ).

For the force-pulse task, half of the trials were rejected because of visible counter-movement prior to the pulse and finger slips off a sensor. The 12 accepted trials were aligned by the time ( $t_0$ ) when derivative of  $F_{\text{TOT}}$  exceeded 5% of its maximal value during that trial. The analysis of multi-finger synergies stabilizing the  $F_{\text{TOT}}$  profile assumed that the central nervous system (CNS) manipulated a set of elemental variables, finger forces or finger modes (hypothetical commands to fingers, Danion et al. 2003), to stabilize  $F_{\text{TOT}}$ . Inter-trial variance of the elemental variables was partitioned into two components, within the uncontrolled manifold ( $V_{\text{UCM}}$ ; which did not affect  $F_{\text{TOT}}$ ) and orthogonal to it ( $V_{\text{ORT}}$ ; which affected  $F_{\text{TOT}}$ ).

The enslaving matrix  $\mathbf{E}$  was used to convert the  $4 \times 1$  force data vector  $\mathbf{f}$  ( $\mathbf{f} = [f_I, f_M, f_R, f_L]^T$ ) into a set of finger modes:  $\mathbf{m} = \mathbf{E}^{-1}\mathbf{f}$  where  $\mathbf{m}$  is the  $4 \times 1$  vector for each sample. The analysis was performed in two spaces, forces ( $\mathbf{f}$ ) and modes ( $\mathbf{m}$ ). Variance across trials was computed for each time sample, and quantified within the uncontrolled manifold (UCM; Scholz and Schöner 1999) and orthogonal space (ORT) separately. The index of synergy ( $\Delta V$ ) was computed as:

$$\Delta V = \frac{V_{\text{UCM}}/3 - V_{\text{ORT}}/1}{V_{\text{TOT}}/4} \quad (2)$$

where  $V_{\text{TOT}}$  is total variance. The  $\Delta V$  values were z-transformed prior to statistical analysis ( $\Delta V_Z$ ). Means and standard deviations (SD) were computed for  $\Delta V_Z$  within the steady-state (SS) defined as a 0.5-s time window from  $-1.5$  s to  $-1.0$  s before  $t_0$ .

ASAs were defined as a drop in  $\Delta V_Z$  prior to  $t_0$ . We computed the time of ASA onset ( $t_{\text{ASA}}$ ) as the time when  $\Delta V_Z$  decreased by two SDs below the average value computed over SS. Changes in the index of synergy ( $\Delta \Delta V_Z$ ) and variance indices ( $\Delta V_{\text{UCM}}$  and  $\Delta V_{\text{ORT}}$ ) over the ASA, were computed as the differences between the values during SS and  $t_0$ .

To quantify the unintentional force drifts, we averaged  $F_{TOT}$  over the three trials and computed the drift magnitude ( $\Delta F_{TOT}$ ) as the difference between two 1-s windows, just before the time when visual feedback had been removed and just before the end of the trial.

For statistical analysis, we used the Singlims\_ES.exe (Crawford et al. 2010) which implements methods for comparing a single-case value to values obtained in a small control sample with the help of multiple Monte-Carlo simulations.

## RESULTS

We present the data in comparison to the female subjects in Shinohara et al. (2003) and Park et al. (2012) ( $n = 6$  for both samples). GL's MVC force was 51.86 N, 5 SD higher compared to somewhat older control females ( $25 \pm 5.0$  N;  $p < 0.01$ ). Analysis of enslaving showed larger values for the two "lateral" fingers, I (0.513) and L (0.451), compared to the "central" fingers, M (0.344) and R (0.231). This pattern was atypical compared to controls as illustrated in Figure 2. In particular, the  $E$  indices for the I and L fingers were  $>4$  SDs above the control mean (I:  $0.15 \pm 0.071$ ; L:  $0.14 \pm 0.054$ ;  $p < 0.01$  for each).

<Figure 2 >

During steady-state force production, inter-trial variance within the uncontrolled manifold ( $V_{UCM}$ ) was consistently higher than inter-trial variance orthogonal to the uncontrolled manifold ( $V_{ORT}$ ) in both force ( $\mathbf{f}$ ) space and mode ( $\mathbf{m}$ ) space, resulting in positive values of the synergy index (Fig. 3),  $\Delta V_Z = 1.33$  and 2.21 for the  $\mathbf{f}$ -space and  $\mathbf{m}$ -space analysis, respectively. The latter value was within one SD from the mean value in controls ( $2.11 \pm 0.2$ ;  $n = 6$ ). Prior to the force pulse, there was a drop in the synergy index (ASA, Fig. 3) starting at  $t_{ASA} = 0.432$  s (controls:  $t_{ASA} = 0.310 \pm 0.115$ ). The magnitude of the drop in  $\Delta V_Z$  during the ASA was 0.623 (controls:  $\Delta \Delta V_Z = 0.85 \pm 0.063$ ).

<Figure 3>

Removing visual feedback led to a slow  $F_{TOT}$  drift toward lower magnitudes. The total drift magnitude was 0.248 when normalized by the task force magnitude, close to the values seen in control subjects ( $0.17 \pm 0.08$ ;  $n = 6$ ; Jo et al. 2016).



## DISCUSSION

### **The origin of finger enslaving**

Changes in enslaving with aging are counter-intuitive: It has been reported to decrease in older persons, thus corresponding to better finger individuation (Shinohara et al. 2003; Kapur et al. 2010). Compared to age-matched females (Shinohara et al. 2003), the pattern of enslaving observed in our study showed atypically high values for the I and L fingers (Fig. 2). In contrast, the R-finger enslaving was of a relatively modest magnitude ( $< 0.3$ ), lower than for any other finger of the hand, whereas the R finger typically shows the highest enslaving (Zatsiorsky et al. 2000; Shinohara et al. 2002). Given that there are no reasons to expect major changes in peripheral inter-finger connective tissue links and anatomy of multi-finger extrinsic muscles in deafferented persons, this atypical pattern suggests a predominant role of supraspinal mechanisms in the phenomenon of enslaving, possibly reflecting changes in cortical finger representations (cf. Schieber and Santello 2004), **ALTHOUGH CHANGES AT THE SPINAL LEVEL CANNOT BE RULES OUT.**

The patient's atypical pattern of enslaving could reflect a central adaptation to the somatosensory loss (cf. Hypothesis-1). Indeed, somatosensory loss impairs manual dexterity (Rothwell et al. 1982). Note that the central fingers, M and R, are responsible primarily for grip force and resultant force production, whereas the lateral fingers, I and L, specialize for rotational action, i.e. moment of force production (Zatsiorsky and Latash 2008). This suggests a patient's strategy of over-gripping the hand-held object thus increasing the rotational apparent stiffness of the hand with the object and decreasing kinematic consequences of possible errors in the applied moment of force. This can be achieved by coupling neural commands to lateral fingers and central fingers, which results in large enslaving indices for lateral fingers as observed in our study.

### **The role of sensory feedback loops in multi-finger synergies**

Our observations of unchanged indices of multi-finger synergies stabilizing  $F_{TOT}$  falsify Hypothesis-2 and fit theoretical schemes of synergic control that do not rely on feedback from peripheral receptors, e.g., those based on the idea of central back-coupling (Latash et al. 2005). This idea assumes the presence of within-the-CNS loops with modifiable gains that provide very

short-latency feedback from the outputs of a pool of neurons back to those neurons, somewhat similar to the system of Renshaw cells. Note that optimal feedback control schemes rely on sensory signals about the ongoing action (Diedrichsen et al. 2010). We cannot address the controversy between optimal feedback control schemes and ideas of control with RCs (equilibrium-point control) within this brief note; this controversy has been addressed recently (Feldman 2015; Latash 2017). However, if one accepts the postulates of the optimal feedback control schemes, our observations suggest that such mechanisms can function based on artificially-created feedback, e.g., visual feedback on  $F_{TOT}$  rather than on natural somatosensory feedback.

These conclusions are in line with recent studies showing that removal of visual feedback leads to quick loss of stability and low synergy indices even in the presence of veridical continuous feedback from somatosensory endings (Parsa et al. 2016; Reschechtko and Latash 2017). This dominance of visual information for stability of prehensile tasks suggests that the documented poor coordination in deafferented persons (Rothwell et al. 1982; Sainburg et al. 1993; Sarlegna et al. 2010) may partly be due to the loss of performance-stabilizing synergies when salient variables produced by the effector cannot be monitored closely with visual information.

Our finding of unchanged ASAs confirms Hypothesis-3 and is in line with earlier reports on feed-forward adjustments in deafferented patients (Forget and Lamarre 1995). They extend these previous findings to feed-forward adjustments of synergies that are seen in the absence of changes in magnitudes of any of the performance variables and can be seen only in patterns of inter-trial co-variation of elemental variables. This is not a trivial finding given that ASAs show significant changes in patients with supraspinal neurological disorders (reviewed in Latash and Huang 2015) and suggests that central and peripheral insults to the nervous system may have qualitatively different effects on feed-forward control of action stability.

### **Control of action in conditions of deafferentation**

Within the physical approach to biological actions, movements are produced by changes in parameters of respective laws of nature, for example, threshold of the stretch reflex ( $\lambda$ ) that defines the dependence of active muscle force on muscle length; these parameters have been associated with RCs for the effectors (Latash 2010, 2017; Feldman 2015). The action of reflex

loops from proprioceptors forms the basis for this scheme, and this mechanism is expected to be destroyed in conditions of deafferentation. How are movements controlled in such conditions?

An answer was suggested in studies of movements by deafferented monkeys (Polit and Bizzi 1978; Bizzi et al. 1982; see also Levin et al. 1995), which formed the basis for the  $\alpha$ -model within the equilibrium-point hypothesis. The  $\alpha$ -model assumes that the neural controller specifies the output of the  $\alpha$ -motoneuronal pools. Within the  $\alpha$ -model, changes in the control signals to opposing muscle groups can lead to changes in effector's force-coordinate (or torque-length) characteristic thus making movements possible and demonstrating some features of unimpaired control, e.g. equifinality in cases of transient perturbations. This mode of control is, however, in principle different from specifying RCs for the involved muscles during movements by persons with intact somatosensory feedback. The switch to this unusual mode of control may be a major contributor to the severe movement deficits in deafferented persons. Without visual feedback, control variables ( $\alpha$ ) are expected to move to zero reflecting the natural tendency of all physical systems to move toward states with lower potential energy (Latash 2017). This is consistent with the observed force drift for the deafferented patient, a drift similar to that of healthy persons (Vaillancourt and Russell 2002; Ambike et al. 2015).

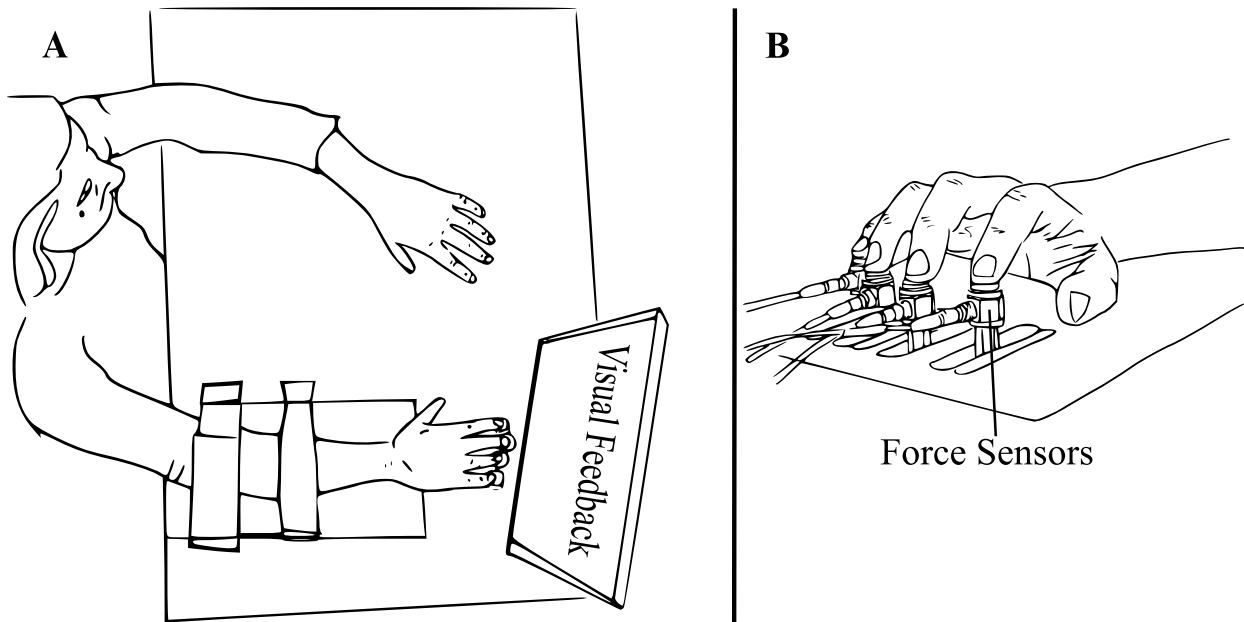
As suggested earlier, the concept of performance-stabilizing synergies is compatible with the theoretical scheme of hierarchical control with RCs (Latash 2010). Our results suggest that synergies stabilizing performance can be built on mechanisms that do not necessarily require intact somatosensory feedback and use different control variables for the participating muscles.

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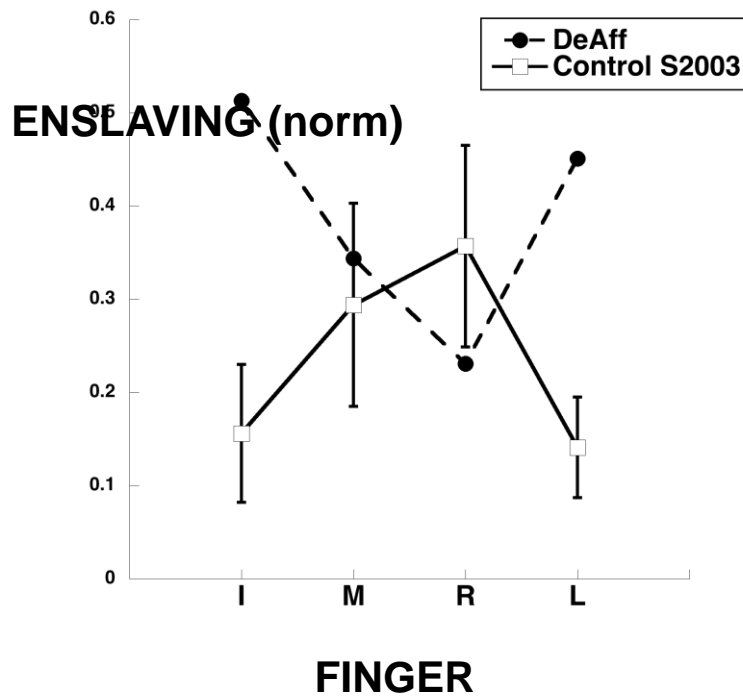
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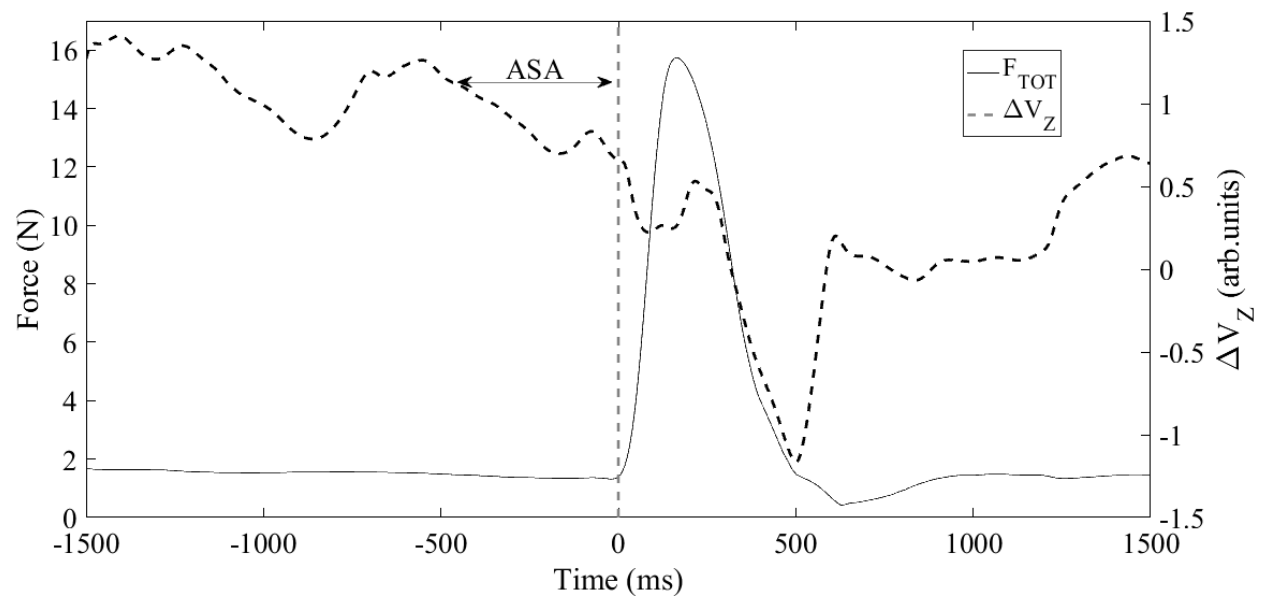
**FIGURES**



**Figure 1:** Schematic illustration of the setup. A: Position of the subject and visual display. B: Hand configuration and force sensors.



**Figure 2:** Enslaving values are presented for each finger for the deafferented patient (closed circles, DeAff) and controls (values from Shinohara et al. (2003; 6 right-handed, healthy females, age=75 ± 5 years) are presented with standard deviation bars (open squares, Control S2003). Note the qualitatively-different patterns and DeAff's larger enslaving for the index (I) and little (L) fingers.



**Figure 3:** Results of the force-pulse task. Average force pulse ( $F_{TOT}$  across 12 trials) and the z-transformed synergy index ( $\Delta V_z$ ) are shown. ASA stands for anticipatory synergy adjustment.