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Maintaining rotational equilibrium during object manipulation: linear behavior of a highly non-linear system

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Abstract

We address issues of simultaneous control of the grasping force and the total moment of forces applied to a handheld object during its manipulation. Six young healthy male subjects grasped an instrumented handle and performed its cyclic motion in the vertical direction. The handle allowed for setting different clockwise (negative) or counterclockwise torques. Three movement frequencies: 1, 1.5 and 2 Hz, and five different torques: $-1/3$, $-1/6$, 0, $1/6$ and $1/3$ Nm, were used. The rotational equilibrium was maintained by two means: (1) Concerted changes of the moments produced by the normal and tangential forces, specifically anti-phase changes of the moments during the tasks with zero external torque and in-phase changes during the non-zero-torque tasks, and (2) Redistribution of the normal forces among individual fingers such that the agonist fingers—the fingers that resist external torque—increased the force in phase with the acceleration, while the forces of the antagonist fingers—those that assist the external torque—especially, the fingers with the large moment arms, the index and little fingers, stayed unchanged. The observed effects agree with the principle of superposition—according to which some complex actions, for example, prehension, can be decomposed into elemental actions controlled independently—and the mechanical advantage hypothesis according to which in moment production the fingers are activated in proportion to their moment arms with respect to the axis of rotation. We would like to emphasize the linearity of the observed relations, which was not prescribed by the task mechanics and seems to be produced by specific neural control mechanisms.

Keywords

Prehension; Grip force; Load force; Finger; Synergies; Rotation equilibrium; Cyclic arm movement; Principle of superposition; Safety margin

Introduction

The control of orientation of handheld objects is important for everyday activities. For instance, when drinking from a glass, one needs to control the glass orientation in such a way that the liquid is not spilled out.

The orientation control during prehension has been examined mainly in static tasks (Zatsiorsky et al. 2002a, b; 2003a, b; Shim et al. 2003; Pataky et al. 2004a, b; Zatsiorsky and Latash 2004). The grip force has been shown to increase with an increase in the external torque (Zatsiorsky et al. 2002a, b, 2003a, b). The external torque was counterbalanced by the moments produced by both normal and tangential forces with each of them generating approximately 50% of the total moment (Zatsiorsky et al. 2002a). Because the normal forces produced by the thumb and by the fingers are not collinear, the finger forces generate the moments of force with respect to the thumb as a pivot. The fingers that are located above and below the thumb, for instance, the index and the little fingers, generate moments in opposite directions (Li et al. 1998a, b). Moments in a desired direction—those that resist the external torque—have been termed the *agonist moments*, while moments in the opposite direction—assisting the external torque—have been termed *antagonist moments* (Zatsiorsky et al. 2002a, b). We will call fingers that generate agonist and antagonist moments with respect to a given task (external torque) the *agonist* and *antagonist fingers*, respectively.

The digit force production during static prehension in humans conforms to the principle of superposition (Shim et al. 2003; Zatsiorsky and Latash 2004; Zatsiorsky et al. 2004), according to which some actions can be decomposed into elemental actions that are controlled independently. Following this principle reduces the amount of required computation and simplifies the control (Arimoto et al. 2001). Two independent commands have been hypothesized: “grasp the object stronger/weaker to prevent slipping” and “maintain the rotational equilibrium of the object”. The effects of the two commands are summed up. The principle of superposition has been validated for both planar and three-dimensional prehension tasks (Shim et al. 2004a, b). Effects of changes in the external tangential torque and tangential load on the grip force have also shown linear superposition (Kinoshita et al. 1997).

In static tasks requiring pronation or supination efforts, the force of the “peripheral” fingers (with longer moment arms with respect to the point of thumb contact, i.e., index and little) depends mainly on the torque, while the force exerted by the “central” (middle and ring) fingers depended both on the external load and torque (Zatsiorsky et al. 2002a, b). These facts led to formulating the “mechanical advantage” hypothesis, according to which, in moment production, the fingers are activated in proportion to their moment arms with respect to the axis of rotation (Shim et al. 2004a, b). This hypothesis has been confirmed in some static tasks, including three-dimensional tasks (Shim et al. 2005), and was only in partial agreement with the data obtained during torque production on a mechanically fixed object when the distances from the fingers to the axis of rotation were systematically varied (Shim et al. 2004a, b).

In dynamic tasks—during vertical movement of a vertically oriented handle—the grip force increases with load force. The tight coupling between the grip force (G)—the total normal force exerted by all the fingers against the thumb—and the load force (L) was revealed in diverse experimental conditions. In particular, G is modulated by the inertial forces acting during lifting an object (Johansson and Westling 1984), shaking and point-to-point arm movements (Flanagan and Wing 1993, 1995; Tresilian et al. 1993; Flanagan and Tresilian 1994; Kinoshita et al. 1996) and during locomotion (Gysin et al. 2003). It is also modulated by the weight of the object (Johansson and Westling 1984; Winstein et al. 1991), abrupt load perturbations (Cole and Abbs 1988; Eliasson et al. 1995; Serrien et al. 1999), friction conditions (Cole and Johansson 1993; Cadoret and Smith 1996; Burstedt et al. 1999), tangential torques (Kinoshita

et al. 1997) and gravity changes during parabolic flights (McIntyre et al. 1998; Hermsdorfer et al. 1999; Augurelle et al. 2003). G has been assumed to be adjusted to expected L (Johansson and Westling 1984; Flanagan and Wing 1995). Hence, the G – L coupling is mainly controlled by a feed-forward mechanism, while feedback based G adjustments are triggered by cutaneous sensation when necessary (Johansson and Westling 1984; Flanagan and Wing 1995). During object manipulation, the effects of the static weight and inertial forces on G are not identical (Zatsiorsky et al. 2005). Three fractions of G have been quantified: (1) static, (2) dynamic and (3) stato-dynamic. When an object is being moved in the vertical direction G : (1) is on average higher than in static tasks—the difference between G values at the instances of zero vertical acceleration and in statics was called the stato-dynamic fraction of the G ; and (2) changes with object acceleration (and, hence with the tangential forces at the fingertips)—the corresponding fraction of the G force was called the dynamic fraction. The dynamic fraction may be characterized by the slope of a G – L linear relation. In the above studies, the external torque exerted on the object was zero.

The rotational equilibrium during object manipulation was addressed in only one study dealing with the internal forces (Gao et al. 2005). The elements of an internal force vector cancel each other and, hence, do not contribute to the resultant force and moment acting on the object (Mason and Salisbury 1985; Kerr and Roth 1986; Yoshikawa and Nagai 1991; Murray et al. 1994). It has been shown that during the performance, people exert internal moments on the object such that the moments of the normal and tangential forces (M^n and M^t , respectively) change in opposite directions in synchrony and cancel each other. As a result, the total moment exerted on the object is close to zero and rotational equilibrium is preserved.

Problem statement

Imagine a person grasping a vertically oriented object of an irregular shape such that the hand needs to resist a load force L and a non-zero moment M to hold it statically (see Fig. 1). The object is grasped by a prismatic precision grip in which the tips of the fingers and the thumb oppose each other (Fig. 1, left panel). We limit the consideration to planar static tasks. We assume that friction at the digit-object interface is sufficiently large to prevent the object from slipping at all values of the digit forces exerted in the present experiment; $[F_i^n - |F_i^t|/\mu] \geq 0$, where μ is the coefficient of friction, superscript n represents normal force, t represents tangential force and subscript i represents i th digit.

For the system to be at rest, the sum of all forces and moments acting on the handle should be equal to zero. Hence, the following three requirements should be satisfied:

1. The sum of the normal forces of the four fingers (the grip force G) equals the normal force of the thumb

$$F_{th}^n = F_i^n + F_m^n + F_r^n + F_l^n = \sum_{f=1}^4 F_f^n \quad (1)$$

2. The sum of the digit tangential forces equals the weight of the handheld object (the load L)

$$L = F_{th}^t + F_i^t + F_m^t + F_r^t + F_l^t \quad (2)$$

3. The total moment produced by the digit forces is equal and opposite to the external static moment M_{st} exerted on the object

$$M_{st} = \underbrace{F_{th}^n d_{th} + F_i^n d_i + F_m^n d_m + F_r^n d_r + F_l^n d_l}_{\text{Moment of the normal forces} \equiv M^n} + \underbrace{F_{th}^t r_{th} + F_i^t r_i + F_m^t r_m + F_r^t r_r + F_l^t r_l}_{\text{Moment of the tangential forces} \equiv M^t} \quad (3)$$

where the subscripts *th*, *i*, *m*, *r* and *l* refer to the thumb, index, middle, ring and little finger, respectively; the superscripts *n* and *t* stand for the normal and tangential force components, respectively; *L* is load (weight of the object), M_{st} is the external moment/torque and coefficients *d* and *r* stand for the moment arms of the normal and tangential force with respect to a pre-selected center, respectively. Note that the normal finger forces produce moments of force with respect to the thumb acting as a pivot. In the configuration shown in Fig. 1 left panel, the fingers that are located above the thumb—the index and middle—generate moments in the counterclockwise direction, while the fingers that are located below the thumb—the ring and little—produce the moments in the clockwise direction. Hence, depending on the direction of the external torque (location of the suspended load along the horizontal beam) some fingers generate the moments that resist the external torque (and hence contribute to the rotational equilibrium maintenance), while moments of other fingers act in the same direction as the external torque and hence increase its action. The fingers that resist the external torque have been called *torque agonists* or simply *agonists*, while the fingers that assist the external torque have been called *torque antagonists* or simply *antagonists* (Zatsiorsky et al. 2002a,b).

During the motion of the object in the vertical direction, both the *L* and *M* change as a function of acceleration. During the movement, the load force equals

$$L(t) = W + ma(t) \quad (4)$$

where *W* is the total weight of the object, *m* is its mass, *t* is time and *a*(*t*) is the acceleration. The object is represented as a combination of two masses. One is located on the vertical axis passing through the hand and does not produce a time varying moment. The other (*m*_{load}) is off that axis by a distance *l*. The external moment *M* equals

$$M(t) = M_{st} + m_{load} l a(t) \quad (5)$$

where M_{st} is the static moment. Hence, both *L*(*t*) and *M*(*t*) change in proportion to the acceleration. Such a task imposes conflicting demands on the individual normal finger forces. To maintain a sufficiently high and constant safety margin, the grip force *G*—the force generated by *all* the fingers—should change in synchrony with *L* (such a *G*–*L* coupling has been found in many studies, in which the subjects oscillated a handle with zero external torque, e.g., Johansson and Westling 1984; Flanagan and Wing 1993, 1995). In contrast, to compensate for the *M*(*t*) increase—to maintain the rotational equilibrium of the object—the forces of only the agonist fingers should rise with *a*. The increase of the force of the antagonist fingers will increase the moment acting on the handle and hence—if not compensated—would induce the handle rotation. The question is how does the CNS sort out these two conflicting demands?

Methods

Six healthy right-handed male university students (27 ± 6 years, 75 ± 9 kg) volunteered to be subjects in this study. Subjects had no previous history of neuropathies or trauma to the upper extremities. All subjects gave informed consent according to the procedures approved by the Office for Regulatory Compliance of The Pennsylvania State University.

Experimental setup

An aluminum handle composed of two horizontal bars and two vertical pillars was used in this study. The handle was attached to the top edge of an aluminum beam (5.0 cm × 85.0 cm × 0.6 cm) at the midpoint in the medio-lateral direction (Fig. 1). Five six-component force/moment transducers (Nano-17, ATI Industrial Automation, Garner, NC, USA) were mounted on the pillars. The center points of the sensors were evenly distributed with a span of 25 mm. The grip width (the distance between the surfaces of the thumb contact and of the finger contacts) was 60 mm. The surfaces of the transducers were coated with 100-grit sandpaper. The friction coefficient between the skin and sandpaper was between 1.4 and 1.5 (Gao 2002). A tri-axial accelerometer (EGA 3, Entran, USA, range ± 5g, weight 7 g) was mounted on the horizontal bar at the middle of the handle to record the movement of the handle. The total weight of the handle including the load was 9.6 N.

The output cables of the sensors were tied together and hung 20 cm above the top of the handle to avoid interference during the cyclic movement of the handle. The output signals of the sensors were input to two 32-channel 12-bit AD converters (PCI-6033E, National Instruments, Austin, TX, USA). The digital signals were processed using a PC computer (Dell Dimension 8200, USA). The sampling frequency was set at 200 Hz. Data were recorded by a customized program written in LabView 6.1 (National Instruments).

Test procedure

Before the experiment, the subjects cleaned the tips of the digits with alcohol to normalize skin condition. The subjects were instructed to hold the handle statically with the forearm unsupported, the tips of the digits placed over the centers of the sensors before each trial. Before each task condition, the subjects were trained to ensure proper performance. A rhythmic audio signal was provided, and the subjects tried to follow the tempo of the signal. The recording started when the subjects could match the rhythm well. In general, the subjects followed the signals well, and the average frequencies of the cyclic movement when the metronome was set at 1.0, 1.5 or 2.0 Hz, were 0.98 ± 0.12 , 1.44 ± 0.19 and 1.93 ± 0.25 Hz, respectively.

The subjects were instructed to make vertical cyclic arm movements while timing the movements to the beeps generated by the metronome. Two horizontal ropes, 10 cm apart in the vertical direction, showed the target range of the movements. The subjects were instructed to move the handle along a straight line and to keep its orientation constant throughout the trial. The movements of the handle were visually monitored by the experimenter. Based on the visual observation, the handle rotation was assumed negligible. This conclusion was supported by the analysis of the acceleration recorded in the z direction (see Fig. 1 for the axes designation): if the handle is not being translated and is oriented vertically the acceleration equals zero; if the handle is inclined 90° the recorded acceleration equals the acceleration due to gravity $g = 9.81 \text{ m/s}^2$. Any intermediate recorded acceleration value corresponds to a sine of the inclination angle. During the handle manipulation, the acceleration recorded in the z direction equals $a_z = a_{\text{hor}} \cos \alpha + (a_{\text{gravity}} + a_{\text{ver}}) \sin \alpha$, where α is the inclination angle; a_{hor} and a_{ver} are the accelerations of the handle in the horizontal and vertical direction, respectively; a_{gravity} is the acceleration due to gravity (all the accelerations are measured in units of g , and hence $a_{\text{gravity}} = 1.0$). Knowing recorded acceleration in z direction and neglecting the contribution of a_{hor} and a_{ver} , we obtained the upper estimates of the orientation of the handle in the gravity field. The estimated average handle inclination in individual trials was less than three angular degrees and was neglected during the analysis.

Three movement frequencies of 1, 1.5 and 2 Hz and five static moments of $-1/3$, $-1/6$, 0, $1/6$ and $1/3$ Nm were used (suspending the load at different positions caused external moments/

torques in either counterclockwise—positive or clockwise—negative directions; note that the moments exerted on the handle by the subjects are opposite to the external moments).

Each test lasted 15 s; 20-s breaks were given between consecutive trials. The order of the tests was pseudo-randomized. At the beginning of the test for each load condition, the subjects were asked to hold the handle in equilibrium with minimum effort and the static finger forces were recorded for 15 s.

Data analysis

In the transducer-fixed reference system, the G (grip force) was normal to the transducer surface (in the z -direction). The L (load force) was tangential to the surface (along the y -axis), aligned with the vertical pillars. The fingertip-sensor interfaces were modeled as the soft finger contacts (Mason and Salisbury 1985) that allow for displacing the point of digit force application over the sensor surface. The y coordinates of the digit force application with respect to the sensor center were computed as $y_i = m_x^i / F_z^i$ ($i = 1, 2, 3, 4$ and 5 , representing thumb, index, middle, ring and little fingers, respectively), where m_x^i represents the moment of the i th digit with respect to x axis and F_z^i represents the normal force of the i th digit (for brevity, if this does not lead to misunderstanding, we will use the symbol F for the normal forces of individual fingers, omitting the subscript and superscript). The obtained values were then used to compute the moment arms of the digit forces in the handle reference frame. The M^n (moments of the normal finger forces) were computed with respect to the y coordinate of the point of application of the thumb normal force and M^t (the moments of the tangential finger forces) were calculated with respect to the center of the handle. Both moments were calculated in the frontal plane.

Raw data were low-pass filtered at 5 Hz with the fourth-order Butterworth filter. In some trials, low-frequency changes in the normal force were observed. Therefore, a high-pass filter at a cutoff frequency of 0.3 Hz was applied to the normal force and an offset was added such that the filtered force had the same means as the unfiltered grip force.

For each trial, G and F were plotted vs the handle acceleration and the regression of G (or F for individual fingers) on the acceleration was computed. Because both L and M changed in proportion to the acceleration (see Eqs. 1 and 2), using either L or M instead of the acceleration did not change the regression relations; only the scale of the abscissa axis changed. For the zero-torque trials, these relations characterized $G(L)$ and $F(L)$, the effects of L on the grip force G or the individual finger forces F , respectively. The relations for the non-zero torque trials, $G(L, M)$ and $F(L, M)$, represented the combine effects of L and M on the recorded forces. To find the fractional effect of M on G or F , the differences $G(L, M) - G(L)$ and $F(L, M) - F(L)$ were computed and then regressed on L (Fig. 2). The regression slopes characterized the effect of the moment production requirement on the forces of interest. The positive slopes indicated that equal increments of L generated larger force increases than in the zero-torque conditions, while the negative slopes indicated that the force increases were smaller than in the zero-torque task. The slopes were determined in two complementary ways: (1) the changes in the force during a trial were linearly regressed on the changes of L or acceleration, and (2) the major axis of G - L ellipse (or the F - L ellipse, F -acceleration ellipse, etc.) was determined by the principal component analysis. The major axis corresponds to the eigenvector of the relation with the maximal eigenvalue. Error ellipse fitting was applied to the relation and the confidence level was chosen at 85%.

The second regression variable, the y -intercept, was replaced by the difference between $G(L, M)$ and $G(L)$ values at the instances of zero acceleration, $[G(L, M) - G(L)]_0$, which we will address as the “moment-related offset”. The difference was determined for each oscillation cycle and then averaged over all cycles. At the instances of zero acceleration, L equals the static

weight of the object W —which was the same in the zero-torque and non-zero-torque tasks—and M equals the static moment. However, $[G(L, M) - G(L)]_0$ can differ between the static and dynamic tasks. In general, the entire procedure was similar to the technique used previously to partition G into three fractions (Zatsiorsky et al. 2005) with one distinction: instead of the static G – L relation, the dynamic $G(L)$ vs L relation was used.

In the time domain, cross-correlation analysis was performed to examine the phase relations between pairs of performance variables. A two-way, repeated-measures ANOVA with the factors TORQUE (five levels) and FREQUENCY (three levels) was employed. Statistical analysis was conducted in the Statistics toolbox of Matlab 6.1 (The MathWorks, Inc., Natick, MA, USA).

Results

We describe first the moment modulations and then L and M effects on G and F forces.

Moment modulation: the moments of the normal and tangential forces

In zero-torque conditions, the moments of the normal (M^n) and tangential forces (M^t) were not equal to zero; they were in opposite directions (Fig. 3). The moments changed in anti-phase and cancelled each other such that the total moment exerted on the handle did not change, and the rotational equilibrium of the handle was maintained. Hence, M^n and M^t considered together acted as an internal moment; similar facts have been reported previously (Gao et al. 2005).

In contrast, in the non-zero-torque trials, the relations between M^n and M^t were positive (Fig. 4c), the moments added to each other (Fig. 4a). During such tasks, the magnitude of the external torque (and the load L) rhythmically changed in proportion to the handle acceleration. M^n and M^t counterbalanced the external torque and also changed rhythmically. In spite of rhythmic changes of M^n and M^t , their percentage contribution to the total moment in a given trial stayed approximately constant; for instance, in the trial shown in Fig. 4b, the contribution of M^n and M^t to the total moment varied only from 49.2 ± 7 to $50.8 \pm 7.0\%$ (the average values of the two bottom curves in the graph are approximately equal and do not change much in individual cycles). Among the tasks, the percentage contribution of M^n and M^t did not change statistically with either the external torque or frequency.

The average (across task conditions) time lags between M^n and M^t , on the one hand, and acceleration, on the other hand, were -16.9 ± 32.1 and -2.3 ± 18.6 ms, respectively (the minus sign indicates that the M^n and M^t changes preceded the acceleration changes). The time lags did not differ significantly from zero (the Wilcoxon signed rank test). Similar relations were observed for all the other recorded variables: the forces and moments oscillated practically in synchrony with the handle acceleration.

Partitioning normal forces into the L-related and M-related fractions

As explained above, we expected that L fluctuations within the cycles affect all the fingers in the same way (i.e., the G force increases and decreases in synchrony with the L changes), while the effects of M fluctuations were expected to be different for the agonist and antagonist fingers. The question of interest is the effect of concurrent L and M changes. We consider first the effects on the G force and then on the forces of the agonist and antagonist fingers. In both the cases, the combined L and M effects are presented first and then the fractional M effects are considered.

The grip force (G)— G changed systematically both between the tasks and during the tasks. As illustrated in Fig. 5, the between-task relation shows a V-like pattern, which is in agreement with the relation between G and M observed in the static tasks (Zatsiorsky et al. 2002a).

The dependence of G on acceleration in single trials is illustrated in Fig. 6. The slopes of linear regressions between G and the handle acceleration changed—as revealed by a 2-way ANOVA—systematically both with the external torque and the oscillation frequency, while the interaction between the two factors was not significant (for the TORQUE, $F_{4,75} = 10.01$, $P < 0.001$; for the FREQUENCY, $F_{2,75} = 4.56$, $P < 0.05$).

The fractional M effects on the grip force computed from the $G(L, M) - G(L)$ difference—both the regression slopes and the moment-related offsets $[G(L, M) - G(L)]_0$ —depended on both the external torque and frequency (for the slopes $F_{4,75} = 15.66$, $P < 0.05$; $F_{2,75} = 8.9$, $P < 0.05$ and for the offsets $F_{4,75} = 33.35$, $P < 0.05$; $F_{2,75} = 3.97$, $P < 0.05$). The interaction between the two factors was not significant ($P > 0.3$). With changes in the external torque, both variables—the slope and the offset—changed in a V-like manner (Fig. 7). With an increase in the oscillation frequency, the slopes decreased while $[G(L, M) - G(L)]_0$ increased.

Agonist and antagonist finger forces—When the handle acceleration increases, both L and M rise. An increase in L should induce an increase in G and hence an increase in all digit normal forces. In contrast, an increase in M requires increasing the force of only the agonist fingers. When the acceleration (and hence both L and M) increases, the normal forces of the agonist fingers get higher, while the forces generated by the antagonist fingers—especially the “peripheral” fingers, the index and little—do not change substantially (Fig. 8). Hence, for the antagonist fingers, the classical G – L relations can be overridden by torque production requirements.

The slopes of linear regressions between $F(L, M)$ and acceleration or L change systematically with M (Fig. 9).

When a supination torque is needed to be produced, the little finger contributed most to the torque production with the largest slope: the finger force increased with acceleration. In such tasks, the index finger force did not change much with acceleration, that is, when L force increased, the normal force of the index finger stayed more or less constant. On the contrary, in the tasks with the pronation effort, the index finger played the most important role (see Fig. 9). The finger force changed substantially with acceleration due to the combined L and M effects. The little finger force was not modulated much with handle acceleration and, hence, with L .

The middle and ring fingers that have smaller moment arms with respect to the thumb as a pivot than the index and little fingers showed moderate changes of the $F(L, M)$ vs L slopes with external torque. Hence, the modulation of the finger forces during the object manipulation depended on the mechanical advantage (moment arms) of the individual fingers.

The effects of the finger function—whether the finger works as a torque agonist or antagonist—on the F – L coupling are especially evident in the $F(M)$ – L relations (Fig. 10). When a finger works as an agonist, the effects of M fluctuations during a trial are added to the effects of changes in L [the $F(M)$ – L slopes are positive]; when a finger works as an antagonist, the M effects decrease the L effects, and the slopes are negative. The latter is correct for the index, little and middle fingers; the $F(M)$ – L slope for the ring finger does not change much with variation of the external torque.

The $F(L, M) - F(L)$ differences at the instances of zero acceleration were significantly affected by external torque ($F_{4,324} = 42.19$, $P < 0.05$; Fig. 11) as well as by oscillation frequency

($F_{2,324} = 4.74$, $P < 0.05$; not shown in the figure). The interaction effects, however, did not reach the level of statistical significance.

Discussion

We will concentrate on discussing the following issues: (1) How is the rotational equilibrium maintained? (2) The L and M effects on G and F ; and (3) Linear effects in the prehension control.

Maintaining rotational equilibrium

To maintain rotational equilibrium the subject has to manipulate the handle in such a way that the external moment M —that varies in the cycle—is counterbalanced by the sum of moments of digit forces. From the presented data, it follows that the rotational equilibrium is maintained by two main mechanisms: (1) concerted changes of the moments of the normal and tangential forces, specifically the anti-phase changes of M^n and M^t during the zero-torque tasks and the in-phase changes during the non-zero-torque tasks (Fig. 3, Fig. 4), and (2) redistribution of the normal forces among individual fingers such that the agonist fingers increase the force in phase with the acceleration, while the forces of the antagonist fingers with the large moment arms, the index and little fingers, stay put (Fig. 8).

The above changes occur in synchrony with the vertical acceleration of the handle and, hence, with the L force (Fig. 4). Taking into account the time delay necessary for force development, it is natural to conclude that the above-mentioned force and moment adjustments to the M fluctuations are made in an anticipatory fashion. The subject seems to learn the physical properties of the handheld object and automatically retrieves relevant motor commands (Johansson et al. 1999). The controller acts in a feed-forward, anticipatory manner and adjusts digit forces based on expected mechanical effects of the voluntary movements on L and M . These observations are compatible with the idea of an internal model that pre-computes time profiles of forces required to perform a task (Wolpert et al. 1995; Flanagan and Wing 1997; Flanagan et al. 2001). Our results are also compatible with other hypotheses of motor control as long as these hypotheses allow predictive action by the central nervous system. In particular, according to the equilibrium-point hypothesis (Feldman 1966, 1986), such predictive actions can be consequences of time changes in the equilibrium states of the neuromotor system leading to changes in the reference configuration of the effector (Feldman and Latash 2005). An integration of sensory information with previous experience has been suggested as a possible mechanism underlying such finger force adjustments (Kording et al. 2004). Several brain structures have been recently implicated in anticipatory force control including the cerebellum and the frontal and parietal cortices (Imamizu et al. 2000, 2004; Yamamoto et al. 2002). A recent study has suggested, in particular, the importance of cortico-cortical projections in producing motor cortical outputs in relation to the properties of an object manipulated by the hand (Cattaneo et al. 2005).

During the vertical oscillation of a vertically oriented handle, a special role is played by the glabrous skin receptors, especially those of them that are responsible for the reception of tangential force and object slipping (Johansson and Westling 1984). These receptors trigger the feedback mechanisms and correction reactions directed at slipping prevention; the reactions that are manifested as fast increases of G (Johansson and Westling 1984). Other possible sensory contributors to force adjustments are proprioceptors that are also known to be able to trigger short-latency changes in grip force (Traub et al. 1980; Scholz and Latash 1998). Recent studies have suggested that sensory information may be combined with prior experience using Bayesian integration in generating finger force adjustments (Kording et al. 2004). However, maintaining the rotational equilibrium requires much more complex responses than a “simple” G increase. It is not clear what may be the role of the cutaneous skin receptors and

proprioceptors in initiating these responses. Some information on that can be obtained from experiments involving fingertip anesthesia or cooling and muscle vibration. We plan to perform such experiments.

Effects of the L and M changes on the digit force modulations

As expected, in the zero-torque tasks, the L fluctuations were accompanied by parallel changes in G and in the forces of all individual fingers. In contrast, in the non-zero-torque tasks, while G changes were in principle similar to those observed in the zero-torque tasks (G changed in synchrony with L), the F modulations were dissimilar in different fingers. It seems that the G – L coupling in the non-zero-torque tasks was less strong than in the zero-torque tasks (Fig. 12). For instance, as shown in Fig. 12, the coefficients of correlation between the normal and tangential forces in individual cycles were 0.97 and 0.98 for the zero-torque task, while they were only 0.86 and 0.84 in the non-zero-torque task. The differences were, however, significant only for the pronation torques when the load was placed at the right hand side (the conclusion is based on 1-way ANOVA performed on the z -transformed values of the correlation coefficients and their paired comparisons); for the supination torques, the P values were close to significant ($P = 0$).

The F modulations depended on (1) the role played by the finger in the rotational equilibrium control—whether the finger serves as a torque agonist or a torque antagonist, and (2) the mechanical advantage (MA) of the finger in producing the pronation/supination moment. To clarify the main concept behind the suggested explanation, we offer the following rudimentary model. Taking into account that the individual finger forces are scaled linearly with the load L and moment M (Fig. 8) and using the Eqs. 4 and 5— $L(t) = W + ma(t)$ and $M(t) = M_{st} + m_{load}la(t)$ —we can write for each instant of time

$$\begin{aligned}
 F^i &= k_L^i L + k_M^i M \\
 &= \underbrace{k_L^i W + k_M^i M_{st}}_{\text{Force at an instant of zero acceleration}} \\
 &\quad + \underbrace{(k_L^i m + k_M^i m_{load}l)a}_{\text{Dynamic fraction of the force}}
 \end{aligned} \tag{6}$$

where F^i is the normal (grip) force exerted by finger i , k_L^i and k_M^i are scaling coefficients, $k_M^i = kd^i$, where d^i is the moment arm (distance) of the point of application of the i -th finger force from the pivot (d^i accounts for the displacements of the points of application of the thumb and finger forces on the sensors). Note that d^i is positive if the finger serves as a torque agonist and d^i is negative when the finger works as a torque antagonist. Other symbols are explained previously; see Eqs. 4 and 5.

Conceptually, the “force at an instant of zero acceleration” represents the sum of (1) constant forces necessary to counterbalance static load and moment and (2) the so-called stato-dynamic fraction of the grip force (Zatsiorsky et al. 2005), that is, the steady increase of the force above the static level; this fraction is recorded at the instances of zero acceleration of the handle during the trial. The “force at an instant of zero acceleration” is approximately constant during a trial, while the dynamic fraction changes with the acceleration during single oscillation cycles. When it comes to the dynamic fraction of the grip force, the equation predicts the following facts: (1) summation of the L and M effects for the fingers acting as torque agonists [according to $(k_L^i m + k_M^i m_{load}l)a(t)$] and subtraction of the M effects from the L effects in antagonist fingers [according to $(k_L^i m - k_M^i m_{load}l)a(t)$] and (b) larger M effects for the index and little fingers than for the middle and ring fingers (because of the larger d^i values). Both the predictions agree

well with the experimental data (Fig. 8). In individual trials, the forces exerted by the agonist fingers scaled with the handle acceleration, while the forces of the antagonist fingers did not change much or even stay put. The latest result indicates that in the antagonist fingers, the L effects were cancelled by the oppositely directed M effects of equal magnitude. The second prediction from Eq. 6 is essentially the MA hypothesis. The prediction came true: in the “lateral” fingers with the large moment arms—the index and little fingers—the M effects were pronounced to a much larger degree than in the “central” fingers, the middle and ring fingers (Fig. 7, Fig. 8, Fig. 9, Fig. 10).

In general, the data support the MA hypothesis for the specific case of torque production by several fingers. Note that the MA hypothesis was also used to explain the force sharing between individual muscles serving the same joint (for a discussion and review see Prilutsky 2000). The confirmation of the MA hypothesis in the present study provides an additional argument in favor of its broad applicability.

As follows from Eq. 6 and the expressions for the dynamic force fraction discussed above — $[(k_L^i m + k_M^i m_{\text{load}})a(t)]$ for the agonist fingers and $[(k_L^i m - k_M^i m_{\text{load}})a(t)]$ for the antagonist fingers — observed L and M effects on the F forces can be explained by a superposition of two commands. One command whose intensity is determined by L results in stronger/weaker contractions of all involved fingers and hence in a change in G . This command represents the L effect. The second command, representing the M effects, results in a potentiation of the flexion command to the agonist fingers and inhibition of the commands to the antagonist fingers. As a result, the force of the agonist fingers increases and the force of the antagonist fingers decreases. For the antagonist fingers with the large moment arms, the effects of the L -related commands and M -related commands can negate each other such that the outcome force does not change with the L fluctuations, that is, the G – L coupling for these fingers appears to be broken (see Fig. 8, top). While this explanation and the data (Fig. 9, Fig. 10, Fig. 11) agree nicely with the principle of superposition, we cannot claim that the principle is validated in this study because our analysis—specifically partitioning the $G(L, M)$ and $F(L, M)$ forces into the $G(L)/F(L)$ and $G(M)/F(M)$ fractions—was based on this principle. Claiming the proof will be tantamount to circular reasoning (a vicious circle, *circulus in probando*). However, we do say that the application of the principle to the dynamic tasks helped in interpreting the obtained facts.

Linear effects in the control of prehension

The observed relations between the input and output variables in this study were nearly linear (with some noise, e.g., Fig. 5, Fig. 7, Fig. 8). The relations were approximated by linear regression equations. Essentially, we dealt with the linear regressions and their sums. The linearity cannot be deduced from the task mechanics. G is an internal force and can be of any value (provided that slipping is prevented). When L changes, the task mechanics does not require G to change with L in a linear fashion. The same is valid for the rotational equilibrium control: If the sum of the moments exerted by the subject negates the external moment, the equilibrium is maintained. There is nothing in mechanics requiring that the contributing moments, for example, moments exerted by the individual fingers, should change linearly with the handle acceleration or L . It is a choice made by the central controller and, hence, is in the domain of neurophysiological and motor control investigations.

Linear behaviors of the neuromotor system have been described in a number of studies. In particular, Nichols and Houk (1976) have suggested that the role of the tonic stretch reflex could be to linearize the dependence of the muscle force on muscle length. Linear scaling of peak velocity with movement distance during fast voluntary movements could result from the desire of the controller to perform maximally smooth movements in accordance with the

minimum-jerk hypothesis (Hogan 1985; Hogan and Flash 1987). A principle of linear joint torque scaling has been proposed by Gottlieb and his colleagues as a simplifying control strategy for a variety of fast limb movements (Gottlieb et al. 1996). The central nervous system may be aware of the advantages of dealing with linear systems during simple behaviors and it may parameterize control signals to gain this advantage. Presently, one can only speculate on the role of particular neural structures in all these examples of linear behavior of strongly non-linear systems. Modulation of spinal reflexes (Nichols and Houk 1976), operation with spinal primitives (Mussa-Ivaldi et al. 1994; Lemay and Grill 2004) and particular brain mechanisms of predictive behavior (Kawato et al. 2003) have been implicated in tuning elements of the system to simplify control.

Analogies can also be found in engineering. Although most of the control systems exhibit non-linear behaviors, transforming them into linear systems by linearization around equilibrium point has been demonstrated to be a very powerful tool. Linearization is a process by which an approximate linear model that deals with small-scale changes is derived from a non-linear model. The model is derived with the assumption that the excitations perturb the system in the vicinity of a nominal set point (Kailath 1980). The benefits of doing so are twofold. Firstly, linearization can reduce the complexity of controller design and results in lower cost. Secondly, the control theory of linear systems is much better established than that of the non-linear systems and hence the design is easy to track.

Finally, we have to acknowledge some limitations of the current study. In particular: (1) the L and M fluctuations were not independent, (2) the enslaving effects among the fingers were not addressed and (3) the EMG was not recorded (the wiring from the five force sensors and the accelerometer has made this recording cumbersome and the signals noisy). We are planning to overcome these delimitations in future studies.

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Fig. 1.

Schematic drawing of the handle with the horizontal beam. The static moment was computed as the product: $M_{st} = m_{load} \times g \times l = 0.285 \text{ kg} \times 9.81 \text{ m/s}^2 \times l$, where l is the horizontal distance from the handle center to the place of the mass suspension

Fig. 2.

Computing the fractional effect of M on the grip force G by comparing the non-zero and zero-torque tasks. W is the object weight. The $G(L)$ – L relation for a zero-torque task is represented by the straight line. The $G(L, M)$ – L relation for a non-zero-torque task is represented by the ellipse and the regression line. The $G(L, M)$ – $G(L)$ difference is also called the moment-related offset

Fig. 3.

Moments of normal forces (M^n), tangential forces (M^t) and their sum ($M^n + M^t$, the total moment) vs acceleration in a zero-torque task. A representative example (subject #6, 1 Hz, 0 Nm). The acceleration is presented in units of acceleration due to gravity (g , 9.81 m/s^2). When acceleration equals $1g$ the inertial force equals the weight of the object. To determine the load force Eq. 4 should be used; for instance when the acceleration equals $0.4g$ the load force equals 1.4 of the weight of the object

Fig. 4.

Moments in a non-zero task (2 Hz, -0.33 Nm). A representative example. **a** Moments in relation to acceleration. **b** Moments vs time (2 Hz, -0.33 Nm). For easy comparison with the external torque, the absolute values of the total moment $M^n + M^t$ are shown. **c** M^n vs M^t during object manipulation. In panel b, the “overshoots” of the total moment ($M^t + M^n$) over the external torque values at the peaks of the curve and the “undershoots” at the bottom of the curves are seen. The “overshoots” and “undershoots” [i.e., the differences between the total moment ($M^t + M^n$) and the external torque values] are proportional to the angular acceleration of the object. However, because the periods of over- and undershooting are brief and the velocity during these periods is close to zero, the second integrals of the angular acceleration over time

(they equal the angular displacement) are small and the handle maintains approximately vertical orientation. In the present example the handle acceleration in the z direction is $0.046 \pm 0.0659g$, which corresponds to the upper estimate of the average inclination of $2^\circ 35'$. Both the “overshoots” and “undershoots” indicate that at the instances when the movement changes its direction the accuracy of the adjustment of the total moment ($M^t + M^n$) to the external torque deteriorates.

Fig. 5.

Grip force (G) in relation to external torque in different tasks and within the individual trials (a representative example, subject 1, 2 Hz). Note: In this and other figures the torques are described by the load location with respect to the center of the beam, R right, L left, Mi for the middle, 1 designates 1/6 Nm, 2 corresponds to 1/3 Nm. As an example, the symbol R2 represents the load location to the right of the center that results in the moment of $-1/3$ Nm. Such a moment—as seen from the subject—is in the clockwise direction (*negative*). To counterbalance this external moment/torque, the subject should exert a counterclockwise (*pronation, positive*) moment of equal magnitude

Fig. 6.

Dependence of $G(L)$ and $G(L, M)$ on handle acceleration at various M values in a representative subject (2 Hz). When the load is suspended at the middle of the handle (*Mi task*), the torque is zero and, hence, a “pure” effect of changes in the load force L on the grip force G is observed, $G(L)$ relation (the bottom ellipse in the graph). All other relations represent combined effects of the L and M fluctuations on the grip force G in the trial, the $G(L, M)$ relations

Fig. 7. The slope of the $G(M)$ vs L relations (*top panel*) and the moment-related offset $[G(L, M) - G(L)]_0$ (*bottom panel*) for different tasks. Group average and standard errors

Fig. 8.
The dependence of individual finger forces on object acceleration, a representative example. Frequency 2 Hz. Top panel: index and little fingers; bottom panel: middle and ring fingers

Fig. 9.

The slopes of linear regressions between $F(L, M)$ and L for individual fingers under various M conditions (1 Hz, group averages and standard errors)

Fig. 10.

The slopes of $F(M)$ vs L relations at different tasks. Group average and standard errors, frequency 2 Hz. Note that when the fingers work as torque antagonists the slopes are negative: when L increases, $F(M)$ decreases

Fig. 11.
 $F(L, M) - F(L)$ differences at the instances of zero acceleration. Group average and standard errors, 2 Hz

Fig. 12.

Force vectors during single trials. Movement frequency was 2 Hz. *Top panel* zero torque, *bottom panel* torque -0.33 Nm. In the bottom panel, the difference on average tangential forces are exerted by the thumb and the fingers. The difference between these forces is proportional to M^t (see Eq. 5)