Multidigit Control of Contact Forces During Transport of Handheld Objects

Sara A. Winges, John F. Soechting, and Martha Flanders

Department of Neuroscience, University of Minnesota, Minneapolis, Minnesota

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Winges SA, Soechting JF, Flanders M. Multidigit control of contact forces during transport of handheld objects. J Neurophysiol 98: 851–860, 2007. First published June 6, 2007; doi:10.1152/jn.00267.2007. When an object is lifted vertically, the normal force increases and decreases in tandem with tangential (load) force to safely avoid slips. For horizontal object transport, horizontal forces at the contact surfaces can be decomposed into manipulation forces (producing acceleration/deceleration) and grasping forces. Although the grasping forces must satisfy equilibrium constraints, it is not clear what determines their modulation across time, nor the extent to which they result from active muscle contraction or mechanical interactions of the digits with the moving object. Grasping force was found to increase in an experimental condition where the center of mass was below the contact plane, compared with when it was in the contact plane. This increase may be aimed at stabilizing object orientation during translation. In another experimental condition, more complex moments were introduced by allowing the low center of mass to swing around a pivot point. Electromyographic (EMG) activity recorded from several intrinsic and extrinsic hand muscles failed to reveal active feedforward control of contact forces in this situation. Instead, in all experimental conditions, EMG data revealed a strategy of feedforward stiffness modulation. Multiple regression analysis revealed that muscle activity at remote digits (e.g., the index and ring fingers) was highly correlated with the contact force measured at another digit (e.g., the thumb). The data suggest that to maintain grasp stability during horizontal translation, predictable as well as somewhat unpredictable inertial forces are compensated for by controlling the stiffness of the hand through cocontraction and modulation of hand muscle activity.

INTRODUCTION

Control of the hand during the grasping of an object has been widely studied (for reviews see Flanagan et al. 2006; Johansson 1996; Wing 1996) using different types of grips that typically involve two, three, or five digits. For each type of grip, equilibrium constraints must be satisfied to produce and maintain a stable grasp. For a tripod grasp, the horizontal force vectors of the thumb and the two fingers must sum to zero and must intersect at a point termed the force focus (Yoshikawa and Nagai 1991). However, this constraint does not uniquely specify the direction and magnitude of the contact forces at the digits. Although these basic equilibrium constraints remain when an object is transported, additional control issues associated with object stability can arise, such as maintaining object orientation during the movement (Gao et al. 2006).

To examine grasp stability during a movement, the forces associated with equilibrium and transport can be decoupled. During transport, the force on the object can be decomposed into manipulation forces that equal the product of mass and acceleration and internal grasping forces that satisfy equilibrium constraints (Yoshikawa and Nagai 1991). Previous studies using the tripod grip (Smith and Soechting 2005) and a five-digit grip (Gao et al. 2005) have observed changes in the internal grasping force during movement. If in three-digit grasping internal grasp force and manipulation force are coupled in the same way as grip and load force are for vertical two-finger lifting (Westling and Johansson 1984), one would expect that the modulation in grasp force would be associated with object acceleration. However, in these previous studies, the modulation of grasp force appeared to be more closely linked to velocity. Therefore it was suggested that this transient increase in grasping force is associated with object stabilization, constituting a strategy to minimize object tilt (Smith and Soechting 2005). Alternatively, Gao et al. (2005) suggested that the modulation of grasp force may partially be explained as a mechanical artifact or a representation of a neuromuscular strategy.

The current project extends these results by examining how changes in the inertial properties of an object affect the grasp during horizontal transport. When the center of mass is located within the contact plane, the small moments that occur during horizontal transport likely arise from vertical offsets of the three contact points. However, if the center of mass is below the contact plane, larger moments would occur during movement—thus increasing the forces needed to stabilize the object. Therefore if the modulation of internal grasp force during the movement is related to stabilization of the object, this modulation should be affected by the location of the center of mass. Furthermore, if the center of mass is at a fixed point either within or below the contact plane, a feedforward strategy could be used to successfully perform the movement while stabilizing the object orientation because the external moments would be predictable with respect to acceleration (Wing and Lederman 1998). However, a pendular weight placed below the contact plane and allowed to swing freely during the movement induces less-predictable changes in the inertial properties of the object and may change the subject’s strategy.

A comparison between the three center-of-mass conditions (within, below/fixed, below/free) provides an opportunity to describe how the modulation of grasp force is controlled. One possibility is that the modulation of contact force (i.e., the force measured at the transducer) is not actively controlled; rather it may (at least partially) result from a purely mechanical interaction between the object and a stiffened hand (Gao et al. 2005). Furthermore, actively controlled grip force may result from an anticipatory, feedforward strategy or, alternatively, from reflexive muscle contractions. Reflexive changes in grip force and muscle activity have been observed for unexpected load perturbations during two-digit grasping and lifting (Cole...
and Abbs 1988; Johansson and Westling 1984). Therefore to
determine the genesis of the modulation in contact forces, in a
second experiment we examined hand muscle activity and
compared it between conditions where the center-of-mass po-
sition was fixed or free to swing.

**METHODS**

Seven subjects (three male, four female, ages 21–62 yr, five
right-handed and two ambidextrous) participated in the study. Six
subjects participated in the first experiment and four subjects
participated in the second experiment, three of whom also participated in
the first experiment. The experimental protocol was approved by the
University of Minnesota’s Institutional Review Board and all subjects
gave informed consent before the experiment.

**Instrumentation**

Subjects grasped a manipulandum from above (described in Baud-
Bovy and Soechting 2001) with the right hand, using a tripod grasp,
i.e., with the thumb, ring, and index fingers on the transducers (T1, T2,
and T3, respectively; Fig. 1). The contacts were constrained to the
surfaces of three 17-mm-diameter force–torque transducers (ATI
Nano 17 US-6-2) covered with No. 60 sandpaper. The transducers
were arranged equidistant from the center of the manipulandum, on
a circle with a radius of 42 mm, such that forces normal to the contact
surface of each transducer were directed toward the center of the
manipulandum. The contact surface of the thumb sensor (T1) was
aligned with the frontal plane of the subject and perpendicular to the
subject’s sagittal plane (Y-axis). Forces and torques from the trans-
ducers were sampled at 1 kHz and the three-dimensional position of
the object and the weight for the third condition (see following text)
were sampled at 60 Hz using a Polhemus Fastrak system. Force and
position data were low-pass filtered (fourth-order Butterworth, 10-Hz
cutoff frequency) before analysis.

The location of the center of mass (CM) was manipulated by
placing a 220-g weight on the object (Fig. 1). For the control
configuration, the weight was in the base platform (which had a
mass of 200 g) such that the CM of the object was in the plane of the
contact surfaces. In the second object configuration, the weight
was fixed below the base platform so the CM was approximately 4.20 cm
below the horizontal plane of the contact surfaces. For the third object
configuration the CM was also below the plane of the contact surfaces
(−6.50 cm) but the weight was connected to the base platform by a
configuration the CM was also below the plane of the contact surfaces
below the horizontal plane of the contact surfaces. For the third object
configuration, the weight was above the base platform (which had a
placing a 220-g weight on the object (Fig. 1). For the control
configuration, the weight was above the base platform (which had a
weight up and weight down conditions, contact forces must satisfy the
following general equations of motion

\[
F_{\text{pX}} = m_p(a_x + i\dot{\theta}) \\
F_{\text{pY}} = m_pg \\
F_{\text{pZ}} = F_{\text{pX}} + F_{\text{pY}} = 0
\]

where \( m_p \) is the mass of the pendulum, \( i \) is the distance from the pivot
point to \( m_p \), \( \theta \) is the angle of the pendulum’s deviation from the
vertical Z axis (Fig. 1), \( \dot{\theta} \) is the angular acceleration of the pendulum,
and \( a_y \) is the acceleration of the platform of the manipulandum in the
Y-direction, and \( F_{\text{pX}} \) and \( F_{\text{pY}} \) are the forces exerted by the platform
on the pendulum. Equations 1–3 can be simplified to yield

\[
F_{\text{pX}} = -m_p g \dot{\theta} \\
\dot{\theta} + g \theta = -a_y
\]

Note that the force exerted by the pendular mass on the platform is
equal and opposite to \( F_{\text{pX}} \) and that Eq. 5 defines the oscillation of
the pendulum. Thus this configuration served to test the efficacy of
feedback regulation of grasping force.

**Experimental procedures**

Subjects were asked to grasp the manipulandum with their right
hand using a tripod grasp, lift it, and respond to a tone by quickly
moving it 20 cm horizontally from the center point to one of eight
targets equally spaced on the perimeter (center-out). The manipulan-
dum was held at the target point for approximately 1 s, then the
reverse movement was made back to the center point (out-center).
Subjects were given practice before the start of the experiment to
familiarize themselves with the movement. For each manipulandum
configuration, subjects completed five blocks of trials to eight ran-
domized target locations.

**Data analysis**

Our analysis was limited to contact forces in the horizontal plane.
Normal (\( F_{\text{n}} \)) and tangential (\( F_{\text{t}} \)) forces at each digit are defined in Fig. 1
with arrows indicating the direction of positive sign. For both the
weight up and weight down conditions, contact forces must satisfy the
following general equations of motion

\[
\sum F_{\text{n}} = m a_x \\
\sum F_{\text{t}} = m a_y \\
r_i \times F_i = M_i = 0
\]

where \( m \) is the manipulandum mass; accelerations in X-direction and
Y-direction are given by \( a_x \) and \( a_y \), respectively; \( F_{\text{n}} \) and \( F_{\text{t}} \) are forces
in X-direction and Y-direction, respectively, for the \( i \)th contact
point, \( r_i \) is the horizontal vector from the center of mass to the \( i \)th

![Fig. 1. Manipulandum configurations. Side view demonstrates the configurations: weight up, weight down, pendulum. Top view shows transducer (T1, T2, T3) arrangement and positive direction of normal (\( F_{\text{n}} \)) and tangential (\( F_{\text{t}} \)) forces. Free-body diagram of the pendulum illustrates the movement of the pendulum in the \( Y-Z \) plane where \( \theta \) is the angle of the pendulum’s deviation from the vertical axis. \( l \) is the distance from the pivot point to the center of mass, and \( F_{\text{pX}} \) and \( F_{\text{pY}} \) are the forces exerted on the pendulum.](http://jn.physiology.org/doi/10.1152/jn.00592.2006)
contact point; \( F_i \) is the resultant force from the \( i \)th contact point; and \( M_{Zi} \) is the twisting moment about the vertical Z-axis. For the pendulum condition, the inertial forces produced by the pendulum (Eqs. 1 and 2) must also be accounted for by the contact forces; thus the equations of motion are modified as follows for the pendulum condition

\[
\sum F_{xi} = m_x a_{xi} + m_y a_{yi}
\]

\[
\sum F_{yi} = m_x a_{xi} + m_y a_{yi}
\]

where the subscript \( m \) denotes the manipulandum platform and the subscript \( p \) denotes the pendulum.

To examine forces associated with object stabilization alone, horizontal contact forces were partitioned into two components: forces required to move the manipulandum (manipulation force, \( F_{\text{manip}} \)) and forces that satisfy equilibrium constraints to hold the manipulandum (grasping force, \( F_{\text{grasp}} \)). Note that grasping forces are internal force vectors that cancel each other in a tripod grip. We used the scheme proposed by Yoshikawa and Nagai (1990), which provides a geometric solution for the smallest physically plausible manipulation forces, given that the decomposition of forces into these two components does not have a unique solution (Smith and Soechting 2005). The strategy used to determine the grasping forces at each contact point (the center of pressure) first computes the manipulation forces at each contact point (following Yoshikawa and Nagai 1990, 1991). Then the grasping forces at each contact point are found by subtracting the manipulation forces from the contact forces at the corresponding contact point (\( F_{\text{grasp}} = F_{\text{contact}} - F_{\text{manip}} \); for details see Smith and Soechting 2005).

Position data were differentiated to obtain velocity and acceleration of the object during the movement. Movement onset and end were determined as the points when movement speed was 5% of the maximum speed for that movement. Force and position data were then time normalized to 100% of the movement duration.

ANOVA with repeated measures were used to determine the effect of weight location and direction (independent variables) on movement variables and grasp force amplitude (dependent variable). ANOVA was also used to determine the effect of weight location and direction (independent variables) on grasp force amplitude (dependent variable) for individual subjects. Because ANOVA revealed that grasp forces were directionally tuned, we found the amplitude and phase of the directional tuning by fitting our data to a cosine function

\[
F(\theta) = F_x + F_y \cos(\theta - \theta_0)
\]

using linear regression. A significance level of 0.05 was used for all analyses.

**Experiment 2**

To determine the extent to which the modulation of grasp force observed in the first experiment could be attributed to the modulation of muscle activity in addition to the mechanical interaction of a stiffened hand and the manipulandum, in a second experiment, hand muscle activity was recorded for a subset of directions and conditions. For this second experiment, subjects were asked to make only center-out movements to four targets from the first experiment, corresponding to forward, right, back (toward body), and left. Object configurations were limited to those where the weight was fixed and free to move below the contact plane: weight down and pendulum conditions, respectively. For each object configuration, subjects completed two blocks of 40 trials, each with ten randomly ordered trials for each of the four targets.

Electromyographic (EMG) activity was recorded using small bipolar Ag–AgCl surface electrodes, with 2-mm-diameter conductive surfaces placed 10 mm apart (see Fig. 2). These electrodes were purchased from Discount Disposables (St. Albans, VT) and permanently soldered to custom-made, electrically shielded wire leads, connected to standard laboratory amplifiers. The ground electrode was attached to the subject’s contralateral, nonmoving wrist. EMG was amplified (×1,000), band-pass filtered (60–500 Hz), and then sampled at 1,000 Hz.

EMG activity was recorded from three portions of extrinsic finger muscles: a central portion of extensor digitorum (ED) and two portions of flexor digitorum superficialis (FD, FD2). As shown in Fig. 2, the FD portion of the flexor digitorum superficialis was closer to the index finger and FD2 was closer to the ring finger. We also recorded from two intrinsic thumb muscles: abductor pollicis brevis (APB) and flexor pollicis brevis (FPB); and three intrinsic finger muscles: first dorsal interosseus (FDI) and index and ring lumbricals (LUMi, LUMr, respectively). We previously estimated cross talk between the APB and FPB electrodes to amount to <16% of the recorded signal (Klein Breteler et al. 2007). LUMr is beneath a relatively thick layer of tissue.
but is not close to other muscles; LUMi lies above adductor pollicis, but the fibers of this thumb muscle run orthogonal to the axis of the bipolar LUMi electrodes.

Before analysis, EMG for each muscle was rectified and then low-pass filtered at 20 Hz (d’Avella et al. 2006). Treatment of position and force data as well as segmentation and time normalization procedures were the same as for the first experiment. Mean EMG for each muscle was computed across trials for each direction in each condition. Mean EMGs were then normalized to the maximum amplitude observed for that muscle during the experiment. Linear regression with maximum lags of ±25% movement time was used to assess whether fluctuations in EMG activity corresponded to pendulum motion. The effect of the pendular motion was not clearly reflected in the EMG activity, although it was apparent in the force. Therefore to further examine whether the effect of the pendulum observed in the normal contact force was reflected in muscle activity, we used stepwise multiple linear regression. The first model used the EMG activity of APB and FPB to determine the extent to which the modulation of thumb normal force could be explained by the modulation of thumb muscle activity. Alternatively, thumb normal force could at least partially be the result of forces produced by the opposing index and ring fingers pressing toward the stiffened thumb, as a result of constraints of the tripod grasp. Therefore a second model that also included EMG activity from muscles acting on the index and ring finger was used. Because there were high correlations (>0.9) between muscles associated with the same digit, we chose to combine their EMG activity to create a four-variable model. The thumb variable was the sum of EMG activity from APB and FPB; the index variable was the sum of FDI, LUMi, and FD EMG activity; and the ring variable was the sum of LUMr and FD2 EMG activity. The EMG activity of the extensor ED was included as the fourth variable because it acts on both the index and ring fingers. Linear regression was used to assess each model’s fit to the measured force.

Results

Subjects transported the object along horizontal trajectories with a mean vertical deviation of 1.10 ± 0.97 cm; therefore we assumed planar horizontal motion for data analysis. ANOVA revealed no differences between center-out and out-center movements and force profiles; therefore the data for center-out and out-center movements in the same direction were combined for subsequent analysis. Mean movement times were 510 ± 179 ms for the weight up condition, 543 ± 142 ms for the weight down condition, and 700 ± 160 ms for the pendulum condition and were significantly different between each pair of conditions ($P < 0.05$). Differences in acceleration across conditions were consistent with this result. This can be seen by comparing the Y-component of acceleration across conditions in Fig. 3, which shows mean time-normalized data for movements in one of the eight directions [backward direction (−Y), along the midline toward the body] from one subject. The start and end of movements in Fig. 3 are indicated by the vertical dotted lines at 0 and 100%, respectively, on the x-axis. Subjects were not entirely successful in stabilizing the orientation of the manipulandum during the movement (Fig. 3, bottom three rows). Small differences were observed in the amount of rotation (relative to the initial orientation) of the manipulandum across conditions during the movement. Across all subjects and directions the weight down condition had the largest mean (±SE) change in pitch and roll (2.42 ± 0.32 and 2.78 ± 0.26°, respectively), whereas the pendulum condition had the largest mean (±SE) change in yaw of 6.12 ± 0.79°.

Before movement, forces were similar across conditions (compare columns, Fig. 3). The thumb contributed the largest normal force (3.11 ± 0.31 N, 43.4%), whereas the ring and index finger contributions were roughly equal (1.91 ± 0.12 N, 26.4%; 2.14 ± 0.38 N, 30.2%, respectively). Tangential forces were small, with the thumb tangential force being close to zero (−0.05 ± 0.01 N) and the ring and index tangential forces being larger (−0.11 ± 0.04 and 0.17 ± 0.06 N, respectively) because the force vectors were directed toward the thumb. Equilibrium requires that the resultant vector of each of the three grasp forces intersect at a common point termed the force focus. The force focus tended to be located along the normal axis of the thumb and closer to the thumb than to the fingers. It deviated during the movement with the largest deviations occurring along the normal axis of the thumb (Y-axis), with a mean deviation of 0.84 cm across all movement directions.

Consistent with the results of Smith and Soechting (2005), the initial rise in normal contact force at movement onset was attributed to the manipulation force. For example, for the weight up condition in Fig. 3, once the movement began (0%) the normal contact force ($F_n$, solid line) increased at the ring and index fingers corresponding to the force necessary to accelerate the object, i.e., manipulation force. When the manipulation force is subtracted off, the grasp forces ($F_n$, dotted lines) of the ring and index fingers also increased slowly in this example. The thumb normal contact force, which was equal to
the thumb normal grasp force during the early portion of the movement, also increased after a delay. Although the initial increase varied across digits, the peak of the normal grasp force tended to occur close to the point of maximum velocity \( (\alpha v = 0) \).

These trends were consistent across conditions, although there were some notable differences. For the weight down condition, at each digit the initial increase in normal grasp force was steep, with larger peak amplitudes than those of the weight up condition (see Fig. 3). The initial increases in grasp forces for the pendulum condition resemble those of the weight down condition, although the peak amplitudes were not as large. Furthermore, the effect of the pendular oscillations arising from the inertial forces given in Eq. 1 can be seen in the thumb normal grasp force \( (F_n, \text{dotted line, right column}; \text{Fig. 3}) \). Analysis confirmed that during movement, ring and index finger normal grasp force amplitudes were 10–15% larger for the weight down condition than for other conditions for all subjects and directions \( (P < 0.05) \). Although the example shown in Fig. 3 suggests there may be a temporal difference in the modulation of grasp force across conditions, analysis revealed that this was not a consistent trend across subjects or directions.

The difference across conditions in normal grasp force amplitude can be seen in Fig. 4, which contains data from a different subject. Each polar plot contains the mean amplitude of normal grasp force for each direction and condition at different normalized time epochs relative to the start of the movement \( (\text{rows}) \) for each digit \( (\text{columns}) \). For this subject, the normal grasp force of the thumb and index tended to be larger for the weight down condition than for the other two conditions \( (\text{Fig. 4}; P < 0.05) \). Although the pattern of grasp force modulation differed somewhat for each subject, overall, the index and ring grasp force in the weight down condition \( (\text{Fig. 4, blue lines}) \) was consistently larger than the other conditions at 50% of the total movement time and beyond \( (P < 0.05) \).

The normal grasp forces were directionally tuned. This can be seen for the subject in Fig. 4, where the largest thumb and ring normal grasp forces occurred for movements back \( (\text{Y}) \) and to the left \( (\text{X}) \). This trend can first be seen at 25 and 50% of the total movement time for the thumb and ring finger, respectively \( (\text{Fig. 4, rows 3 and 4, left and center columns}) \). At the index finger, the directional tuning changed over time, with a peak initially for movements to the left \( (25\%) \) and thereafter for movements back and to the right for the second half of the movement \( (\text{Fig. 4; compare rows 4 and 5, right column}) \). Although the pattern of directional tuning could differ across digits and time, it remained consistent across conditions \( (\text{Fig. 4; compare colors in each plot}) \).

To further examine differences in grasp force across directions and conditions, the mean amplitude of grasp force for each direction (as shown in Fig. 4) was fit to a cosine function \( (\text{Eq. 1}) \). The resulting phase of the cosine fit is equivalent to the preferred direction \( (\text{PD}) \) of grasp force for each digit at each time epoch. A summary of the PDs computed for normal grasp forces for each subject, digit, and condition is shown in Fig. 5, where each symbol corresponds to a single subject and filled symbols indicate a significant fit \( (\text{linear regression, } P < 0.05) \). For each subject, PDs were similar across conditions, although to some extent each subject exhibited idiosyncratic behavior. Within a single condition \( (\text{Fig. 5, columns}) \) it is clear that the directional tuning of some digits was more variable across subjects than others, particularly for the thumb and index finger. It is also apparent that the directional tuning of the ring finger tended to be more pronounced because there were more significant fits (filled symbols) than for the thumb and index finger. Figure 5 also demonstrates the consistency of subjects’ preferred directions across conditions, such that the angular differences in PD between conditions were typically within one movement direction \( (\text{i.e., } \leq 45^\circ) \) for a single subject \( (\text{Fig. 5, compare columns}) \). This result is consistent with our observation that maximum grasp force amplitudes tended to be similar across conditions \( (\text{compare colors in each polar plot; Fig. 4}) \).

Consistent with previous work, the first experiment demonstrated that during horizontal transport there is a transient increase in grasp force. Furthermore, this experiment revealed that modulation of grasp force amplitude was greatest when a weight was fixed below the contact plane and had a predictable effect on the inertial forces during transport \( (\text{Figs. 3 and 4}) \). Preferred directions of grasp force were also observed and
Contact force could be the result of active force modulation resulting from changes in muscle activation or from the mechanical interaction of the inertial properties of the manipulandum and a stiffened hand (or both). Therefore to examine the extent to which these contact force modulations are the result of active changes in hand muscle activity, in a second experiment we recorded hand muscle activity simultaneously with force and position.

The second experiment studied the weight down and pendulum manipulandum configurations to focus on differences arising from predictable versus less-predictable inertial forces that resulted from a fixed versus variable CM position. Movement directions were limited to center-out: forward, right, backward (toward body), and left. This subset of movement directions was chosen because they result in the extremes of pendulum movement. Because the pendulum was restricted to movement in the Y–Z plane, its effect should be maximal for forward and backward movements and minimal for movements to the right and left.

Figure 7 presents a summary of the EMG and force data collected from one subject during the second experiment. For each muscle and digit, mean EMG and force data, respectively, are shown (clockwise) from the forward, right, back, and left movements from the weight down and pendulum conditions (black and gray lines, respectively). For several muscles, EMG activity was directionally tuned; large early bursts of activity can be seen for some directions, whereas in the opposite direction there is a smaller increase followed by tonic activity through the end of the movement. This pattern of activity is most pronounced in FD (compare left/back to right/forward directions). Directionally tuned activity was also apparent in the thumb muscles; for both APB and FPB, movements to the right had a large initial burst of EMG activity at movement onset.

In principle, the resultant forces and moments acting about the object during transport can be defined by the general equations of motion (Eqs. 6–8). However, in the case of the pendulum, the inertial forces of the pendulum must also be included. The pendular motion depends on the acceleration of the platform of the manipulandum and on the resonant frequency of the pendulum mass (Eq. 5). Figure 6 illustrates the effect of the pendular mass on the inertial forces. The plots illustrate the results for one trial in which the manipulandum was moved in the -Y direction (backward). Figure 6A shows that the acceleration of the pendulum is out of phase with the acceleration of the platform of the manipulandum. For example, the initial acceleration of the manipulandum results in an acceleration of the pendulum in the opposite direction. This illustration also shows that the subject was not able to completely stabilize the manipulandum because the platform as well as the pendulum exhibited damped oscillations.

The contact forces must compensate for the sum of the resulting inertial forces (Eqs. 9 and 10). Indeed, the time course of the sum of the contact forces follows that of the total inertial force (dotted and solid lines, respectively), with oscillations in the contact force reflecting oscillations in the inertial force (Fig. 6B). A regression analysis showed a high degree of correlation between the inertial and contact forces in the Y-dimension for all trials (r² values ranging from 0.82 to 0.96). Thus the effect of the pendulum can be seen in the sum of contact forces in the Y-dimension as is required by Newtonian mechanics.

To what extent are these force oscillations reflected in the contact forces of each of the digits? Figure 6C shows that although not obligatory, in this case oscillations did occur in the contact forces at all three transducers. These oscillations in
difficult to identify a single muscle with a strong relation to the pendulum acceleration, given that the $r^2$ values ranged from 0 to 0.475, with only 12 of 32 cases having a statistically significant fit (Table 1, values in bold). Furthermore, slopes of the regression were modest ($-0.02$ to $0.48$). Similar results were obtained when lags up to $\pm25\%$ of movement time (about 175 ms) were used for the regression. Therefore patterns of activity from single muscles were not related to the oscillation of the pendulum. However, because effects of the pendular oscillation could result in force oscillations at more than one contact point (Fig. 6C), the combined activity of hand muscles may be more capable of representing force oscillations at a single contact point. Therefore stepwise multiple regression was used to examine whether the force modulations were the result of modulations in muscle activity at multiple digits.

The first model in the multiple regression was used to assess whether patterns of thumb muscle activity (APB and FPB) could account for fluctuations in thumb normal force (Thumb-only model). Alternatively, the thumb normal force may also at least partially reflect the activation of ring and index finger muscles, which must push against the thumb because of the constraints of the tripod grasp. Therefore a second model of muscle activity, which included grouped hand muscle activity from each digit (four-variable model; see Methods), was also used to fit thumb normal force. Figure 8 is a summary of results from two subjects for each model and condition. For subject 1 (Fig. 8, top panels) similar weighting for thumb muscles was found across conditions for both thumb-only and four-variable models (bar graphs). Below each bar graph, the force (black line) and model generated fit (gray line) are shown for comparison. The traces are a concatenation of the results for the four directions and span the same time frame used in Fig. 7. For subject 1 the fit is fairly good for both conditions and is similar between models. Note that there is not a marked

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<th>Subject 1</th>
<th>Subject 2</th>
<th>Subject 3</th>
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<td>$\beta$</td>
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<td>$r^2$</td>
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Slope ($\beta$) and $r^2$ values computed from the regression of EMG activity from a single muscle onto pendulum acceleration are shown for each muscle and subject. Values in bold indicate a significant fit ($P < 0.05$).
improvement when additional hand muscles are added, i.e., thumb-only model versus four-variable model. Subject 2 also had similar weighting across conditions (Fig. 8, bottom bar graphs), although the fits of the models were quite different; the result from the four-variable model followed the force data much better than the thumb-only model (compare left and right columns in bottom panels, Fig. 8). Table 2 gives the $r^2$ values for all subjects for the two models and demonstrates that for subject 1 there is only slight improvement from the thumb-only to the four-variable model. This suggests that for subject 1, the force modulation at the thumb results largely from activation of the thumb muscles. For the other three subjects, the fit was improved considerably by the addition of the muscle activity from the other digits (four-variable model). Thus in these instances, the normal force measured at the thumb contact is at least partially explained by the modulation of muscle activity at other digits. Changes in muscle activity could result in increased contact force or stiffness at the corresponding digit during the movement. Furthermore, changes in force and/or stiffness at the index and/or ring finger indirectly affect the contact force measured at the thumb arising from the equilibrium constraints of the tripod grasp.

**DISCUSSION**

**Summary of results**

Consistent with a previous study (Smith and Soechting 2005), horizontal grasp forces tended to increase transiently during transport, appeared to be more closely related to velocity than to acceleration, and were directionally tuned in an idiosyncratic manner for each subject. Comparison across experimental conditions revealed that the amplitude but not the time course of the grasp force modulation was affected by the CM position. Specifically, when the CM was fixed below the contact plane, resulting in the generation of predictable external torques, the amplitude of grasp force increased. However, the idiosyncratic directional tuning was relatively consistent across conditions.

An examination of muscle activity for the weight down and pendulum conditions in the second experiment revealed directional preferences for bursting activity in most hand muscles. However, regression analysis failed to reveal a clear explanation of the effect of the pendular oscillation in the muscle activity (Table 1). Furthermore, multiple regression analysis revealed that muscles other than those of the thumb contributed to the contact force measured at the thumb. These results suggest that the modulation of grasp force is at least partially explained by elastic forces at each of the digits arising from muscle contraction.

**Grasp stability**

Previously, Smith and Soechting (2005) suggested that the increase in grasping force during movement was associated with object stabilization. The results of the current study support this idea because the amplitude of grasp force was increased when potentially larger external torques resulted from the CM position, i.e., in the weight down condition. Results of our second experiment demonstrated that increased muscle activity at one digit can at least partially explain the force observed at the corresponding digit.
modulation of muscle activity at a digit can result in an increase in contact force at an opposing digit due to the stiffness of the hand, i.e., the mechanical interaction of the object and the stiff hand. Therefore as suggested by Gao et al. (2005), the modulation in grasp force is a representation of a neuromuscular strategy and it also arises from mechanical interactions.

The pendulum condition was used to further examine the control strategy for stabilization and to specifically examine the extent to which sensory information played a role in the modulation. Because the pendulum condition resulted in complex external torques, if grasp force was modulated based on sensory feedback, the effect of the pendulum should have been apparent in the EMG with a lag. However, regression analysis revealed no consistent relation between the pendular motion and muscle activity (Table 1), even though the effect of the pendulum was apparent in the forces at each digit (Fig. 6C). An analysis of EMG activity indicated that the forces recorded at each transducer resulted in part from the activation of muscles at remote digits. This analysis suggested that the recorded forces resulted in part from the interaction of the manipulandum with compliant digits. Therefore it seems that grasp stability is maintained even under somewhat unpredictable conditions by altering the stiffness at one or more digits. Stiffness control has also been implicated in other tasks such as pushing on a pivoting stick (Rancourt and Hogan 2001) and catching a ball (Lacquaniti et al. 1992).

We did not observe short-latency EMG responses to the oscillatory load. Such responses have been observed when the load force is altered unpredictably (e.g., Cole and Abbs 1988; Johansson et al. 1992a,b). However, our experimental condition differed in two fundamental aspects. First, the vertical load force did not change; instead the horizontal contact forces were affected by the movement. Furthermore, the changes in force were gradual rather than abrupt. Conceivably, such gradual changes in force could be adequately controlled by an anticipatory mechanism (e.g., Witney and Wolpert 2007; Witney et al. 2000) such as impedance control, even when the prediction is not entirely accurate.

Therefore we propose that for our task, cocontraction of muscles was utilized to compensate for the somewhat unpredictable inertial forces introduced during the movement by altering stiffness at the digits. A diagram illustrating this is shown in Fig. 9, where contact forces can be viewed as the result of altered stiffness at one or more joints through cocontraction of flexor and extensor muscles and/or increased flexor muscle activity. Cocontraction would stiffen each spring and an increase in flexor muscle force at one digit would then produce an increase in recorded force at opposing digits by compressing their springs. As illustrated by comparing the data of two subjects in Fig. 8, the modulations in stiffness allow for the use of different control strategies to achieve the same goal of grasp stabilization, which serves to maintain the object orientation during the grasp. Furthermore, using intrinsic stiffness eliminates the need for precise feedforward prediction (Flanagan et al. 2003; Kawato 1999) and does not suffer from the time delays inherent in feedback.

In conclusion, to maintain grasp stability during horizontal translation, the neuromuscular control system compensates for predictable as well as somewhat unpredictable inertial properties of objects during movement by using the inherent stiffness of the hand through cocontraction and modulation of hand muscle activity.

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REFERENCES


