

# Prehension synergies and control with referent hand configurations

Mark L. Latash · Jason Friedman ·  
Sun Wook Kim · Anatol G. Feldman ·  
Vladimir M. Zatsiorsky

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**Abstract** We used the framework of the equilibrium- referent configuration may be described with a few referent point hypothesis (in its updated form based on the notion of values of variables that influence the equilibrium state, to referent configuration) to investigate the multi-digit syn-which the system is attracted. Moreover, the referent con-ergies at two levels of a hypothetical hierarchy involved in configuration hypothesis can help interpret the data related to prehensile actions. Synergies were analyzed at the thumb and the trade-off between synergies at different hierarchical virtual finger (VF) level (VF is an imaginary digit with the levels.

mechanical action equivalent to that of the four actual fingers) and at the individual finger level. The subjects performed very quick vertical movements of a handle into a target. A load could be attached off-center to provide a pronation or supination torque. In a few trials, the handle was unexpectedly fixed to the table and the digits slipped off the sensors. In such trials, the hand stopped at a higher vertical position and rotated into pronation or supination depending on the expected torque. The aperture showed non-monotonic changes with a large, fast decrease and further increase, ending up with a smaller distance between the thumb and the fingers as compared to unperturbed trials at which all the involved muscles would have achieved zero activation levels, while any deviations from co-variation between digit forces and moments of force across unperturbed trials. Prior to the lifting action, high synergy indices were observed at the individual finger level while modest indices were observed at the thumb level. During the lifting action, the synergies at the individual finger level disappeared while the synergy indices became higher at the thumb level. The results support the basic premise that, within a given task, setting a

Prehension Synergy. Referent configuration. Grip Introduction Recent developments of the equilibrium-point hypothesis and the control of multi-effector and whole-body movements have resulted in the concept of referent configuration (RC; reviewed in Feldman and Levin 2009). RC is a configuration of the thumb and the fingers as compared to unperturbed trials at which all the involved muscles would have achieved zero activation levels, while any deviations from co-variation between digit forces and moments of force across unperturbed trials. Therefore, RC may also be addressed as threshold body configuration. Actual equilibrium body configurations commonly deviate from RC because of external forces (including gravity) and/or constraints that may be imposed by external objects such as rigid obstacles preventing motion of body parts and the body anatomy.

Prehensile tasks have been commonly described in terms of digit forces (reviewed in Johansson and Zatsiorsky and Latash 2008), that is kinetic variables. In a recent study, Pilon and colleagues (2007) have shown that motion of a hand-held object, associated with anticipatory adjustment of grip force, can result from changes in a component of the referent body configuration—the referent arm-hand configuration. In this framework, the normal force during prehension emerges following the difference between the

M. L. Latash (✉) · J. Friedman · S. W. Kim · V. M. Zatsiorsky  
Department of Kinesiology, The Pennsylvania State University,  
Rec.Hall-267, University Park, PA 16802, USA  
e-mail: mll11@psu.edu

A. G. Feldman  
Department of Physiology, Centre for Interdisciplinary Research  
in Rehabilitation, University of Montreal, Montreal, QC, Canada

referent aperture between the opposing digits and the actual aperture constrained by the size of the object between the digits. The purpose of this study is to develop this view, test some of its predictions, and link the RC hypothesis with the idea of multi-digit prehension synergies.

Consider a five-digit prismatic grasp where all the points of digit contact with the hand-held object are in one plane (the grasp plane); an external torque acts in the same plane, i.e. the torque vector is normal to the plane. Such a task has been analyzed as a two-level hierarchy (Arbib et al. 1985; Iberall 1987; Santello and Soechting 2000; Zatsiorsky and Latash 2008; Latash and Zatsiorsky 2009). At the upper level, the task is shared between the thumb and a virtual finger (VF, an imagined digit with the coordinates of the four fingers). At the lower level, the VF action is shared among the four fingers. Consider the task at the upper level: Holding an object statically imposes four constraints. First, the resultant normal force should be zero. Second, the resultant tangential force should be equal in magnitude to the object weight and directed against the force of gravity (load,  $L$ ). Third, the resultant moment of force should be equal in magnitude and directed against the external moment of force ( $M$ ). Fourth, the normal forces should be

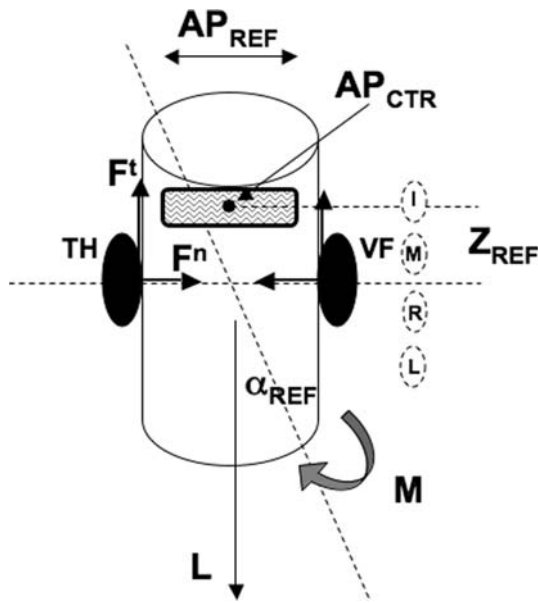


Fig. 1 An illustration of a thumb-virtual finger (TH-VF) grip in a planar case. An external load and moment of force ( $L$  and  $M$ ) act on the hand-held object. The controller sets a referent configuration, which leads to peripheral effects that may be described with four geometric parameters: The size and location of the referent aperture ( $AP_{REF}$  and  $AP_{CTR}$ ), referent vertical position ( $Z_{REF}$ ), and referent orientation ( $\alpha_{REF}$ ). Virtual finger produces force and moment of force equal to the sum of the forces and moments of force produced by the four individual fingers ( $I$ : index,  $M$ : middle,  $R$ : ring, and  $L$ : little)

Note that setting any  $AP_{REF}$  smaller than the actual aperture leads to a discrepancy between the referent and actual digit tip coordinates in the horizontal direction. This discrepancy results in active muscle force production trying to move the digits towards their respective referent point ( $AP_{CTR}$ ; cf. Pilon et al. 2007), referent position in the vertical direction ( $Z_{REF}$ ), and referent orientation of the object with respect to the vertical ( $\alpha_{REF}$ ). Note that setting any  $AP_{REF}$  smaller than the actual aperture leads to a discrepancy between the referent and actual digit tip coordinates in the horizontal direction. This discrepancy results in active muscle force production trying to move the digits towards their respective referent point ( $AP_{CTR}$ ; cf. Pilon et al. 2007), referent position in the vertical direction ( $Z_{REF}$ ), and referent orientation of the object with respect to the vertical ( $\alpha_{REF}$ ). Note that setting any  $AP_{REF}$  smaller than the actual aperture leads to a discrepancy between the referent and actual digit tip coordinates in the horizontal direction. This discrepancy results in active muscle force production trying to move the digits towards their respective referent point ( $AP_{CTR}$ ; cf. Pilon et al. 2007), referent position in the vertical direction ( $Z_{REF}$ ), and referent orientation of the object with respect to the vertical ( $\alpha_{REF}$ ).

Using the described mode of control defined by these, given certain external conditions, characteristics of the overall action of the hand on the object such as grip (normal) force, total load resisting force, and total moment of force. It does not define unambiguously, however, contributions of the individual digits (for example, the thumb and VF forces) to the overall hand action. Across repetitive trials, the digit forces and moments of force may be expected to co-vary, as long as they do not lead to major changes in the resultant force and moment of force acting on the object. Such co-varied changes in elemental variables (forces and moments of force produced by individual digits) that keep important characteristics of the overall hand action unchanged have been addressed as prehension synergies (Santello and Soechting 2000; Zatsiorsky and Latash 2004, 2008).

Several recent studies produced quantitative estimates of prehension synergies at the two introduced levels (Gorniak et al. 2007a, b, 2009). In these studies, an index of synergy was computed reflecting the amount of co-variation among elemental variables across repetitive trials that helped stabilize the mechanical output at that particular level. High synergy indices at the upper level were accompanied by low synergy indices at the lower level suggesting a conflict between synergies at the two levels.

In this study, we test several predictions of the suggested two-level hierarchical scheme and control with RC for an experiment when the subject plans to move a hand-held object quickly and the object unexpectedly happens not to be in the hand. First, we predict that such an unexpected unloading of the hand would lead to a new configuration of

the hand and digits compatible with the idea of unloading of the wrist with the hand extended, and their hand width was referred variables such as  $A_{REF}$ ,  $Z_{REF}$ , and  $\alpha_{REF}$ . The measured between the lateral aspect of the index and little unloading will lead to a decrease in the external forces on the finger metacarpophalangeal (MCP) joints. None of the subjects had a history of neurological or peripheral disorders of the hand or professional training that might affect their hand function, such as playing musical instruments. All subjects gave informed consent according to the procedures approved by the Office for Research Protection of the Pennsylvania State University.

between the thumb and the opposing digits, i.e. the digits moving towards each other and then away from each other.

This prediction is based on the documented transient increase in the grip force in the middle of such actions related to the expected inertial forces (Flanagan et al. 2006; Gysin et al. 2003). We expect the hand to move to a midpoint of the beam in the medio-lateral direction; the higher vertical location similarly to the classical results in handle and beam apparatus created an inverse T shape experiments with arm unloading (Feldman 1966). We also expect the hand to rotate in the direction opposite to the external torque created by the unbalanced load attached to the aluminum handle. The transducers measured the forces and moments of force applied by the fingers (Nano-17) and by the thumb (Nano-25). The moments are recorded with respect to the centers of the contact area of the sensors.

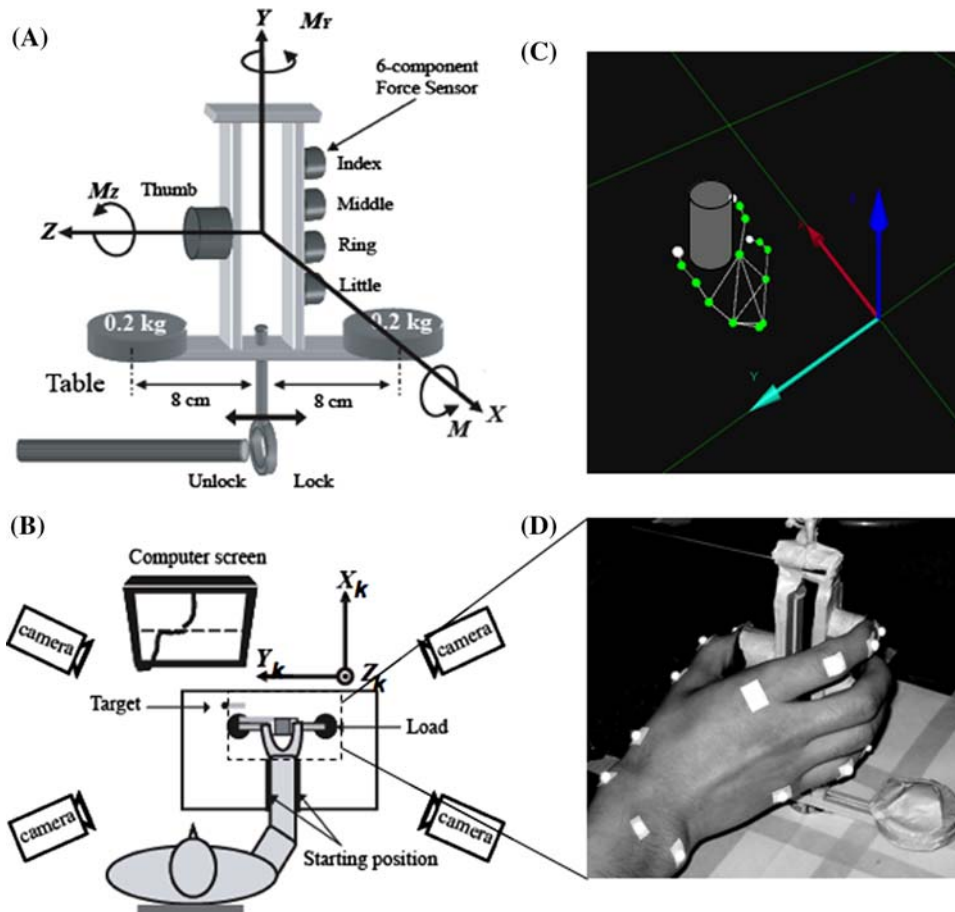
Second, we expect to see strong synergies at the upper level of the hierarchy during the unperturbed lifting actions and while synergies at the lower level may be present or absent (as in Gorniak et al. 2009).

Third, if the subject is asked to produce a certain, low magnitude of the grasping force prior to lifting the object, this task may be associated with setting not a referent coordinate for each of the opposing sets of digits (the thumb and the set of four fingers comprising the VF). Setting a referent VF coordinate defines VF normal force system while it allows finger forces to co-vary as long as VF force corresponds to the difference between the referent and actual VF tip coordinates. Hence, we expect to see a synergy at the lower level stabilizing the VF normal force (in contrast to the second prediction). During this phase, the unloaded handle was determined by suspending the handle at different points. Two loads (0.21 kg) were fixed either symmetrically at the endpoints (zero external torque on the object since keeping the resultant force at zero condition) or there was only one load attached to the left or right endpoint. When the load was placed at the left endpoint, it required a supination effort to keep the handle vertical (SU condition). When the load was placed at the right endpoint, it required a pronation effort (PR condition). The magnitude of the external torque was 0.15 Nm.

## Methods

### Subjects

Ten healthy right-handed university students (five males and five females) participated in this experiment. Subjects were all right-handed according to their hand usage during eating and writing. Their mean (SD) anthropometric characteristics were: age  $27.7 \pm 5.5$  years, weight  $68.1 \pm 13.1$  kg, height  $170 \pm 8.2$  cm, hand width  $7.5 \pm 0.9$  cm, and hand length  $17.5 \pm 1.2$  cm. Each participant's hand length was measured between the middle fingertip and the distal crease between the contact surfaces of the thumb and finger



**Fig. 2** Experimental setup **a** A schematic diagram of the aluminum handle; the force/moment sensors shown as black cylinders were attached to two vertical aluminum bars. The loads (0.21 kg) are shown as black cylinders attached to the long horizontal beam. The external torque conditions were *Left* ( $-0.15$  Nm), *No* ( $0$  Nm), and *Right* ( $0.15$  Nm) external torque conditions. A lock system was attached to a metal loop and was secured with an eyehook directly underneath the table in the medial direction. **b** The approximate location of four cameras and the wrist markers. Note that there are two coordinate systems:  $X^k$  and  $Z^k$  are fixed relative to the handle, and  $Y^k$  and  $Z^k$  are fixed relative to the laboratory table.

sensors in the horizontal direction, was 86 mm. The plane containing the centers of all five sensors will be referred to as the grasp plane.

Smooth nylon pads were placed on the round contact surface of each sensor in order to decrease the friction between the skin and the nylon pads. To measure the static friction coefficient ( $\mu$ ) between the skin and the nylon pads, the subjects were asked to grasp the handle with their thumb and index finger and then decrease the grasping force as slowly as possible. Slips were detected by a sudden decrease in the tangential force at the thumb and index fingers. The friction coefficient was computed as the ratio between the normal force and the tangential force at slip (Johansson and Westling 1984; Aoki et al. 2006). The friction coefficient ( $\mu$ ) was  $0.6 \pm 0.07$ .

markers were recorded and identified with the Qualisys visually presented target (20 cm from the top of the handle) Track Manager (Qualisys, Gothenburg, Sweden) on a self-paced manner and then hold the handle naturally on another desktop computer (Dell Dimension 8300, Austin, TX, USA). A customized LabView program was used for the data acquisition, and Matlab programs were written for data processing.

### Experimental procedure

The subjects cleaned and dried their hands to normalize the skin condition. Before testing, the subjects were given an orientation session that explained the apparatus and the procedure to ensure that they were able to accomplish the task properly. Light-weight spherical retro-reflective markers (3 mm in diameter) were attached to the dorsal aspect of the hand.

Due to limitations in the experimental setup, data were recorded only from the thumb, index and little fingers. For these three digits, markers were adhered to consistent identifiable and palpable surface landmarks: to the center of each fingernail, to the three joints of each digit, to the radial and ulnar styloids, and to the midpoint between the two wrist markers (a total of 15 markers, see Fig. 1). We used the Pngertip markers to track the position of the handle during the task. Finger flexion and extension, abduction and adduction, and hand pronation and supination movements were calculated from the motion capture data.

During the experiment, the subject sat on a chair, faced the testing table and rested his/her elbow and wrist on the table with his/her upper arm at approximately 45° abduction in the frontal plane and his/her forearm at approximately 135° flexion in the sagittal plane. The forearm was supinated 90° thus, the hand was positioned in a natural grasping position. The handle was placed on the table and aligned with the right shoulder of subject. The subject was requested to place his/her forearm in a starting position prior to each trial (Fig. 2c). The starting forearm position was identified by a drawing on a board and defined by the size of each subject's forearm, but his/her forearm was not constrained by any physical means. In the starting position, the fingers were close to, but not touching, the sensors as the subject prepared to grip the inverse T-shaped handle.

During the testing, the computer generated a warning beep (alerting subjects to get ready), and a yellow cursor showing the total normal force produced by all four fingers (I, M, R, and L) started to move along the screen. The subjects were asked to statically grasp the handle and match their total finger normal force with the horizontal line (10 N) shown on the monitor. This force was much smaller than typical forces generated during the object motion (see Fig. 5; Results). The second time interval, which started after the trial initiation, was shown as a thick dotted vertical line. At any time within this interval, the subjects were asked to lift the handle up rapidly to match a

voluntary action was identified using the thumb normal rotation ( $\Delta\theta$ ) between perturbed and unperturbed trials was finger force. The time of action initiation ( $t_0$ ) was defined as defined as the difference between the maximal hand rotation the time when the time derivative of the thumb normal force in a perturbed trial and in the averaged unperturbed reached 5% of its peak level for that trial. All trials were trials. The hand rotations in the counterclockwise direction aligned by  $t_0$  for further analysis. Note that  $\Delta\theta$  was calculated (pronation) were designated as positive. from the force data rather than the position data, because the increase in grip force preceded the handle movement.

The kinetic and kinematic data processing was performed using Matlab. Three time intervals were identified within each action:

- (1) The constant force phase was the period of time when the fingers produced about 10 N before the lifting movement was initiated (before  $t_0$ ).
- (2) The lifting phase was defined as the period between the onset of the movement ( $t_0$ ) and the time of peak height ( $H_{PEAK}$ ) computed as the height when the average tangential velocity of the wrist markers crossed zero after reaching the peak velocity.
- (3) The holding phase was defined as the last 1 s of the movement.

**Kinematic analysis**

The vertical movement distance ( $D_z$ ) was defined as the height reached, after the movement was complete, by the thumb marker as measured by the cameras (in the direction in the lab-fixed reference system). In the unperturbed conditions,  $D_z$  was close to the target height (20 cm). For perturbed conditions,  $D_z$  could vary substantially. The difference ( $\Delta D_z$ ) between  $D_z$  in a perturbed trial and its averaged value in unperturbed trials was computed for each perturbed trial. Positive values of  $\Delta D_z$  indicate that in the perturbed condition, the hand was higher than in the unperturbed condition.

Grip aperture ( $W$ ) was defined as the minimal distance between the thumb and the line connecting the centers of the index and little finger sensors. This distance was unchanged in unperturbed trials because of the constraints imposed by the handle,  $9.4 \pm 3$  mm across subjects; it differs from the handle width because the sensors were placed on the top of the fingernails. The aperture could change in the perturbed trials as a function of time. For each perturbed trial, the change in grip aperture ( $\Delta W$ ) was defined as the difference between the constant aperture in the unperturbed trials and the minimum value ( $W(t)$ ) in that trial. Positive values of  $\Delta W$  indicate that the aperture was smaller in the perturbed condition.

Rotation of the line connecting the carpometacarpal (CMC) and MCP joint markers was described using Euler angles, with the  $X - Y' - Z''$  sequence (Zatsiorsky 1998). Hand rotation was defined as the maximum rotation about the  $X$  axis in this decomposition. The change in hand

**Kinetic analysis**

The forces of the individual force sensors were first transformed into the coordinate system of the handle. In the transducer-fixed reference system, the normal force (where the subscript refers to individual digits) corresponds to the  $Z$ -direction. In the initial position,  $F_i^n$  was oriented horizontally with respect to the global coordinate system. The  $Z$ -axis of each transducer was aligned with the vertical axis. The force along the  $Z$ -axis will be referred to as tangential force  $F_i^t$ .

The normal and tangential forces of the individual digits,  $F_i^n$  and  $F_i^t$ , and the resultant force can be represented as:

$$\begin{bmatrix} F_{VF}^n \\ F_{VF}^t \end{bmatrix} = \begin{bmatrix} \sum_{i=1}^4 F_i^n \\ \sum_{i=1}^4 F_i^t \end{bmatrix}, \quad i = \{I, M, R, L\} \tag{1}$$

$$\begin{bmatrix} F_{TOT}^n \\ F_{TOT}^t \end{bmatrix} = \begin{bmatrix} \sum_{j=1}^5 F_j^n \\ \sum_{j=1}^5 F_j^t \end{bmatrix}, \quad j = \{I, M, R, L, T\} \tag{2}$$

where I, index; M, middle; R, ring; L, little; and T, thumb. The resultant (subscript TOT) normal force of the five digits was expected to be close to zero, while the resultant tangential force of the five digits was expected to be close to the load when the handle was not moving.

Since each finger makes soft finger contact with the sensor surface (Mason and Salisbury 1985), the digits could roll on and push against the sensor surfaces, but they could not pull on the sensors. The position of the point of normal digit force application with respect to the sensor center (the center of pressure, CoP) was calculated as  $CoP_x = m_x / F_z$  and  $CoP_y = m_y / F_z$ , where CoP stands for the center of pressure;  $m_x$  and  $m_y$  signify the moments of force about the local  $X$ - and  $Y$ -axis with respect to the center of the sensor surface. The moments of individual finger forces and the resultant moment acting on the handle about the  $Z$ -axis passing through the center of the handle were calculated:

$$M^j = d_Y^j \cdot F_Z^j - d_Z^j \cdot F_Y^j \tag{3}$$

$$M = \sum_j M^j \tag{4}$$

where  $j$  stands for all digits including the thumb (I, M, R, L, T),  $F$  is force,  $d$  is a moment arm, and  $M$  stands for

moment of force about the axis. Upward tangential forces normal forces,  $\Delta V_{F,j}(t)$ , was also computed. Further, an and counterclockwise moments (PR moments) were index of force co-variation at the lower and higher levels defined as positive. In the text, moments of force exerted were computed as:  
by the subjects, not produced by external loads are presented.

$$\Delta V_{F,IF}(t) = [\Sigma \text{Var} F_j(t) - \text{Var} F_{VF}(t)] / \Sigma \text{Var} F_j(t) \quad (9)$$

*Analysis of force and moment-of-force stabilizing synergies*

$$\Delta V_{F,HAND}(t) = [\text{Var} F_{VF}(t) + \text{Var} F_T(t) - \text{Var} F_{TOT}(t)] / [\text{Var} F_{VF}(t) + \text{Var} F_T(t)] \quad (10)$$

The purpose of this analysis was to compute indices of co-variation of elemental variables (forces and moments of force) produced by sets of effectors that reflect the stabilization of combined effector outputs. This analysis was performed at two levels: the individual finger (lower) level and the VF+thumb (upper) level. Note that at the upper level, four constraints of statics have to be satisfied to keep the object motionless in the hand:

Likewise, indices for moment of force co-variation at the two levels were computed as:

$$\Delta V_{M,IF}(t) = [\Sigma \text{Var} M_j(t) - \text{Var} M_{VF}(t)] / \Sigma \text{Var} M_j(t) \quad (11)$$

$$\Delta V_{M,HAND}(t) = [\text{Var} M_{VF}(t) + \text{Var} M_T(t) - \text{Var} M_{TOT}(t)] / (\text{Var} M_{VF}(t) + \text{Var} M_T(t)) \quad (12)$$

$$0 = F_{VF}^n + F_T^n \quad (5)$$

$$-L = F_{VF}^t + F_T^t \quad (6)$$

$$-M = \underbrace{F_T^n d_T + F_{VF}^n d_{VF}}_{\text{Moment of the normal forces } M^n} + \underbrace{F_T^t r_T + F_{VF}^t r_{VF}}_{\text{Moment of the tangential forces } M^t} \quad (7)$$

$$k F_{VF}^n > F_{VF}^t; k F_T^n > F_T^t \quad (8)$$

where the superscripts refer to normal and tangential forces,  $d$  and  $r$  are moment arms of the normal and tangential forces respectively, and  $k$  is a friction coefficient.

Note that  $\Delta V > 0$  implies predominantly negative co-variation among forces (or moments of force) produced by the individual digits. We interpret such values as signs of a force (or moment of force) stabilizing synergy (Gorniak et al. 2007a b; Kang et al. 2004; Shim et al. 2005). Larger positive  $\Delta V$  values correspond to larger amounts of negative co-variation, thus a stronger synergy. A result of  $\Delta V = 0$  implies independent variation of digit forces (or moments of force), and correspondingly the absence of a synergy, while  $\Delta V < 0$  may be interpreted as co-variation of elemental variables destabilizing their combined output. The normalization limits the value of  $\Delta V$  indices by +1 for perfect force (or moment) stabilizing synergies (the individual elemental variables change their value in time but variance of the performance variable equals zero).

At the lower level, co-variation of elemental variables produced by individual fingers was studied, while at the upper level, co-variation of elemental variables produced by the VF and the thumb was studied. The index of co-variation was computed as the difference between the sum of the variances of elemental variables  $\Sigma [\text{Var}(EV)]$  and the variance of the total output of these elemental variables  $[\text{Var}(\Sigma EV)]$ . According to the Bienaymé theorem (Loève 1955), for independently varying variables, the two values should be equal to each other. Hence positive values of the index corresponded to predominantly negative co-variation among the elemental variables, which we interpret as stabilization of their combined output.

*Analysis of apparent stiffness*

For each condition and subject, there were at least 12 acceptable unperturbed trials. Hence, exactly 12 trials were chosen for each condition and each subject for this analysis. These trials were aligned by the moment of action initiation ( $t_0$ ). The VF normal force was computed as the sum of the magnitudes of the four finger normal forces at each time sample. The time profiles of the variances of each individual digit normal force ( $\text{Var} F_j(t)$ ,  $j = I, M, R, L, T$ ), the VF normal force [ $\text{Var} F_{VF}(t)$ ], and the total normal force [ $\text{Var} F_{TOT}(t)$ ] were computed across the trials at each point in time for each condition and subject separately. The time profile of the sum of the variances of the individual finger

We will use the term "apparent stiffness" (see Latash and Zatsiorsky 1993; Zatsiorsky 2002) defined as the change in force (or moment of force) per unit of linear displacement (or rotational displacement) imposed by a change in the external loading conditions. For simplicity, we assume linear relations between changes in displacements and forces (moments of force).

Previous studies of the apparent stiffness of the fingers (Kao et al. 1997; Hajian and Howe 1997; Milner and Franklin 1998) and of a grasping hand (van Dorpe 1998; Friedman and Flanagan 2007) used small perturbations of the fingers in order to calculate the stiffness matrices. In this study, a different approach was used. In the perturbed conditions, motion of the hand to a higher location, motion of the thumb and fingers towards each other, and rotation of the hand in pronation/supination was observed (see Results). During these perturbed trials, the fingers were no longer on the force sensors, and so it was not possible to

measure the actual change of force corresponding to the  $Phase$  factor were defined as the average over change of hand posture. Rather, we assume that the  $Pr_{00}$  ms of steady state before and after  $t_0$ . Appropriate position corresponded to zero force applied by the fingers. Pair-wise contrasts and post-hoc Tukey's Honestly Significant Difference (HSD) tests were used to further analyze significant effects of ANOVA. The level of significance was set at  $p < 0.05$ .

In particular, tangential apparent stiffness ( $K_T$ ) was defined as the change of tangential force per unit of the change in the hand height:  $\Delta F_{TOT}^T = K_T(\Delta D_Z)$ . Aperture apparent stiffness ( $K_A$ ) was defined as a change in the normal VF force per unit of change in the aperture:  $\Delta F_{TOT}^n = K_A(\Delta W)$ . Rotational apparent stiffness ( $K_R$ ) was defined as the change of the moment of force about the handle-fixed-axis per unit of change in the rotation of the hand:  $\Delta M = K_R(\Delta\theta)$ . All computations were performed between the individual perturbed trials and the average values across the unperturbed trials.

### Statistical analysis

The data are presented in the text as means and standard errors of the mean. Mixed-effects ANOVA with the factors *Torque* (three levels: PR, ZERO, and SU) and *Condition* (two levels: perturbed and unperturbed) and *Digit* (three levels: thumb, index, and little) were used.

To estimate the effects on the apparent stiffness indices  $K_A$ ,  $K_T$ , and  $K_R$ , an ANOVA was run with the factors *Torque* (three levels: PR, ZERO, and SU) and *Condition* (two levels: perturbed and unperturbed) and then averaged across trials for a typical subject. Panel A illustrates the increase of height of the hand during the task, with the hand moving higher in the perturbed case. Panel B shows the approximately constant

For  $\Delta V$  analysis, a three-way repeated measures ANOVA was run with the factors *Index* (two levels:  $\Delta V_F$  and  $\Delta V_M$ ), *Level* (two levels: VF-TH and IMRL), and *Phase* (two levels: before and after the perturbation). The level

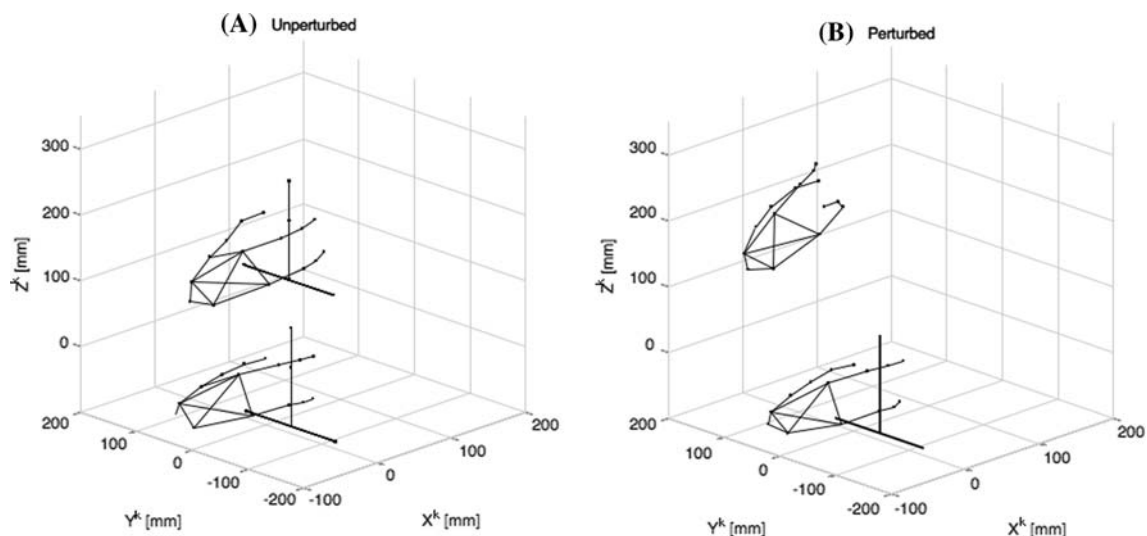
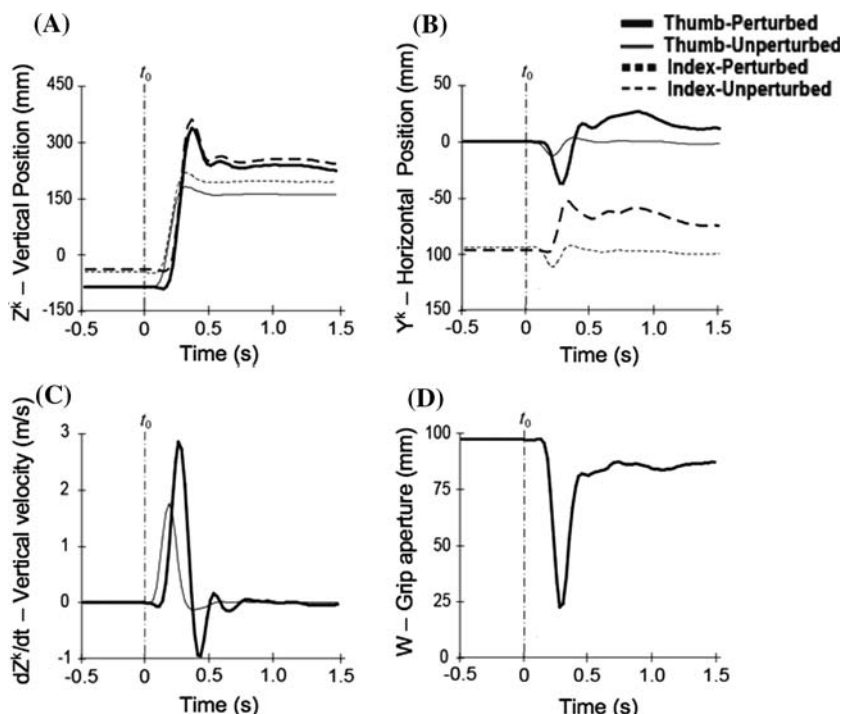


Fig. 3 Initial and final 3D hand locations. a Shows the hand and the T-shape handle at the start position and at the final steady state position during results presented are from the no external torque condition a typical unperturbed movement. The handle is shown as an inverse

**Fig. 4** Kinematic patterns for the average of three perturbed (thick lines) and three unperturbed (thin lines) trials performed by a typical subject. **a** The vertical position ( $Z^k$ ) of the thumb (thick solid lines) and index (dashed lines) fingertips. **b** The horizontal ( $Y^k$ ) position of the thumb and index fingertips. **c** The vertical velocity ( $dZ^k/dt$ ) of the thumb. **d** The grip aperture ( $W$ ) of the thumb and index fingers, for a perturbed trial. The onset ( $t_0$ ) of the movement was defined by 5% of the peak derivative of grip force. The data are for the zero external torque condition

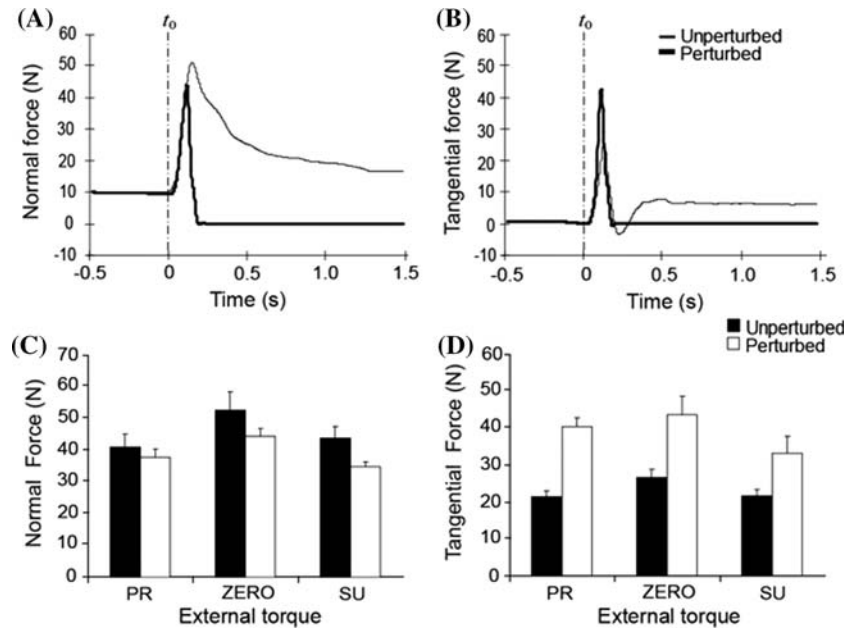


horizontal positions of the thumb and index finger for Maximal deviations of trajectories from a perfect vertical unperturbed movements, and the large changes in the local path more than doubled in the perturbed trials as compared to the unobstructed trials (10.4 vs. 21.2 ± 0.4 cm). These deviations were also higher in the perturbed case. Panel C shows an approximately bell-shaped vertical velocity profile in the unperturbed case, and a correction for an overshoot in the perturbed case. Panel D shows a decrease in the grip aperture during the perturbed trial (aperture is constant in the unperturbed case). Note that in the perturbed trials, the hand took longer to start moving because it had to overcome the friction between the digit tips and the sensors.

Statistical analysis has shown an increase in both the peak height of the hand (measured at the time of the largest overshoot) and the ultimate steady-state height in the unloaded trials. On average, the peak height increased from 0.25 ± 0.15 to 0.30 ± 0.2 m, while the steady-state height showed an increase simultaneously with the tangential force (load force). Typical time profiles of the two forces are shown in Fig. 5a and b. Note that the final steady-state value of the grip force is elevated as compared to the initial prescribed value of 10 N. In perturbed trials, the initial changes in the two forces followed closely those observed in the unobstructed trials (compare the thick and thin lines in Fig. 5a, b). After the digits slipped off the sensors, about 100 ms after the action initiation, both grip and load force data became zero.

The increase in movement amplitude was accompanied by an increase in the peak velocity (on average, from 1.79 ± 0.14 to 2.53 ± 0.24 m/s) and in the peak acceleration (on average, from 25.4 ± 2.5 to 73.0 ± 5.6 m/s<sup>2</sup>). Both results have been confirmed by similar two-way ANOVAs that showed main effects of Condition ( $F_{[1,18]} > 5.71; p < 0.01$ ) without an effect of Torque and without an interaction. The peak value of the grip (normal) force was smaller in the perturbed trials, on average by 15.4% (Fig. 5c), while the peak value of the load (tangential) force was higher in the perturbed trials, on average nearly by 41 ± 3% (Fig. 5d). Both differences were significant

**Fig. 5** a The total normal (grip) force of the four fingers (IMRL) and b tangential (load) forces as a function of time in the perturbed (thick lines) and unperturbed (thin lines) trials. The movement started at time  $t = 0$  s ( $t_0$ ). c Peak normal and d tangential force in the unperturbed (black bars) and perturbed (white bars) conditions. The data was averaged over 12 trials (unperturbed) and two trials (perturbed) for each subject and further averaged across all subjects. Data averaged across subjects are shown with standard error bars



according to the two-way ANOVA that showed significant value before returning to a new steady state. If the thumb effects of *Torque* ( $F_{[2,36]} > 7.2, p < 0.01$ ) and *Condition* ( $F_{[1,18]} > 15.41, p < 0.001$ ), without a significant interaction.

#### Apparent stiffness

The tangential apparent stiffness ( $K_A$ ) was estimated as the ratio of the increase in the hand displacement ( $\Delta D_z$ ) to the change in the tangential forces ( $\Delta F_{TOT}^t$ ) in the perturbed trials as compared to the unobstructed trials. These two quantities are plotted in Fig. 6. They are both higher in the ZERO external torque condition compared to the PR and SU conditions, confirmed by an ANOVA *Torque*  $\times$  *Condition*. There was a significant effect of *Torque* on  $\Delta D_z$  ( $F_{[2,18]} = 3.86, p < 0.05$ ), and on  $\Delta F_{TOT}^t$  ( $F_{[2,18]} = 20.32, p < 0.01$ ).

Across the external torque conditions, the value was, on average,  $3.33 \pm 0.75$  N/cm (PR  $3.64 \pm 0.75$  N/cm; ZERO  $3.01 \pm 0.81$  N/cm; SU  $3.36 \pm 0.71$  N/cm). This value was significantly positive ( $p < 0.01$ ; Wilcoxon  $\tilde{O}$ s test). These values are comparable to those found for two finger pinching in Kao et al. (1997): 2.99 N/cm, three finger pinch in Van Doren (1998): 4.82 N/cm, and for grasping a cup from the side in Friedman and Flanagan (2007): 6.52 N/cm.

Changes in the grip aperture ( $\Delta W$ ) in the perturbed trials were quantified using the distance between the thumb and the line joining the tips of the index and little fingers. Recall that in the unperturbed trials, the digit tips stayed on the sensors and the aperture remained constant depending on the handle geometry. The grip aperture reduced from its initial value (prescribed by the handle width) to a minimum

contacted one of the other digits, the aperture would be expected to dwell at the minimum for some time before moving to the new steady state. However, this was never observed.

In the perturbed trials, the minimum grip aperture was on average  $7.1 \pm 0.6$  cm less than in the unperturbed case. This difference was significant as confirmed by an ANOVA, *Condition*  $\times$  *Torque*, that showed main effect of both *Condition* ( $F_{[1,18]} = 24.2; p < 0.001$ ) and *Torque* ( $F_{[2,18]} = 3.75; p < 0.05$ ). The latter effect reflected the significantly larger  $\Delta W$  under the SU condition as compared to the PR condition. There was no significant interaction.

After reaching the minima, the hand aperture increased to a magnitude that was, on average,  $\pm 0.6$  cm less than in the unperturbed case. This difference was statistically significant according to a two-way ANOVA, *Condition*  $\times$  *Torque*, which showed an effect of condition ( $F_{[1,18]} = 5.5, p < 0.05$ ) without any other effects.

The apparent aperture stiffness ( $K_A$ ) was estimated as the ratio of the decrease in the hand aperture ( $\Delta W$ ) to the grip forces ( $\Delta F_{TOT}^t$ ) in the unperturbed trials. These two quantities are plotted in Fig. 6. On average,  $K_A$  was  $7.0 \pm 0.7$  N/cm; it did not depend on external torque.

When the external torque was zero, there was no difference in the magnitude of the hand rotation in the frontal plane between the unobstructed and perturbed trials, the average difference was less than  $1^\circ$ . When the torque was non-zero, however, unobstructed trials showed significant differences from the perturbed ones. In particular, when the subjects planned a movement against a SU load, they showed hand rotation into SU that

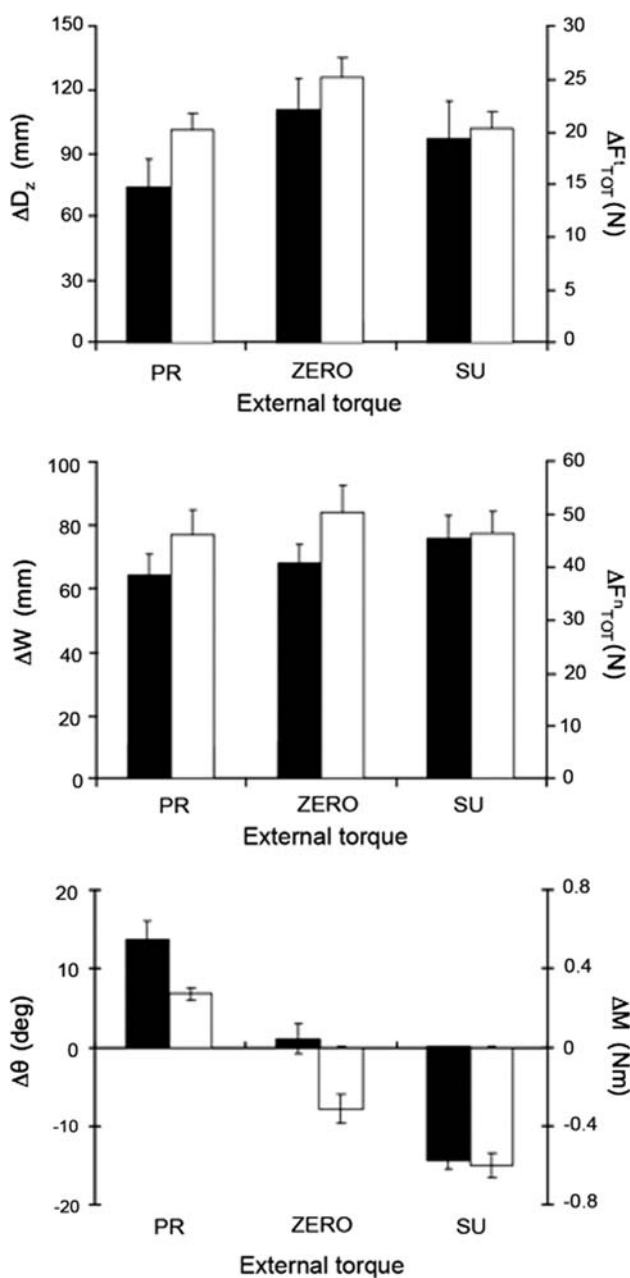


Fig. 6 a Changes of path height  $\Delta D_z$  (black bars) and peak tangential forces  $\Delta F_{TOT}^1$  (white bars). Both quantities are higher in the presence of a ZERO external torque as compared the PR and SU conditions. b Changes in aperture  $\Delta W$  (black bars) and grip forces  $\Delta F_{TOT}^2$  (white bars). c Changes in hand rotation  $\Delta \theta$  (black bars) and moment about the x-axis  $\Delta M$  (white bars). Data are averaged across subjects, standard error bars are shown

was, on average,  $13.8 \pm 2.5$ , as compared to the unobstructed trials. In contrast, under the PR load, the perturbed trials showed excessive hand rotation into PR that was, on average,  $17.2 \pm 2.6$ , as compared to the unobstructed trials. There was a main effect of torque ( $F_{[2,18]} = 39.36$ ;  $p < 0.001$ ) without other effects.

The apparent rotational stiffness of the hand ( $K_x$ ) was estimated as the ratio of the change in the hand rotation ( $\Delta \theta$ ) in the frontal plane to the moment about the x-axis ( $\Delta M$ ) applied by the fingers. These two quantities are plotted in Fig. 6c. As the change in hand rotation for the zero external torque case was close to zero, was not calculated for this condition. The average magnitude of  $K_x$  for the other two conditions was  $1.77 \pm 0.28$  Nm/rad. (PR  $1.32 \pm 0.25$  N/cm; SU  $2.22 \pm 0.31$  N/cm). This value was significantly positive ( $p < 0.01$ ) and not different across the two torque conditions as confirmed by ANOVA.

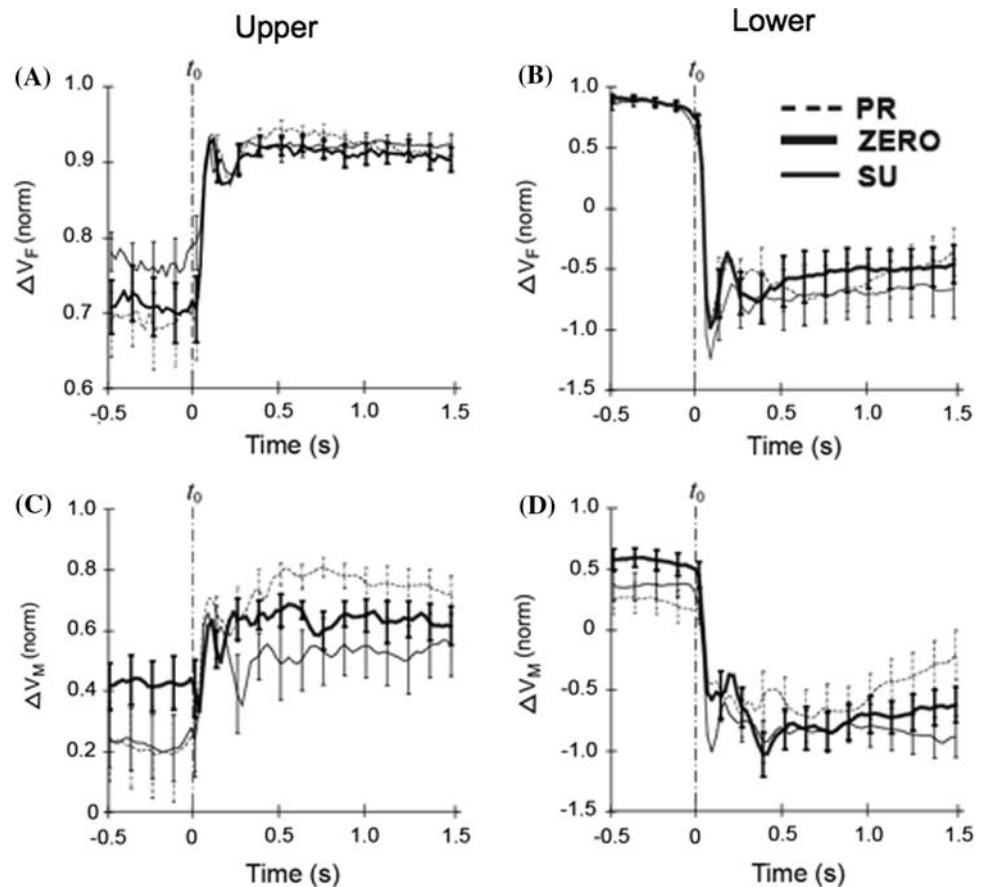
### Analysis of multi-digit synergies

We used two indices  $\Delta V_F(t)$  and  $\Delta V_M(t)$ , to assess effects of co-variation of individual digit forces and moments across trials on stabilization of the total grip force and total moment of force produced by the digits and acting on the handle. To remind, these indices represent the normalized difference between the sum of the variances in the space of elemental variable (individual digit forces/moments) and the variance in the performance variable (total force and total moment). Their positive values correspond to negative co-variation of elemental variables that stabilizes the performance variable. Such analyses were performed at the upper level (thumb and VF) and at the lower level (individual four fingers) of the assumed hierarchy (see Introduction and Methods).

When the subject gripped the handle on the table, both total grip force and total moment of force were stabilized by co-varied adjustments of finger forces and moments of force across trials. This was reflected in positive  $\Delta V_F(t)$  and  $\Delta V_M(t)$ . At the initiation of the lifting action ( $t_0$ ), the values of  $\Delta V_F$  and  $\Delta V_M$  both increased at the upper level and dropped at the lower level. As a result, at the new steady state, both the total grip force and the total moment of force were strongly stabilized at the upper level ( $\Delta V > 0$ ), while they showed positive co-variation potentially destabilizing the output of the four fingers at the lower level ( $\Delta V < 0$ ).

Figure 7 illustrates the time profiles  $\Delta V_F(t)$  and  $\Delta V_M(t)$  at the two levels over all three torque conditions. Note the similarity of the graphs for the PR, ZERO, and SU torques. Note the positive  $\Delta V$  values prior to the action; on average,  $\Delta V$  indices averaged over the 0.5 s interval during the first steady state were  $0.72 \pm 0.03$  for  $\Delta V_F$  at the upper level,  $0.85 \pm 0.03$  for  $\Delta V_F$  at the lower level,  $0.28 \pm 0.08$  for  $\Delta V_M$  at the upper level, and  $0.38 \pm 0.08$  for  $\Delta V_M$  at the lower level. After the action, at the upper level  $\Delta V_F$  increased to  $0.63 \pm 0.05$ . At the same time, at the lower level,  $\Delta V_F$  dropped to  $-0.55 \pm 0.15$  while  $\Delta V_M$  dropped to  $-0.63 \pm 0.14$ .

**Fig. 7** Indices of digit force covariation,  $\Delta V_F(t)$ , at the upper (a) and lower (b) levels. Indices of digit moment of force covariation,  $\Delta V_M(t)$ , at the upper (c) and lower (d) levels in the unperturbed condition. The onset (dashed vertical lines) of hand lifting was at time  $t = 0$  s ( $t_0$ ). Different lines show data during lifting the hand in different external moment conditions, PR (dashed line), ZERO (thick solid line), and SU (solid line)



These findings were supported by a three-way ANOVA the object was unexpectedly fixed to the table, the loading that showed significant effects of all three factors, conditions changed, and we observed new configurations of the hand and digits reproducible across subjects. In particular, we observed non-monotonic pattern of changes in the grip aperture, and new values of the hand height, hand rotation in pronation–supination, and grip aperture at the final steady state. These observations confirm our first prediction. In the following sections, we discuss relationships of the results to the RC hypothesis and address the issue of synergies at different levels of a control hierarchy.

## Discussion

### Moving towards the referent configuration

Our experiments confirmed the main predictions formulated in the Introduction. In the initial condition, before the lifting action, we observed strong force and moment of force stabilizing synergies at the lower level of the assumed models that predict and implement requisite forces moving hierarchy (i.e., at the level of four individual finger actions) the system from the initial state to a desired final state corresponding to our third prediction. There were also force and moment of force stabilizing synergies at the higher level (i.e., at the level of thumb and VF actions). According to the alternative view, the CNS defines time After the movement initiation, both synergies at the lower level disappeared, while the synergies at the upper level of neuronal pools, while all the performance variables became stronger (as quantified by the index). These observations correspond to our second prediction. Whether the neuromotor processes within the body and between the

body and the external force field (Kugler and Turvey 1987; Schmidt and McGowan 1980; Latash and Gottlieb 1990; Feldman and Levin 1995; Latash 2008). Arguments in favor of or against these schemes have been published recently (Hinder and Milner 2003; Ostry and Feldman 2003; Feldman and Latash 2005; Feldman and Levin 2009). Along similar lines, the removal of the external torque (in the PR and SU conditions) was expected to lead to a new hand orientation in space (closer to  $Z_{REF}$ , Fig. 1). All these predictions were confirmed (see Figs 4, 5 and 6).

In our experiment, the unexpected unloadings of the hand resulted in the finger tip forces becoming zero immediately after the fingers slipped of the sensors. The disappearance of the rigid walls of the handle was expected to lead to motion of the digit tips towards each other resulting in a new steady-state value of the grip aperture (see Pilon et al 2007). However, we also observed a less trivial, reproducible non-monotonic pattern of changes in the grip aperture: The digits flexed and then extended. Although we did not record electromyographic signals (a shortcoming of the study), the extension motion of the digit was likely produced by activation of the extensor muscles. Within the framework of the RC hypothesis, this could happen if, in the unloaded trials, extensor muscles transiently became longer than their referent (threshold) length for activation. Note that in the unperturbed trials, the walls of the object did not allow the digits to move and stretch the extensor muscles. As a result, their actual length was always shorter than the referent length and no major phasic activation was expected that could reverse the motion direction (here we ignore the relatively minor co-activation of extensors during typical lifting actions).

There is one more physiological reason for an unchangeable time pattern of RC to lead to non-monotonic changes in the aperture in the unloaded trials: Sudden unloading of finger muscles may lead to a silent period in the flexor muscle spindle discharge, resulting in a temporal decrease in the flexor muscle activation and reversing the movement direction (especially in the low-inertial fingers). Indeed, a geometric consequence of using an unchanged RC pattern may be an unchanged (or only slightly changed) time pattern of referent aperture ( $A_{REF}$  in Fig. 1). It has a minimum soon after the movement initiation corresponding to a transient peak in the grip force and then it settles at a new steady-state value (see Pilon et al 2007). In the unloaded trials, actual aperture showed a non-monotonic time profile similar to that of  $A_{REF}$ . To our knowledge, the flexion–extension pattern of digit motion, after the hand slipped off the sensors and moved up without the handle, would not be predicted by other hypotheses on grip force control.

According to the RC-hypothesis, RC (a combination of activation thresholds for relevant neuronal pools) is reflected in a set of referent variables  $D$  coordinates, which the effectors tend to move (see Fig. 1). It also leads to certain stability properties of the effectors about those coordinates (Feldman and Levin 1995, 2009; cf. impedance control, Hogan 1985). We quantified this second component of RC using indices of apparent stiffness (Latash and Zatsiorsky 1993). The reproducible results across subjects suggest that these indices do reflect common features of

These interpretations hinge on the mentioned assumption of non-intervention by the subjects. It is possible that, despite the instruction, the subjects showed triggered (pre-programmed) reactions that led, in particular, to the observed non-monotonic changes in the digit aperture (Traub et al. 1980; Johansson and Westlin 1984). As shown in Fig. 4, the thumb and the fingers moved towards each other and reached a minimum of the aperture value soon after the movement initiation, and later the hand opened and reached a new steady-state aperture, smaller than the initial aperture value. We would like to note that pre-programmed reactions are known for their phasic nature and inconsistent amplitude if perturbations are unexpected (Marsden et al. 1981). In contrast, the steady-state new aperture values were consistent both within and across the subjects.

Several recent studies explored motor synergies based on quantitative analysis of variance in kinetic, kinematic, and electromyographic spaces (reviewed in Latash et al. 2007). In a redundant system of elements, variance in the space of elemental variables may be viewed as consisting of two components defined with respect to a particular, potentially important performance variable produced by the system. One of the components does not affect the performance variable; it has been addressed as compensated, goal-equivalent, or, simply, “good” variance. The other component leads to changes in the performance variables (uncompensated, non-goal-equivalent, or “bad”,  $V_{BAD}$ ). Analysis of the two variance components has been developed within the uncontrolled manifold (UCM) hypothesis (Scholz and Schoner 1999; reviewed in Latash et al. 2002b), which assumes that the space of elemental variables is organized by the controller into two sub-spaces, compatible (UCM) and incompatible with a desired value of a performance variable.

The existence of the mentioned two variance components associated with synergies similar to those seen in one-person tasks; however, these synergies showed lower coefficients of variation indices (Gorniak et al. 2009). It is possible that the controller facilitates a group of RCs that are consistent with the task demands and then, in each trial, a randomly selected RC from this set. Then, RC variability hierarchically controlled system, synergies at different levels of the hierarchy may be in conflict with each other for a motor task, i.e., in proportionally higher variance of the VF output. Consider a strong synergy stabilizing a performance variable (for example, resultant horizontal force) at the upper (thumb and VF) level of a hierarchy within the task context.

Second, it is possible that a single RC specifies activation means that  $V_{\text{GOOD}} > V_{\text{BAD}}$ . As such, large  $V_{\text{GOOD}}$  contribution thresholds for neuronal pools that are reflected in attributes to stronger synergies. Note, however, that both higher-order variables such as, for example, referent  $V_{\text{GOOD}}$  and  $V_{\text{BAD}}$  contribute to variance of each of the aperture, while elemental variables (forces and moments of elemental variables at the higher level; in particular, large force) produced by elements (individual digits) are free to vary in a sub-space compatible with the referent aperture at the lower level of the hierarchy. At that level, variance and external conditions (cf. Pilon et al. 2007). So, the variance of the VF output, by definition, corresponds to  $V_{\text{BAD}}$ . So, existence of the two variance components is a natural consequence of choice of a RC (or RC set) that meets the task demand.

In our study (see the simple illustration in Fig. 1), we asked to produce a certain magnitude of the total normal force by the VF. This was expected to be accomplished by setting an adequate RC that produced a referent coordinate  $\hat{O}$  reflecting mechanical constraints for keeping the object perfectly vertical and perfectly motionless. Note, however, that these constraints could be (and very likely were) violated in experiments, for example, if the handle was slightly rotated or if the object trembled a bit. So, there was no specific requirement for the moment of force expected to see, across trials, a certain amount of  $\hat{O}$  produced by the VF in the initial position. It is reasonable to assume that a natural, default action would correspond to zero net moment of force (cf. minimization of secondary moment of force. These constraints, however, are compatible with any amount of  $\hat{O}$  variance. So, themselves, they do not necessitate synergies (in a sense  $V_{\text{GOOD}} > V_{\text{BAD}}$ , see Latash et al. 2007).

Several studies have suggested that synergies may be seen in the absence of such explicit constraints, i.e. reflecting preference by the controller that may not have an obvious mechanical interpretation (Latash et al. 2001; Niu et al. 2007). More-  
over, sometimes synergies in similar tasks are seen in some subjects but not in others; they can also emerge in the process of practice (Latash et al. 2002a; Kang et al. 2004; Scholz et al. 2003). These observations suggest that some of the synergies may be related to setting a referent moment of force at the upper level. At the same time, the value of a variable that is not easy to guess and that may not have a straightforward mechanical interpretation.

Imagine now that a similar grasping task is performed by two persons such that the opposing digits (thumb and VF) are controlled by different brains. In such a case, referent coordinates have to be set separately for the thumb and VF. This may or may not lead to their synergic adjustment (for example, based on afferent information) such that the equations of statics are satisfied. Indeed, a recent study has shown that two-person tasks may be

The initiation of the lifting action is associated with a qualitative change in the control: The combined thumb and VF action has to satisfy task requirements, and the upper control level becomes leading. This was indeed associated with much stronger synergies stabilizing both force and moment of force at the upper level. At the same time, the synergies at the lower level disappeared as expected from the trade-off between synergies at the two hierarchical levels, as described earlier. Taken together, these observations support the earlier hypothesis on a trade-off between synergies at different hierarchical levels (Gorniak et al. 2007a, b).

Typical studies of multi-joint actions forming the basis of the force-control view involved movements by a kinematically non-redundant effector (typically, a two-joint system performing a two-dimensional task, e.g., Shadmehr

and Mussa-Ivaldi 1994; Hinder and Milner 2003; Kluzik et al. 2008). As a result, the problem of motor redundancy and the associated issue of synergies have not been addressed within this line of studies. As shown in a recent study of multi-joint synergies in the process of practicing reaching movements in an unusual force field (Yang et al. 2007), such synergies show non-trivial changes involving increased self-motion (joint motion leading to no motion of the endpoint) that looks wasteful and meaningless within the force-control view. This study has shown limitations of the force-control ideas in handling natural movements by redundant systems of effectors. The interactions between synergies at the two hierarchical level demonstrated in our study can be addressed within the RC hypothesis, while such issues have been beyond the level of analysis within the force-control approach.

### Concluding comments

The main goal of this study has been to explore how the concept of prehension synergy can be naturally incorporated into the idea of control with RC. Our observations are overall compatible with the basic premise that, within a given task, setting a RC may be described with a few referent variables that influence the equilibrium state to which the system is attracted. Moreover, the RC control can help interpret the data related to the trade-off between synergies at different hierarchical levels. Further controlled studies are necessary with mechanical perturbations applied to redundant motor systems (see Adamovich et al. 2001; Rossi et al. 2002). Unfortunately, so far, most perturbation studies with well controlled kinetics and kinematics have studied non-redundant motor tasks such as, for example, planar movements of two-joint systems (Shadmehr and Mussa-Ivaldi 1994). There are a few notable exceptions (e.g., Yang et al. 2007). However, most of those studies focused on processes of adaptation to perturbations rather than using perturbations to discover the nature of control variables and their task-specific patterns.

We have to admit several shortcomings of the current experimental design. First, we used only a few unexpectedly unloaded trials and could not track likely adjustments in the strategy of control in anticipation of a change in the loading conditions. We used such short sequences of unloaded trials for two reasons. First, to minimize the chances for the subject to realize that such trials could happen with a 50% probability. Second, to avoid fatigue. Avoiding fatigue was also the main reason why we used the 50:50% ratio of unperturbed and unloaded trials, not a less frequent presentation of unloaded trials, for example 20:80%, which could have an advantage of preventing changes in the lifting strategy as compared to the preceding trials without any unexpected events.

Another relatively artificial manipulation was setting a target pressing force prior to lifting the object. This could potentially have an effect on the control of the lifting phase. We used this particular experimental design to be able to quantify finger coordination (synergies) prior to the lift-off, which would be impossible to do if the fingers only touched the sensors producing effectively zero forces. As in several earlier studies (e.g., Asatryan and Feldman 1965; Latash 1994), we relied on the subjects' ability not to intervene when the external conditions changed. In earlier studies, this assumption was tested by additional control tests in which the timing and spatial gradients of unloading were varied, yielding invariant torque-angle characteristics (Latash and Gottlieb 1991, 1992; Feldman and Levin 1995). These tests were difficult to conduct in the present study. However, we would like to note that the reproducibility of the subjects' behavior in the unloaded trials and its compatibility with the predictions formulated assuming non-intervention offer indirect support for the assumption that the subjects did not intervene.

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