Multi-Digit Control of Contact Forces During Rotation of a Hand-Held Object

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Winges SA, Eonta SE, Soechting JF, Flanders M. Multi-digit control of contact forces during rotation of a hand-held object. J Neurophysiol 99: 1846–1856, 2008. First published January 30, 2008; doi:10.1152/jn.01238.2007. Rotation of an object held with three fingers is produced by modulation of force amplitude and direction at one or more contact points. Changes in the moment arm through which these forces act can also contribute to the modulation of the rotational moment. Therefore force amplitude and direction as well as the center of pressure on each contact surface must be carefully coordinated to produce a rotation. Because there is not a single solution, this study sought to describe consistent strategies for simple position-to-position rotations in the pitch, roll, and yaw axes. Force amplitude and direction, and center of pressure on the contact surfaces (and thus the moment arm), were measured as human subjects rotated a 420 g force-transducer instrumented object, grasped with the thumb, index and ring fingers (average movement time: 500 ms). Electromyographic (EMG) activity was recorded from five intrinsic and three extrinsic hand muscles and two wrist muscles. Principal components analysis of force and EMG revealed just two main temporal patterns: the main one followed rotational position and the secondary one had a time course that resembled that of rotational velocity. Although the task could have been accomplished by dynamic modulation of the activity of wrist muscles alone, these two main dynamic EMG patterns were seen in intrinsic hand muscles as well. In contrast to previous reports of shifting in time of the phasic activity bursts of various muscles, in this task, all EMG records were well described by just two temporal patterns, resembling the position and velocity traces.

INTRODUCTION

To rotate a hand-held object, forces and moments must be carefully coordinated to produce the desired rotation while maintaining a stable grasp. The partitioning of forces and moments will be dependent on the type of grip used to hold the object. In the simplest case, the thumb opposes a finger in a two-digit grip, and a moment about the desired axis is produced. This could be achieved by altering the direction and amplitude of the force vector at one or both digits. Additionally, changes in the moment arm achieved through adjustments to the centers of pressure at the contact points could also contribute to the moment about the object. Thus even for the simplest grip type, rotation of a hand-held object can be achieved in several different ways.

Previous studies have found that when objects are rotated using a thumb-index grip, grip forces change in proportion to the amplitude of rotation about a horizontal axis (Goodwin et al. 1998; Johansson et al. 1999) and angular speed of wrist motion (Werremeyer and Cole 1997) and are linearly related to the load force at each digit. For a thumb-index grip combined with wrist flexion, Werremeyer and Cole (1997) also found that two finger muscles, first dorsal interosseus (FDI) and flexor digitorum superficialis (FDS), are recruited along with a wrist flexor, flexor carpi radialis (FCR). Thus recruitment of both intrinsic and extrinsic finger flexors may contribute to the increase in grip force observed during wrist flexion movements. Therefore even in the simplest case of a two-digit grasp, the patterns of force and muscle activity may vary depending on the specific task requirements.

If rotation of a hand-held object is performed using a three-digit tripod grip, the number of possible solutions (in terms of patterns of forces and muscle activity) increases substantially. A static tripod grasp is characterized by opposing horizontal forces that intersect at a force focus within the plane of the contact points (Baud-Bovy and Soechting 2001; Yoshikawa and Nagai 1991), and the sum of the moments with respect to the pitch, roll, and yaw axes must equal zero to prevent rotation. Therefore to produce a rotation from a static hold, characteristics of the contact forces such as direction and amplitude must be modulated at one or more contacts. Changes in static or dynamic moments of force can also be produced by altering the center of pressure locations at each contact point, resulting in a change in the moment arm through which the applied forces act on the object. Therefore force direction and amplitude as well as the center of pressure at each contact point must be coordinated to produce the desired rotation. Because rotation of a hand-held object could be achieved by using various combinations of forces, it is unclear whether specific strategies are preferred for certain rotations. Furthermore, patterns of muscle activity during rotation could reflect a contribution to the grip force and/or a general stiffening of the hand resulting in a specific force pattern due to the interaction of the object and a stiffened hand as demonstrated during object translation (Winges et al. 2007).

This study was designed to examine the extent to which unique strategies are utilized to produce rotations of a hand-held object. Specifically, we examined patterns of center of pressure, force direction, and amplitude as well as arm and hand muscle activity during hand-held object rotation using a tripod grip. We found that grip force increased monotonically for all rotations following the time course of the rotation. We also found changes in the direction of grip force and center of pressure that result primarily from the interaction of a stiff hand with a rigid object rather than from active muscular control. Activity in finger flexors was consistent with increases in grip force and thus dynamic stiffening of the hand during the rotation.

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METHODS

Nine subjects (4 male, 5 female, 21–62 yr, 1.58–1.83 m in height, 6 right-handed, 1 left-handed, and 2 ambidextrous) participated in the study. The experimental protocol was approved by the University of Minnesota’s Institutional Review Board, and all subjects gave informed consent prior to the experiment.

Instrumentation

Subjects grasped an instrumented 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-diam 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 parallel to the frontal plane of the subject. Forces and torques from the transducers were sampled at 1 kHz, and the three-dimensional orientation of the object was sampled at 60 Hz using a Polhemus Fastrak system. Force and orientation data were low-pass filtered (4th-order Butterworth, 10-Hz cut-off frequency) prior to 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 above the base platform (which had a mass of 200 g; illustrated in Fig. 1D) so 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 (illus-
averaged across subjects. Results from individual subjects were then compared with the overall average. The center of pressure (CP) at each digit was computed as

$$\text{CP}_x = \frac{M_{x_i}}{F_{yi}}$$

$$\text{CP}_z = \frac{-M_{z_i}}{F_{yi}}$$

where $M_{x_i}$ and $M_{z_i}$ are the torque measured at the $i$th contact point in the $x$ and $z$ dimensions, respectively, and $F_{yi}$ is the normal force measured at the $i$th contact point. Force vectors were computed as the resultant of the normal and tangential forces and were assumed to originate from the CP at the respective digit.

ANOVA's were used to determine the effect of weight location and rotation (independent variables) on movement variables and force amplitude relative to baseline (dependent variable). A significance level of 0.05 was used for all analyses. All values are mean ± SE unless otherwise noted.

The EMG signal for each muscle was rectified and then low-pass filtered at 20 Hz (d'Avella et al. 2006) prior to analysis. Mean EMG traces for each muscle were computed across trials for each rotation in each condition. These mean EMG waveforms were then normalized to the maximum amplitude observed for that muscle during the entire experiment.

FIG. 2. Force, angular velocity, and rotation. Time-normalized mean data from all subjects for each condition are shown for forward and backward rotations. Dashed vertical lines, onset and offset of rotation as defined by 5% of the peak velocity. Solid black line, weight-up condition; dashed black line, weight-down condition; gray lines (bottom panels), “off-axis” angular velocity and rotation and show that rotations were primarily about the “target” axis. Mean forces $(F_x, F_y, \text{ and } F_z)$ measured at the thumb (T), ring (R), and index (I) transducers are shown. y-axis ranges for $F_y$, $F_z$, and $F_x$ are 2.0–8.0 N, 1.0–5.0 N, and 1.0–1.0 N, respectively. On $F_x$ and $F_z$ plots, gray y-axis ticks denote 0 N.
Principal component analysis

Principal component (PC) analysis was used to characterize the patterns of forces utilized for producing object rotations for each object configuration, i.e., weight up and weight down. A PC analysis was performed using the Matlab “princomp” function as described in Klein Breteler et al. (2007). The inputs to the PC analysis of force were the contact forces (\(F_x, F_y, \text{and } F_z\)), from 25% before rotation onset to 25% after rotation offset (from individual subjects and averages over all subjects) for each digit and each rotation. In this analysis, we used the covariance matrix of 54 force traces (3 digits \(\times 3\) forces \(\times 6\) rotations). Each force waveform could be perfectly reconstructed as the average force magnitude of each contact force for each dimension (\(F_x, F_y, \text{and } F_z\)) plus a weighted sum of the 54 PCs. Cross-correlations of weighting coefficients were performed to illustrate which forces tended to change together. PC analysis revealed that PC1 accounted for \(>85\%\) of the variance and PC2 accounted for \(\sim 13\%\) of the variance. PC3 never contributed \(>1\%\), therefore only PC1 and PC2 were included in the cross-correlation analysis.

PC analysis was also performed on EMG data; however, the input for the EMG PC analysis was the mean amplitude normalized EMG signal, over the same time interval, computed across weight-up and -down object configurations, for each subject. The PC analysis was performed on individual subjects because EMGs tended to be more variable across subjects. The analysis used the covariance matrix from 60 EMG traces (10 muscles \(\times 6\) rotations). Each EMG trace could be perfectly reconstructed as the average EMG magnitude of each muscle plus a weighted sum of the 60 PCs. To examine patterns across subjects, the mean PCs as well as the weighting coefficients were computed. Cross-correlations of the mean weighting coefficients were performed to illustrate which muscles tended to change together. Similar to the force PC analysis, PC1 accounted for \(>80\%\) of the variance, PC2 accounted for \(<10\%\) of the variance, and PC3 never contributed \(>3\%\) of the variance. Therefore only PC1 and PC2 were included in the cross-correlation analysis.

Results

As shown in Fig. 2 for pitch, subjects performed six different target rotations with mean (\(\pm SD\)) rotations of \(68 \pm 7\) and \(65 \pm 5^\circ\) for the weight up (solid lines) and weight down (dashed lines) condition (see Fig. 1, C and D). The mean off-axis rotations were small with a range of \(0–10^\circ\). There was no difference in the extent of the target rotation (\(P = 0.52\)) in the two conditions; however, larger off-axis rotations were observed for the weight down compared with the weight up condition (\(6 \pm 4, 3 \pm 3^\circ\), respectively; \(P < 0.05\)). During pitch and roll rotations, translations of the object’s center of mass ranged from \(7–11\) and \(2–5\) cm for the weight-up and -down conditions, respectively. Although the translations were larger for the weight-up condition, they were on the same order of magnitude and of the same sign as translations that would result from a rotation about the wrist with a rigid hand. Translations during the yaw rotations were smaller than the pitch and roll rotations and were similar across conditions. The mean movement times were \(482 \pm 20\) and \(533 \pm 42\) ms for the weight-up and -down conditions, respectively, and there were no significant differences across condition or rotation. Accordingly, there were no differences in peak angular velocity across condition or rotation (\(P > 0.05\)).

Contact forces

The force patterns reflect changes due to gravitational and angular acceleration components during the rotations. For example, during pitch rotations, the load is transferred from \(F_z\) at all contacts to \(F_x\) at one or two contacts resulting in a relatively slow monotonic increase in \(F_x\) at the respective digits (Fig. 2). For forward (positive pitch) rotations, the load is transferred to the thumb, which is reflected as a large increase in amplitude of \(F_{Rx}\) during the rotation. Conversely, during backward rotations (negative pitch) the load is transferred to the ring and index finger contacts (\(F_{Ry}\) and \(F_{Rz}\)). The rotations also required that the contact forces produce a force couple. When the CM was in the plane of the contact points (weight up), the inertial torque due to angular acceleration was small (\(<0.005\) Nm). In the weight-down condition, the inertial torque for pitch and roll was larger (\(<0.015\) Nm). By comparison, the static gravitational torque in the weight-down condition for pitch and roll was an order of magnitude larger (\(<0.09\) Nm). Assuming a contact force of 5 N, a change in its moment arm on the order of 1–3 mm could produce inertial torques for a rotation. By contrast, for the weight-down condition, balancing the gravitational torque would require a substantially larger change in moment arm (\(<18\) mm).

Force patterns during roll rotations exhibited similar patterns with respect to changes in load distribution and modulation due to angular acceleration. In roll rotations, the load was transferred to the thumb and one digit, either the ring or index finger during left or right rotations, respectively. This was reflected by expected changes in the tangential force at the thumb contact and changes in the normal force at the ring or index finger. Although the load on the thumb after rotation was tangential to the contact surface (\(F_{Rx}\)), increases in thumb normal forces were also observed during roll rotations. The average (\(\pm SD\)) increases in thumb normal force during left and right rotations were \(1.99 \pm 1.63\) N and \(3.96 \pm 2.42\) for the weight-up condition and \(5.44 \pm 1.90\) N and \(7.88 \pm 2.17\) N for the weight-down condition.

For yaw rotations, where the load direction remains the same, changes in tangential force (\(<1.0\) N) were observed at each digit, consistent with the direction of rotation. Monotonic increases in normal force at each contact that peaked after 50% of the rotation were also observed during yaw rotations. Average (\(\pm SD\)) increases in normal force during yaw rotations were \(2.00 \pm 0.24\) N for the thumb, \(1.68 \pm 0.70\) N for the ring finger, and \(1.26 \pm 0.12\) N for the index finger. One exception to this observation was \(F_{Ry}\) as the average (\(\pm SD\)) increases during roll rotations were \(2.17 \pm 0.87\) N. During clockwise rotations for the weight-up condition, which peaked around 25% of the rotation, the load was transferred from \(F_{Rx}\) to \(F_{Ry}\) at all contacts to \(F_{Rx}\) at one or two contacts resulting in a relatively slow monotonic increase in \(F_x\) at the respective digits (Fig. 2). For forward (positive pitch) rotations, the load is transferred to the thumb, which is reflected as a large increase in amplitude of \(F_{Rx}\) during the rotation. Conversely, during backward rotations (negative pitch) the load is transferred to the ring and index finger contacts (\(F_{Ry}\) and \(F_{Rz}\)). The rotations also required that the contact forces produce a force couple. When the CM was in the plane of the contact points (weight up), the inertial torque due to angular acceleration was small (\(<0.005\) Nm). In the weight-down condition, the inertial torque for pitch and roll was larger (\(<0.015\) Nm). By comparison, the static gravitational torque in the weight-down condition for pitch and roll was an order of magnitude larger (\(<0.09\) Nm). Assuming a contact force of 5 N, a change in its moment arm on the order of 1–3 mm could produce inertial torques for a rotation. By contrast, for the weight-down condition, balancing the gravitational torque would require a substantially larger change in moment arm (\(<18\) mm).

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Results of the PC analysis captured these observations of force patterns. For the weight-up and -down conditions, PC1 accounted for 86 and 95% of the variance, whereas PC2 accounted for 12 and 4% of the variance, and PC3 accounted for 1 and 0.7% of the variance, respectively. The time course of PC1 was very similar to the time course of rotation with a temporal offset, PC1 leading rotation by \(<100\) ms (cf. Fig. 2). This was also indicated by large \(R^2\) values from regressions of PC1 onto rotations for individual subjects (mean \(R^2 = 0.87\), range: 0.39–1.00) and averaged data (mean \(R^2 = 0.89\), range: 0.85–0.92). For weight-up and -down conditions, PC1 had a
similar temporal pattern, namely a gradual monotonic change in amplitude, with a larger amplitude for the weight down condition (Fig. 3A). Thus the monotonic increase observed in PC1 is associated with the gravitational component of the rotation. The weighting of each force variable onto PC1 is shown in Fig. 3B for the weight-down condition. Positive weighting of this component for normal forces at each contact for all rotations reflects the tendency for normal forces to increase during the rotation, even for yaw rotations when load did not change (Fig. 3B, top). Furthermore, larger weightings occur when the load was transferred to that contact, for example, the thumb normal force has a larger weighting on PC1 for the forward compared with backward rotation. Paired t-test revealed $F_{Ty}$ weights were 95% higher for forward versus backward rotations ($df = 18, P < 0.05$), $F_{Rx}$ weights were 81% higher for left versus right rotations ($df = 18, P < 0.05$), and $F_{Tx}$ weights were 83% higher for right versus left rotations ($df = 18, P < 0.05$) for the weight-up condition. Smaller nonsignificant differences ranging from 38 to 73% were observed for the weight-down condition. Relatively large negative PC1 weightings for $F_{Tz}$, $F_{Rx}$, and $F_{Ty}$ for the forward, left, and right rotations, respectively, denote rotations where there was an obligatory sign change at that contact (see Fig. 2, $T_z$, forward rotation).

PC2 reached its maximum coincident with the peak angular velocity, similar to the modulation in grasp forces observed during translation (Smith and Soechting 2005; Winges et al. 2007). This component was substantial for $F_{x}$ and $F_{z}$ for pitch and roll rotations (Fig. 3B), and these forces could contribute to pitch and roll rotations by producing moments. Regression analysis was performed to examine the extent to which PC2 was associated with angular velocity. Mean $R^2$ values from regressions of PC2 onto angular velocity were 0.79 (range: 0.22–0.99) for individual subjects and 0.90 (range: 0.83–0.96) for averaged data. The third PC, which was consistently small, resembled the angular acceleration profile, reflecting the inertial component of the motion. Regression analysis of PC3 onto angular acceleration revealed a weak relation with mean $R^2$ values of 0.34 (range: 0.02–0.76) for individual subjects data and 0.45 (range: 0.33–0.59) for averaged data.

**EMG**

We recorded EMG activity from five extrinsic and five intrinsic hand and wrist muscles during the rotations (Fig. 4). Although the magnitude of muscle activity for a given muscle varied across subjects for a single rotation, consistent temporal patterns of muscle activity were observed across subjects and conditions. In the following, we will describe the patterns of muscle activity that were common across all subjects. For each rotation, specific sets of muscles tended to have activity characterized by monotonic increases around the onset of the rotation to a peak near 50% of the rotation, followed by a gradual decay to a level higher than that at the onset of rotation.

![Fig. 3. Principal components and weights. A: principal components (PCs) 1–4 are shown for the weight-up and -down condition for the force analysis and the electromyographic (EMG) analysis (left to right, respectively). The time course is ~25–125% of the rotation with vertical dashed lines indicating rotation onset and offset (0 and 100%, respectively). B: weightings of force variables onto PC1 (top) and PC2 (bottom) for each rotation (color legend). C: weightings of EMG variables (color legend) onto PC1 (top) and PC2 (bottom) for each rotation.](http://jn.physiology.org/)

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This pattern of activity was exemplified by ED and ECU during forward rotations. Other muscles such as FCU (FWD rotation) and LUMr (BWD and LFT rotation) exhibited a sustained increase in activity. Rotation specific muscle activation patterns were observed for all extrinsic hand muscles we recorded (Fig. 4, 1st–5th rows). For pitch rotations, ED and ECU were activated during forward rotations but showed only small changes in activity during backward rotations; conversely, activity in FD, FD2, and FCU increased by a small amount during forward rotations with much more marked activity during the opposite backward rotation (Fig. 4, 1st and 2nd columns). Thus these sets of muscles appear to be antagonistic for pitch rotations, but this pattern is not maintained for roll and yaw rotations. For example, during roll rotations to the right and yaw clockwise rotations, ECU was activated in concert with FD, FD2, and FCU.

Rotation specific patterns of muscle activation are expected for extrinsic hand muscles because they contribute to wrist motion. However, although there was more variability across subjects than for the extrinsic hand muscles, similar patterns were also observed in the intrinsic hand muscles (Fig. 4, 6th–10th rows). For pitch rotations, all intrinsic muscles exhibited some increase in activity, but their patterns of activation were not consistent across subjects. For left roll rotations, each of the intrinsic muscles tended to have a sustained increase in activity in all subjects. Finally, during clockwise yaw rotations, LUMr exhibited an increase in activity in all subjects that reached a peak at 25–50% of the rotation followed by a decay to a level higher than that at rotation onset. Other intrinsic muscles showed small changes in activity that were not consistent across subjects. Note that although not typical, for the subject shown in Fig. 4, the thumb muscles (APB and FPB) also exhibited increased activity for the weight-up condition during clockwise rotations. During counterclockwise yaw rotations, in all subjects APB and FPB exhibited large increases in activity that peaked around 50% of the rotation followed by a gradual decay, while FDI exhibited a similar pattern with a smaller amplitude increase.

Therefore extrinsic as well as intrinsic hand muscles are actively controlled in a manner that is specific to the direction of the rotation being performed.

Because the patterns of EMG activity tended to be similar for the two conditions (weight up and weight down), the PC analysis was performed on EMG averaged across conditions. The resulting PCs for EMG were similar to those obtained in the force PC analysis (Fig. 3A) and were consistent with our observations of the EMG activation patterns. PC1, which accounted for 80% of the variance, reflects the monotonic increase to a peak, followed by a gradual decay described in the preceding text. PC2, which accounted for 9% of the variance, was phasic, with an early onset of EMG activity peaking after peak acceleration. The weighting of each muscle’s EMG onto PC1 and PC2 is shown in Fig. 3C. For pitch rotations, the weighting coefficients of PC1 were largest for
ED and ECU in the forward direction but were near zero in the backward direction, whereas the opposite pattern was seen in FD, FD2, and FCU. The FDI was the only intrinsic muscle with a relatively large difference in weighting across pitch rotations, i.e., nearly zero for forward rotations and the largest weighting among intrinsic muscles for backward rotations (Fig. 3C, top). For roll rotations, FD, FD2, and FCU had small weightings for the left rotations that increased threefold for the right rotations, whereas the opposite was observed for ECU. APB, FPB, and LUMr had relatively large weightings that were consistent across roll rotations, whereas FDI and LUMi weightings were small but larger for right compared with left rotations. For the yaw rotations, ECU, followed by FCU and LUMr, had the largest weighting coefficients for clockwise rotations but were near zero for the counterclockwise rotations. The opposite was observed for APB, FPB, and FDI (Fig. 3C, top).

PC2 weightings were positive and relatively large for LUMr during both yaw rotations and ECU during clockwise rotations; this is consistent with the early onset of EMG activity observed for these muscles (Fig. 4). Relatively large negative PC2 weighting of APB and FPB for the left rotations is consistent with the late onset of phasic EMG observed during this rotation. In summary, the weighting of the first two PCs for EMG data described above captured the overall EMG patterns (Fig. 3), suggesting that two basic rotation specific EMG patterns can account for the control of hand-held object rotation.

Force and EMG patterns

To examine the extent to which patterns of force (in different digits) and EMG modulation (in different muscles) were consistent across rotations, we performed cross-correlations on the PC1 and PC2 weighting coefficients for pairs of force components and EMGs (Fig. 5). We computed a cross-correlation matrix and reordered the columns and rows of this matrix to show highly correlated variables next to each other. The warm colors (i.e., red) indicate positive correlations between weightings while the cool colors (i.e., blue) indicate negative correlation. A strong positive correlation between weights from two or more input variables may indicate a synergistic relation between the respective pairs of forces or muscles.

The most obvious patterns among the force weightings were illustrated by a strong positive correlation of normal force ($F_n$) across pairs of digits (Fig. 5, left). The strongest positive correlations across pairs of EMG weighting coefficients are found for combinations of FD, FD2, FCU, LUMi, and LUMr. Additionally, intrinsic hand muscles exhibit strong positive correlations with other intrinsic muscles that act on the same digit, i.e., FDI and LUMi, as well as APB and FPB (Fig. 5, top right). Weaker positive correlations are observed across the thumb and index intrinsic muscles (APB, FPB and FDI, LUMi). This pattern is consistent with force patterns since these muscles contribute to the production of normal force ($F_n$) at the contacts which are highly correlated with one another. However, APB and FPB have strong negative correlations with FD, FD2, and LUMr indicating reciprocal activation across these muscles for hand-held object rotations.

The strength of correlations across force variables for PC2 was similar to PC1 although the correlations were stronger when RZ was paired with IY or TY. Correlations across EMG PC2 weights also had similar patterns to PC1, although the strength of correlations between LUMi and APB or FPB was stronger, whereas correlations between LUMi and FD or LUMr were weaker. Because PC2 is associated with early onset of EMG, strong relations between intrinsic thumb and index finger muscles suggest that intrinsic thumb and index muscles tend to have similar onset times. The finding of correlations across both extrinsic and intrinsic muscles is important because it shows active control of the intrinsic muscles with respect to the rotation movement, the alternative being co-contraction among all intrinsic hand muscles to maintain a stiffened hand during the rotation.

CP and force direction

As noted in the INTRODUCTION, a moment of force could be produced by shifting the CP at one or more digits. CP changes in the horizontal x dimension were largest during yaw rotations.
and were consistently in the direction of the rotation at all three contacts (Fig. 6, bottom), whereas changes in the z direction tended to be larger for pitch and roll rotations. There was no difference across conditions (weight up and weight down) in the magnitude of CP changes for CP_x or CP_z at any contact (P > 0.05). Overall, mean (±SD) changes in CP were small: 2.00 ± 0.91 and 2.39 ± 0.31 mm for the x and z dimensions, respectively. At the thumb contact, CP_x changes were largest for clockwise rotations (4.42 ± 0.22 mm; P < 0.001) whereas CP_z changes were largest for forward and backward rotations (2.95 ± 0.23 and 2.65 ± 0.23 mm, respectively; P < 0.001). At the ring finger contact, CP_x changes were larger for clockwise compared with right rotations (3.10 ± 0.31 and 1.54 ± 0.31 mm, respectively; P < 0.05), whereas CP_z changes were largest for left rotations (4.25 ± 0.32; P < 0.001). CP_x changes at the index finger contact were largest for clockwise and counterclockwise rotations (3.08 ± 0.24 and 2.43 ± 0.24 mm, respectively; P < 0.001) whereas there was no difference in CP_z changes across rotations.

If a force couple responsible for the rotation was produced merely by changing the location of the CPs, one would expect that these changes should be largest for the weight-down...
condition and for pitch and roll rotations and smallest for yaw rotations. Furthermore, one would expect the CP to change only at one digit or to change in opposite directions at opposing digits. Therefore the results show that the force couples did not result purely from an active control of the location of the CP.

In addition to changes in force magnitude and CPs at individual contact points, changes in the direction of force vectors could contribute to the moment required to produce a rotation of a hand-held object. The force vector within the grip plane was computed for each digit to examine how force direction changes with respect to rotation and condition. The largest changes in force vector direction tended to occur ~25% of normalized movement time (Fig. 6, yellow arrows). Furthermore, the results show that the thumb force vector was directed close to perpendicularly to the contact surface (pitch and yaw) or it was directed toward the finger contact to which the load was transferred during roll rotations (Fig. 6, middle). In the latter case, it is noteworthy that this change in the direction of thumb force anticipates the rotation by 50–100 ms in all subjects. During the rotation, the index force vector exhibited the largest direction changes (especially for yaw rotations), whereas the ring force vector exhibited the smallest direction changes that were similar across all rotations.

The mean (±SD) change in force direction was 7.72 ± 2.67° and ranged from 3.62 to 16.45° across all digits, rotations, and conditions. The change in thumb force direction was slightly larger for the weight-up versus -down condition (8.64 and 6.38 ± 0.50°, respectively; P < 0.002), whereas there were no differences across condition for the ring or index force vectors. Figure 6 shows force vectors for each digit from the weight-up condition to illustrate changes in force vector magnitude and direction during the rotations. The change in thumb force direction differed across rotation such that larger changes were observed for the backward and left rotations compared with the forward, clockwise, and counterclockwise rotations (9.83 and 11.58 ± 0.86° vs. 3.64, 6.02 and 6.04 ± 0.86°, respectively; P < 0.001; Fig. 6). The right rotation also had a larger thumb force direction change compared with the forward rotation (7.96 and 3.64 ± 0.86°, respectively; Fig. 6, A and B). There were no differences across rotations for the change in ring force direction (P > 0.05). For the index force vector, direction changes were larger for clockwise and counterclockwise rotations than forward and right rotations (14.62 and 14.47 ± 1.35° vs. 6.98 and 6.33 ± 1.35°, respectively; Fig. 6), and larger for left compared with right rotations (12.40 and 6.33 ± 1.35°, respectively; P < 0.001; Fig. 6B).

Together these results indicate that at the thumb and index, changes in CP and force direction are both utilized to varying degrees for specific rotations. However, as we argue in the DISCUSSION, these changes in CP and force direction are due largely to the interaction of a stiff hand with a rigid object rather than active control.

DISCUSSION

Summary of results

The modulation in grasp forces as well as in the muscle activity of extrinsic and intrinsic hand muscles during object rotation reflects a very simple temporal pattern of control because two principal components were able to account for >80% of the variance. For most rotations, the first PC in force as well as in EMG reflected changes in gravitational load because it was largely similar to the time course of rotation. The second PC, which was phasic, had a time course that was similar to the angular velocity. The description of forces and muscle activity using only two PCs is indicative of synergistic control. Scaling of the amplitude of muscle patterns related to the rotational position and to the angular velocity could account for the modulation of muscle activity observed during hand-held object rotations. Furthermore, rotation specific patterns of muscle activation were expected for extrinsic hand muscles because they contribute to wrist motion; however, these patterns were also observed for intrinsic hand muscles. Therefore extrinsic as well as intrinsic hand muscles are actively controlled with respect to the rotation being performed. The highly negative correlation between the intrinsic thumb muscles and the extrinsic finger muscles and ring lumbral also supports the idea of active control in the intrinsic muscles.

Force patterns

Rotation of a hand-held object can be produced using a variety of strategies. However, across all subjects there were some distinct patterns that emerged for rotations about each axis. For changes in pitch, the thumb and finger force vectors opposed one another. Similar to static grasping, the thumb force vector was typically directed between the two fingers, which is consistent with the thumb opposing a virtual finger created by the resultant of the finger force vectors (Baud-Bovy and Soechting 2001). However, for changes in roll, the thumb tended to oppose only one digit, i.e., the one that would share in supporting the object’s weight at the maximum rotation. For pitch and roll rotations, as force amplitude increased during the rotation, there was very little shift in the CP and the largest changes in force direction tended to occur around 25% of the normalized movement time (see Fig. 6, A and B, yellow arrows). This general strategy was consistent across the weight-up and -down conditions, although the amplitude of the force change was smaller for the weight-up condition.

A different strategy was utilized to produce yaw rotations. Because the object was rotated about the vertical axis, there are no changes in load force thus changes in grip force would not be required to maintain a stable grasp (Burstedt et al. 1999). Nevertheless during the rotation, the magnitude of the force vectors did increase for both weight-up and -down conditions although not to the extent observed for pitch and roll rotations. For yaw rotations, the force direction changed very little at the thumb and ring finger, whereas the CP at each contact did shift to a large extent during the rotations. For clockwise rotations (negative yaw), the CP shifted in the negative direction, whereas the opposite was observed for counterclockwise (positive yaw) rotations. These shifts in CP occurred at all digits and are consistent with rolling of each digit over the surface. This suggests that these changes are passive in nature.

Thus simple force strategies were observed for each rotation. With respect to the grasp plane, forces increased during the rotation whether it was required due to changes in load (for pitch and roll rotations) or not (for yaw rotations). While the CP and force direction also changed at each digit for all rotations, the extent of these changes could be very small.
Furthermore changes in CPs did not always go hand in hand with changes in force direction, rather each rotation tended to be dominated by one or the other. Finally, the observed force patterns were consistent with grasp force being the reflection of a neuromuscular strategy as well as a mechanical interaction between the object and a stiffened hand (Winges et al. 2007). Forces related to acceleration (PC3) were small even though the rotation movements were fast, and rotation specific changes in forces in the contact plane reflected primarily the monotonic shifts in position and/or gravitational load (PC1) and angular velocity (PC2).

Modulations in grip force with load force have been described previously (e.g., Flanagan and Wing 1993; Witney and Wolpert 2007). For example, Zatsiorsky et al. (2005) observed that grip force modulations during vertical cyclic arm movements accounted for changes in load force during the movements. Our results are also relevant to the theoretical studies on robotic grasp control by Arimoto and colleagues (2000, 2001), subsequently extended to human experimental work by Zatsiorsky and colleagues (2004). These authors suggested that the forces generated at the contact surfaces result from the superposition of two commands: one controlling grasping strength and the other controlling object position. Our analysis instead subdivides the forces that rotate and hold the object into those actively controlled by muscle contraction (as reflected in the 1st 2 PCs), those produced by passive interaction between a compliant hand and a rigid object and those due to passive (rolling) changes in the CP.

Patterns of muscle activity

A previous study found that co-contraction and modulation of hand muscle activity contributed to the maintenance of a stable grasp during translation movements by adjusting the stiffness at one or more digits (Winges et al. 2007). Similar to horizontal translation movements, the rotation task could have been completed by co-contracting the intrinsic thumb and finger muscles to maintain a stiffened hand, while wrist and arm muscles produced motion at the wrist. However, EMG recorded from wrist, extrinsic, and intrinsic finger muscles demonstrated a rotation specific pattern for each subject. PC analysis confirmed this observation and revealed that a PC with a slow monotonic increase during the rotation could account for ≥80% of the variance. The time course of this PC was similar to that revealed in the PC analysis of force. Cross-correlation of PC weights for all muscles and rotations revealed synergistic relations across extrinsic and intrinsic finger and wrist flexor muscles across all subjects. Although their task was different, this finding is consistent with the observations of Werremeyer and Cole (1997), who demonstrated parallel changes in the activity of a primary wrist flexor, i.e., flexor carpi radialis, and FDS and FDI, which are extrinsic and intrinsic finger muscles, respectively, during a rapid wrist flexion movement.

If intrinsic muscles are primarily responsible for maintaining a stiffened hand, a relatively strong correlation among all intrinsic muscles might be expected. However, intrinsic finger muscles were more weakly correlated to intrinsic thumb muscles than to other intrinsic finger muscles. This is consistent with force strategies we observed such that for pitch rotations, the thumb opposed the fingers as a unit or a virtual finger, while in roll rotations the thumb opposed only one of the fingers. Therefore these results indicate that intrinsic as well as extrinsic hand muscles are actively controlled during the rotation of a hand-held object.

Although modulation of muscle activity was typically consistent with changes in force, there was no difference in the amplitude of EMG across conditions, whereas this difference was very apparent in the force data. Therefore the modulation of hand muscle activity may be more closely associated with maintaining stiffness at a particular digit to compensate for additional loads as in the case of pitch and roll rotations. This is consistent with observations from a hand-held object translation task where co-contraction and modulation of muscle activity compensated for inertial forces by controlling the stiffness of the hand (Winges et al. 2007).

The simplicity of control of hand muscle activity during hand-held object rotation was evidenced by two PCs accounting for >85% of the variance. In other tasks, previous studies have required three to five PCs to account for a similar amount of variance in muscle activity. Four or more PCs (or muscle synergies) were required to account for 80% of the variance in EMG patterns for dynamic finger spelling (Klein Breteler et al. 2007) and fast reaching movements (d’Avella et al. 2006), whereas static finger spelling and object grasp (without lift) required three to four PCs (Weiss and Flanders 2004) to account for a similar amount of variance in static EMG levels. The results of the current study indicate that two PCs were capable of describing the muscle activation patterns to a large extent during object rotation. In contrast, previous studies have found that multiple muscle synergies are needed to account for the temporal shift in activation of pairs of asynchronously active muscles (d’Avella et al. 2006; Flanders 1991; Flanders et al. 1996; Klein Breteler et al. 2007). Therefore the main difference is that for our task, groups of muscles can be controlled through amplitude scaling of a simple command without a temporal shift, whereas other tasks require additional commands to account for the temporal shift in activation patterns of groups of simultaneously active muscles. Thus our results suggest that a very simple control strategy is utilized for the modulation of wrist and hand muscles during unidirectional object rotations.

One explanation for the simple control strategy we observed is that the muscles are being controlled primarily to counteract the changes due to gravity. This is similar to the static component of EMG found during vertical plane reaching movements, such that the EMG amplitude changes reflected the effect of gravity at different positions in the vertical plane (Flanders et al. 1996). Additionally, Flanders and Hermann (1992) found that two PCs could describe muscle activation patterns during point-to-point movements in the frontal and sagittal plane. They also found that their two PCs could be transformed into tonic and phasic components that could correspond to the forces required to counteract gravity and those that would produce increases in velocity to produce the movement. Thus it seems reasonable that if the hand maintains a rigid posture during unidirectional object rotations, the largest factor governing muscle control could be described by one component concerned with changes due to gravity. Thus a relatively simple control strategy would be sufficient because it would not require the inclusion of asynchronous muscle acti-
vations, something that is an important factor for fast linear movements.

Postural muscle synergies

Other tasks such as those related to posture and balance control have also demonstrated that muscle activation patterns can be reduced down to a few useful control components that are capable of describing muscle activation patterns. During walking, Ivanenko et al. (2004) found that five components could describe patterns of activation for ≤20 muscles during walking. Krishnamoorthy et al. (2003a,b) found that postural adjustments due to shifts in CP during standing could be described by only three PCs. Control of balance has also been studied in cats, and it has been revealed that a small number of muscle synergies are used to control balance when perturbations are made from many different directions (Ting and Macpherson 2005). Thus many tasks that are performed by controlling a large number of muscles and joints can be explained using a few simplified patterns of muscle activity, suggesting that synergistic groups of muscles are utilized to simplify otherwise highly complex control requirements.

Research has shown that for kinematic and kinetic variables associated with grasping, a relatively small number of coordination patterns emerge among digits of the hand (for review, see Schieber and Santello 2004). Synergic activation of muscles and thus production of forces appears to be a consistent component of control for tasks that require a control strategy that encompasses a large number of degrees of freedom. One possible mechanism underlying these coordinated muscle activation and force production patterns is a common neural signal delivered to pools of motor neurons innervating different muscles (i.e., across-muscle synchrony). Modeling has indicated that a moderate level of across-muscle synchrony could contribute to the coordination of hand muscles and the forces they produce (Santello and Fuglevand 2004). Across-muscle synchrony has been observed across extrinsic and intrinsic hand muscles with varying strengths during grasping (Hochensmith et al. 2005; Keen and Fuglevand 2004; McIsaac and Fuglevand 2006; Wang and Santello 2004; Winges et al. 2006, 2008). Although there is still some question as to the extent to which the strength of this common neural input is modified with respect to task, it seems there may be a fixed gradient among hand muscles during static grasping tasks such that common neural input is strongest across extrinsic hand muscles and weakest across combinations of intrinsic hand muscles (Winges et al. 2008). This type control signal could be one of the mechanisms underlying the synergistic control across hand muscles that would allow for the use of a relatively simple control strategy for tasks involving object grasping and manipulation.

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REFERENCES


