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Accurate production of time-varying patterns of the moment of force in multi-finger tasks

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Abstract

We investigated the production of time profiles of the total moment of force produced in isometric conditions by the four fingers of a hand. We hypothesized that these tasks would be associated with multi-finger synergies stabilizing the time profile of the total moment across trials but not necessarily stabilizing the time profile of the total force produced by the fingers. We also expected the multi-finger synergies to prevent an increase in the moment variability with its magnitude. Seated subjects pressed on force sensors with the four fingers of the right hand and produced two time profiles of the total moment of force, starting from a certain pronation effort, leading to a similar supination effort, and back to the initial pronation effort. One of the profiles was a sequence of straight lines (M-Ramp) while the other was a smooth curve (M-Sine). The subjects showed an increase in the total force during each task. This was accompanied by an increase in the force produced by the fingers opposing the required direction of the total moment—antagonist fingers. Variability of the total force and of the total moment showed complex, non-monotonic changes with the magnitude of the force and moment, respectively. In both tasks, the subjects showed patterns of co-variation of commands to fingers that stabilized the required moment profile over trials. The time profile of the total force was stabilized to a lesser degree or not stabilized at all. The share of fingers with larger moment arms (index finger for pronation efforts and little finger for supination efforts) was higher when the fingers acted to produce moments in a required direction but not necessarily when they acted as antagonists. The results demonstrate the existence of multi-finger synergies stabilizing the combined rotational action. They fit a hypothesis that stabilization of rotational actions may be a default strategy conditioned by everyday experience. The data also suggest that the mechanical advantage hypothesis is valid for sets of effectors that act in the required direction but not for sets of effectors that act as antagonists.

Keywords

Synergy; Finger; Force production; Moment of force; Hand

Introduction

Finger action of the human hand has been used in recent studies to address the problem of motor redundancy (Li et al. 1998; Zatsiorsky et al. 1998). In particular, multi-finger action has been analyzed as an example of a motor synergy, a task-specific neural organization of elemental variables that stabilizes an important performance variable (Gelfand and Latash 2002; Latash et al. 2003). Elemental variables were associated either with forces and moments

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of forces produced by individual digits (Shim et al. 2003) or with hypothetical commands to the fingers (finger modes, Latash et al. 2001; Danion et al. 2003). Changes in a finger mode leads to changes in forces produced by all four fingers of the hand because of the phenomenon of enslaving, that is, unintended finger force production (Kilbreath and Gandevia 1994; Li et al. 1998; Zatsiorsky et al. 2000).

To analyze multi-finger synergies that stabilize the total force and total moment produced by a set of fingers during pressing tasks the framework of the uncontrolled manifold (UCM) hypothesis (Scholz and Schoöner 1999) has been used (Latash et al. 2001, 2002a, b; Scholz et al. 2002). The UCM hypothesis assumes that the neural controller acts in a space of elemental variables and creates in that space a sub-space (a UCM) corresponding to a particular desired value of an important performance variable. Then, the controller allows relatively large across-trials variability of elemental variables within the UCM, but not orthogonal to the UCM.

In several earlier studies (Latash et al. 2001; Scholz et al. 2002), the subjects were required to produce particular time profiles of the total force while pressing with the four fingers of a hand on force sensors, and they were given visual feedback on the current value of the total force. Unexpectedly, the subjects stabilized much better the total moment produced by the fingers about the longitudinal axis of the forearm/hand (further addressed as simply “moment” for brevity) although they were not instructed to do so and were given no feedback on the moment magnitude. These findings led the authors to a hypothesis that moment-stabilizing multi-finger synergies are conditioned by everyday experience that imposes much more strict constraints on possible variations of the rotational hand action as compared to those imposed on the gripping action. For example, if one takes a sip from a glass, the gripping force should only be above the slipping threshold and below the crushing threshold, while the rotational action should be controlled precisely to avoid spilling the contents of the glass.

In the current study, we inverted the task and analyzed the ability of humans to produce a prescribed time pattern of the moment of forces generated by a set of fingers when the subjects are explicitly instructed to do so and provided with adequate visual feedback. Given the mentioned importance of accurate moment production in everyday tasks, we see this modification as an important element of novelty of the study. No instruction or feedback was provided on the total force produced by the fingers. As in an earlier study with force production (Latash et al. 2002a), we used both smooth and ramp-like time profiles of the total moment. We expected the subjects to show strong multi-finger synergies stabilizing the moment–time profile while synergies stabilizing the total force were expected to be weak or absent.

The study has also allowed us to address the issue of relations between the magnitude of a mechanical variable and its trial-to-trial variability. Proportional or close to proportional relations between the magnitude of force and indices of force variability have been reported for tasks when a single effector produced different force levels (Newell et al. 1984; Slifkin and Newell 1999). An increase in force variability with force during multi-digit grasping has also been reported (Sosnoff et al. 2005). This relation, however, showed a tendency to break down when slow force changes were produced by a set of digits pressing in parallel (Latash et al. 2002a, b; Shinohara et al. 2004). In such tasks, indices of force variability showed an increase with force at low force levels and then remained unchanged over a wide range of forces. In multi-finger prehension, the trial-to-trial variability of the normal forces increased with force magnitude while for the tangential forces V-like relations between the force magnitude and variability were observed (Shim et al. 2003). The apparent differences in conclusions drawn in these studies could result from the differences in the tasks (cf. Rearick et al. 2003). To our knowledge, there have been no studies of relations between the magnitude of moment of forces and its variability in multi-finger tasks with purposeful production of accurate moment patterns.

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We hypothesized that multi-finger synergies would prevent an increase in the moment variability with its magnitude.

Methods

Subjects

Twelve healthy volunteers (26.4 ± 2.9 years old, six males and six females) participated as subjects in the experiments. The weight of the subjects averaged 69.5 ± 16.6 kg, and their height was 171.9 ± 9.5 cm. All the subjects were right-handed according to their preferred hand use for writing and eating. The right hand width (measured at the metacarpophalangeal joint level) averaged 8.4 ± 0.9 cm, and the right hand length (measured from the midpoint of the transverse wrist crease to the tip of the middle finger) was 18.7 ± 1.5 cm. All subjects gave informed consent according to the procedures approved by the Office for Research Protection of the Pennsylvania State University.

Apparatus

The experimental setup is illustrated in Fig. 1b. Four unidirectional piezoelectric force sensors (model 208C02; Piezotronic Inc.) with the diameter of 1.5 cm were used to measure forces produced by each of the four fingers of the right hand. Each sensor was mounted on an aluminum post and covered with a cotton pad to increase friction and prevent the influence of finger skin temperature on the measurements. The sensors were placed within an aluminum frame (65 × 120 mm inner size) placed insides a groove made on a wooden board to assure the stable position of the sensors. The sensors were medio-laterally distributed 30 mm apart within the frame. The position of the sensors within the frame could be adjusted in the forward–backward direction to fit the individual subject's anatomy. Analog output signals from the sensors were processed by separate AC/DC conditioners (M482M66, Piezotronic Inc.) with the ± 1% error range over the typical epoch of recording of a constant signal. The force measured by each sensor was sampled at 200 Hz, with the 12 bit resolution by a desktop IBM compatible computer. The sensors were calibrated 30 min before each testing.

During testing, the subject sat comfortably in a chair facing the testing table with his/her right upper arm at approximately 45° of abduction in the frontal plane and 45 of flexion in the sagittal plane, the elbow at approximately 45° of flexion (full extension corresponds to 0°). The wooden horizontal board supported the wrist and the forearm; two pairs of Velcro straps were used to prevent forearm or hand motion during the tests. A custom-fitted wooden piece was placed underneath the subject's right palm to help maintain a constant configuration of the hand and fingers. One more pair of Velcro straps ensured that the wooden piece was stable with respect to the board. A 17″ LCD monitor was placed approximately 65 cm in front of the subject. It displayed both the task (a target total moment time profile) and the actual total moment in pronation/supination (PR/SU) produced by the normal finger forces with respect to the midpoint between the middle and ring fingers (effort into PR was considered positive, and effort into SU was considered negative).

Procedure

There were two auxiliary force production tasks and two main experimental tasks (Fig. 1a). The first auxiliary force production task required the subjects to produce maximal pressing forces by fingers (maximal voluntary contraction, MVC). MVC tests were performed with each individual finger of the right hand separately (I, index; M, middle; R, ring; L, little) and with all four fingers acting together (IMRL). During MVC tests, a sound signal generated by the computer informed the subject to get ready. Then a trace showing the total force produced by the explicitly involved finger(s) (master fingers) started to move across the screen. The subjects were asked to produce peak force within a 2-s time window shown on the screen and

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then to relax. In one-finger MVC trials, the subjects were instructed to pay no attention to possible force generation by other, explicitly non-involved fingers, as long as the master finger produced maximal force. The subjects were not allowed to lift fingers off the sensors at any time. For each MVC task, two trials were performed with 30 s intervals between the trials, and the data for the trial with the highest force of the instructed finger(s) were used for further analysis.

The second force production task required the subject to follow a thick blue template line shown on the screen with the cursor showing the current value of the force produced by a specified instructed finger. The template line was a combination of straight line segments: a horizontal segment corresponded to zero force for the first 2 s, it was followed by an oblique line going up to 10% of the participant's individual MVC in the four-finger test over 4 s, then, another horizontal line corresponded to this constant force level for 2 more seconds. Each finger performed one force ramp trial after two practice trials.

The two main tasks required the subjects to produce accurate time profiles of the total PR/SU moment (M_{TOT}) computed on-line using force sensor signals as:

$$M_{TOT}=d_I F_I+d_M F_M-d_R F_R-d_L F_L \tag{1}$$

where d_i and F_i stand for the force and the lever arm for finger I, respectively (i=I, M, R, L). The lever arms were measured with respect to the mid-point between the middle and ring fingers such that $d_I = d_L = 4.5$ cm, $d_M = d_R = 1.5$ cm. This approximation assumes no changes in the points of force application on the sensor surfaces in the medio-lateral direction.

For the ramp moment production task (M-Ramp task, Fig. 1c), the target template line started with a 3-s horizontal segment corresponding to the subject's 10% of the product of the maximal force produced by the index finger in the MVC_I task by the lever arm of this finger ($d_I = 4.5$ cm) into PR. Then the target oblique line led to the same absolute value of the total moment into SU over 3 s. Then, another horizontal segment corresponded to 2 s of constant SU moment production. Further, an oblique line led back to the same PR moment as early in the trial. Finally, a horizontal line corresponded to 2 s of constant PR moment production.

For the sine moment production tasks (M-Sine task, Fig. 1d), the same levels of target moment were connected with a smooth sine wave. The total duration of the M-Sine task was smaller because of the lack of the middle constant moment production segment in the middle of the M-Ramp task. For both M-Ramp and M-Sine task, 25 trials were performed. The intervals between the trials were 8 s. The intervals between the tasks were at least 1 min. Prior to each task, five practice trials were performed.

Initial data processing

Data processing was performed off-line using MATLAB 7.0, Excel, Minitab, and SPSS 13.0 software. In the MVC tests, peak forces were measured at the time when the sum of the forces produced by the instructed finger(s) reached its peak. For the M-Ramp and M-Sine tasks, moments of force produced by the individual fingers (M_I, M_M, M_R, M_L) were computed as the products of the finger forces and the moment arms (d_i, i = I, M, R, L). Further average time profiles for force and moment variables as well as variability indices such as standard deviation and variance were computed (across trials for each time sample).

UCM analysis

The analysis was performed in the framework of the UCM hypothesis (Scholz and Schoöner 1999; reviewed in Latash et al. 2002b). The hypothesis assumes that the controller organizes

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covariation among independent elemental variables to stabilize a certain value of a performance variable (F_{TOT} or M_{TOT} in our study). Individual finger forces cannot be considered independent elemental variables because of the phenomenon of enslaving, i.e. unintended force production by fingers when other fingers of the hand produce force (Li et al. 1998). Hence, the first step was to convert the data sets from time series of finger forces to time series of elemental variables, force modes.

Force modes were defined similarly to the previous studies (Latash et al. 2001; Scholz et al. 2002). Briefly, single-finger force ramp trials were used to compute the enslaving matrix **E** for each subject. The entries of the **E** matrix were computed as the ratios of the change in the force of each finger to the change in the total force over the ramp duration. As in earlier studies, we have not introduced explicitly the phenomenon of force deficit (Li et al. 1998) into the analysis since it results only in proportional scaling of all finger forces (Zatsiorsky et al. 1998). The **E** matrix was used to compute changes in the vector of hypothetical independent commands to fingers (force modes, **m**) based on force changes.

Further analysis was done across repetitive trials performed by a subject at a given task for each time sample over the duration of the task. For each time, t_i, the average vector of force modes, m_{AV} was computed. Then, for each trial j, the deviation ($\Delta\mathbf{m}_j$) between $\mathbf{m}_j$ and $\mathbf{m}_{AV}$ were computed. Variance of the $\Delta\mathbf{m}_j$ data set was then computed along a direction orthogonal to the UCM computed for the average value of F_{TOT} at that time slice (force-stabilization hypothesis) and for the average value of M_{TOT} (moment-stabilization hypothesis). We will refer to these indices as $V_{ORT\text{-}F}$ and $V_{ORT\text{-}M}$, respectively. This was done using the Raleigh fraction:

$$\mathrm{V}_{\mathrm{ORT}}=\frac{\mathbf{J}_{\mathrm{m}}\mathrm{cov}\,(\mathbf{m})\,\mathbf{J}_{\mathrm{m}}^{\mathrm{T}}}{\mathbf{J}_{\mathrm{m}}\mathbf{J}_{\mathrm{m}}^{\mathrm{T}}}=\frac{\mathbf{J}\mathbf{E}^{-1\mathrm{T}}\mathbf{E}^{-1}\mathrm{cov}\,(\mathbf{f})\,\mathbf{E}^{-1\mathrm{T}}\mathbf{E}^{-1}\mathbf{J}^{\mathrm{T}}}{\mathbf{J}\mathbf{E}^{-1\mathrm{T}}\mathbf{E}^{-1}\mathbf{J}^{\mathrm{T}}}, \tag{2}$$

where **J** is a Jacobian matrix relating small changes in modes ($\mathbf{J}_m$) or forces (**J**) to changes in the selected performance variable, total force or total moment, cov(**m**) is the covariance matrix in the mode space for the demeaned sets of vector **m**, cov(**f**) is the covariance matrix in the finger force space for the demeaned sets of vector **f**, and T is the sign of transpose. For force-stabilization hypothesis, **J** = [1, 1, 1, 1], while for moment-stabilization hypothesis, **J** = [d_I, d_M, $-d_R$, $-d_L$], see Eq. 1. Note that **J**s are written as vector-rows. $\mathbf{J}_m$ can be computed as: $\mathbf{J}_m = \mathbf{J}\mathbf{E}^{-1T}$, where $\mathbf{E}^{-1T}$ is a transpose of the **E** inverse.

We used the **E** matrix obtained in the single-finger force production trials at this stage of analysis. This approach is justified by a number of studies that showed robustness of enslaving phenomena over a wide range of finger forces and multi-finger tasks (Li et al. 1998; Zatsiorsky et al. 2000; Latash et al. 2001; Scholz et al. 2000). In one of the studies, the enslaving matrix obtained in single-finger pressing tasks was even successfully used to model force production patterns in multi-digit grasping tasks (Zatsiorsky et al. 2002b).

V_{ORT} reflects the amount of mode variance in the data set that corresponds to a change in the selected performance variable. The difference between the total amount of variance (V_{TOT}) and V_{ORT} corresponds to variance that does not affect the average value of the performance variable. We will address this variance as V_{UCM} (variance within the UCM): $V_{UCM} = V_{TOT}-V_{ORT}$. Note that the finger mode space is four-dimensional, V_{ORT} lies along a one-dimensional sub-space, while V_{UCM} lies in a three-dimensional sub-space. Therefore, to compare the amounts of variance per dimension, the following index was used:

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$$\Delta V = \frac{(V_{UCM}/3 - V_{ORT})}{V_{TOT}/4} \tag{3}$$

Normalization by the total amount of variance per dimension ($V_{TOT}/4$) was used to compare the data across subjects who could show different amounts of the total variance. Note that positive values of ΔV correspond to proportionally higher V_{UCM} than V_{ORT}. Hence, values $\Delta V > 0$ may be interpreted as a reflection of a multi-mode synergy stabilizing that performance variable. If $\Delta V = 0$, this means that the amount of variance per dimension is the same in directions that correspond to a change in the selected performance variable and those along directions that keep the variable unchanged. $\Delta V < 0$ may be interpreted as covariation among changes in finger modes contributing to a change in the selected performance variable or destabilizing it (cf. Bienaymé equality theorem, Loeve 1977).

Statistical analysis

Standard methods of parametric statistics were used. Analysis of variance (ANOVA) with and without repeated measures was used with factors: *Time* (1-s time intervals), *Task* (M-Ramp vs. M-Sine), *Direction* (PR-SU vs. SU-PR), and *Index* (ΔV_F vs. ΔV_M). Different ANOVAs involving *Time* as a factor were used for the two tasks because of their different duration. Post hoc tests (*t* tests with Bonferroni corrections and Tukey's honestly significant difference tests) and contrasts were used to further analyze significant effects. The data were checked for violations of sphericity due to unequal pairwise correlations across levels of a within-subject factor. We used the Huynh–Feldt criterion to reduce the degrees of freedom when necessary. Data expressed in percent were subjected to *z*-transformation before using parametric methods of statistical analysis. Some of the data of one of the subjects were not included into statistical analysis (see details in Results section) since those data differed from the mean of the rest of the subjects by over five standard deviations.

Results

Each trial started with the subjects sitting relaxed. Over 1 or 2 s, the subjects reached the prescribed initial level of the moment into pronation. All the subjects were able to reach the initial steady-state PR moment within the first 2 s after the trial initiation. Therefore, data recorded were analyzed starting with the third 1-s interval for both M-Ramp and M-Sine tasks.

General patterns of the total force and total moment

The accurate production of the total moment was challenging for all subjects. However, after the practice trials, they were all able to perform the tasks rather accurately. Figure 2 shows typical patterns of the total force (F_{TOT}, thick solid line) and total moment (M_{TOT}, thin solid line) for two representative subjects performing the Ramp-task (Fig. 2a) and the Sine-task (Fig. 2b). Average traces are shown over 25 trials by each subject with standard error bars. Note the rather close correspondence of the average M_{TOT} profile with the template (shown as the thin dashed line) for both tasks. The total force shows an increase over the duration of the task such that it is higher at the end of the task when the subjects produced the same PR moment as at the trial initiation.

Figure 3 shows the same regular features of M_{TOT} and F_{TOT} averaged across the subjects with standard error bars in two tasks, M-Ramp (Fig. 3a) and M-Sine (Fig. 3b). Dashed line indicates each template shown on the screen to the subjects, a solid line closely matching the template represents the average M_{TOT} produced by the subjects (left *y*-axes), and the other solid line shows the average F_{TOT} produced by the subjects (right *y*-axes). On average, F_{TOT} nearly doubled over the trial duration. It increased from 8.07 ± 3.59 N at the beginning of the trial to 15.5 ± 8.05 N at the end of the trial in the M-Ramp task and from 9.07 ± 4.75 N at the beginning to 17.82 ± 9.86 N at the end of the trial in the M-Sine task. The beginning and the end of each task refer to 1-s time intervals immediately prior to the initiation of moment change and after the subjects returned to the original M_{TOT} level into PR. The increase in F_{TOT} over the trial duration was statistically significant as confirmed by a two-way ANOVA, *Task* × *Time*. In this analysis, *Time* had two levels, which refer to the 1-s intervals immediately prior to the initiation of PR–SU moment change and immediately after the SU–PR segment of the task was complete. F_{TOT} was averaged over those time intervals. There was a main effect of *Time* ($F_{[1,11]} = 45.0$; $P < 0.001$). Besides the generally increasing magnitude of F_{TOT}, both tasks appeared to have a local F_{TOT} minimum approximately 0.5–1 s prior to the time when the total moment changed its direction from PR to SU and from SU to PR (see the time intervals indicated in Fig. 3 by the vertical dashed lines and horizontal arrows). Eleven out of 12 subjects showed such local minima or inflection points in both tasks ($P < 0.05$ according to the sign test). However, these minima occurred at different times in different subjects, and ANOVA failed to confirm their existence.

Patterns of force and moment variability

Variability of F_{TOT} (V_F) and M_{TOT} (V_M) was computed for each subject over the 25 trials at each task. V_F and V_M were further averaged over 1-s time intervals shown in panels a and b in Figs. 4 and 5, respectively. Figures 4 and 5 present the averaged V_F (V_M) across the 12 subjects as a function of time and as a function of F_{TOT} (M_{TOT}). Panels c and d of Figs. 4 and 5 show the relations between F_{TOT} and V_F and between M_{TOT} and V_M, respectively. The relations were complex and not necessarily monotonic.

Figure 4 shows the time profile of averaged V_F across 12 subjects with standard errors (Fig 4a, b) and relation between V_F and F_{TOT} (Fig. 4c, d) also averaged across subjects. Figure 4a, c shows the data for the M-Ramp task, while Fig. 4b, d shows the data for the M-Sine task. Thick solid lines in Figure 4c, d, represent the intervals from PR to SU (PR–SU), while thin solid lines represent the intervals from SU to PR (SU–PR), with arrows showing the directions of real time changes and the open circles showing the onset of the tasks.

V_F increased sharply at the beginning of either task and then did not change by much over the rest of the task. From the 1-s steady-state interval prior to the moment change to 1-s interval about the time when the moment was close to zero (changing its direction), V_F increased, on average, from 0.72 ± 0.18 N^2 to 5.88 ± 3.26 N^2 for the M-Ramp task, and from 1.84 ± 0.62 N^2 to 6.05 ± 3.07 N^2 for the M-Sine task. Both changes were significant ($P < 0.01$; paired *t* tests).

Figure 5 shows the time profiles of V_M averaged across subjects (Fig. 5a, b) and the relations between V_M and M_{TOT} (Fig. 5c, d). Similarly to Fig. 4, Fig. 5a, c shows the data for the M-Ramp task, while Fig. 5b, d shows the data for the M-Sine task. In Fig. 5c, d, the circles and arrows indicate the onset of tasks and real time changes respectively. The data show that there was no monotonic relation between the total moment and its variability. In particular, V_M during the 1-s time interval when PR moment changed into SU moment was higher than at other time intervals in both tasks despite the average magnitude of the total moment being lower than over any other time interval. We also explored relations between V_M and the total force produced by the agonist fingers (those that generated moment in the prescribed direction, see Methods) and between V_M and the variance of the agonist finger force. None of these relations approached significance; they were typically non-monotonic.

For further analysis, we identified the following 1-s time intervals: steady-state interval at PR ($T_{PR\cdot SS}$), interval of PR during moment changes ($T_{PR\cdot CH}$), interval about the time of switch of

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the moment direction (T_{SWITCH}), interval of SU during moment changes ($T_{SU·CH}$), and steady-state interval at SU ($T_{SU·SS}$; note that this interval was present only in the M-Ramp task). A two-way ANOVA with repeated measures *Direction* × *Time* showed main effects of *Time* for both tasks ($F_{[3,10]} = 11.818$, $P < 0.001$ for the M-Ramp task and $F_{[2.3,10]} = 33.28$, $P < 0.001$ for the M-Sine task; the sphericity assumption was not met so the Huynh–Feldt correction was applied). Moment variance, V_M was on average 70% higher at T_{SWITCH} than at both $T_{PR·SS}$ and $T_{SU·SS}$ for both tasks ($P < 0.01$).

The ANOVA also showed a significant main effect of *Direction* ($F_{[1,10]} = 7.87$, $P < 0.01$) for the M-Ramp task corresponding to higher moment variance during the PR–SU moment change as compared to SU–PR change. For the M-Sine task, V_M showed a similar tendency, but this difference did not reach significance ($F_{[1,10]} = 3.38$, $P = 0.07$). In this analysis, we used the data of only 11 subjects because the data of subject #10 differed from the other subjects' data by over five SDs (see Methods).

Agonist and antagonist moments

We would like to introduce two terms: (1) *Agonist moment* (M_{AG}) is the moment produced to meet the moment production task requirement; (2) *Antagonist moment* (M_{ANT}) is the moment produced in the direction opposite to the required moment. When the subjects were required to produce the total moment into PR, moments generated by the forces of the index (*I*) and middle (*M*) fingers added up to M_{AG}, while moments generated by the ring (R) and little (L) finger forces produced M_{ANT}. The role of the two finger pairs switched when the subjects had to produce the total moment into SU, IM produced M_{ANT}, while RL produced M_{AG}.

M_{AG} and M_{ANT} were averaged over 0.5-s time intervals for each subject separately and further averaged across subjects. Figure 6 shows the time profiles of averaged M_{AG} (stripe bars) and M_{ANT} (dark bars) with standard error bars in the M-Ramp (Fig. 6a) and M-Sine (Fig. 6b) tasks, respectively. For both M-Ramp and M-Sine tasks, the amplitude of M_{ANT} increased significantly from the steady-state PR moment production at the initiation of the trial to steady-state production of the same PR moment at the end of the trial. The change was more than sixfold for the M-Ramp task and about fourfold for the M-Sine task. This observation has been confirmed by a one-way ANOVA on M_{ANT} with the factor *Time* (ten levels for the M-Ramp task and eight levels for the M-Sine task) for both tasks (main effect $F > 12.3$; $P < 0.001$; the sphericity assumption was not met so the Huynh–Feldt correction was applied) followed by post hoc Tukey's tests ($P < 0.05$). The Tukey's test also confirmed that M_{ANT} reached its local maximum when the total moment was close to zero: there were significant differences between the data for those time intervals and its immediate neighboring time intervals ($P < 0.05$).

Moments produced by individual fingers

Earlier studies have suggested the mechanical advantage hypothesis (Buchanan et al. 1989; Prilutsky 2000; Zatsiorsky et al. 2002a; Shim et al. 2004a, b), which states that effectors (muscles or digits) with longer lever arms contribute more to the total rotational action as compared to effectors with shorter lever arms. In our study, two fingers (I and M) produced PR moments while two other fingers (R and L) produced SU moments. Note that I and L finger forces had moment arms that were three times longer than those for M and R fingers and, therefore, I and L fingers be expected to produce over 50% of the total moment into PR and SU, respectively.

To test this hypothesis, we computed the percentage of the PR moment produced by the I finger M_I_PR and the percentage of SU moment produced by the Lfinger M_I_SU in both tasks. M_I_PR and M_I_SU were averaged over 1-s time interval and then further averaged across subjects. Figure 7 shows the averaged M_I_PR and M_L_SU across subjects with standard error

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bars in the M-Ramp (Fig. 7a) and M-Sine tasks (Fig. 7b). The top panels display the task templates. Note that when the task required PR (SU) moment generation the I and M fingers produced M_{AG} (M_{ANT}) while R and L fingers produced M_{ANT} (M_{AG}).

Figure 7 shows that over the whole task duration, both M_I_PR and M_I_SU contributed more than 50% of the total PR and SU moment respectively. However, their contributions to the PR and SU moments were particularly high when these fingers acted as agonists (produced M_{AG}), and they were lower when these fingers were antagonists (produced M_{ANT}). This pattern was confirmed by a two-way, *Time* × *Task* ANOVA on M_I_PR and M_L_SU separately. In this analysis, *Time* had two levels, which refer to the two-second steady-state intervals in PR and in SU. M_I_PR and M_L_SU were averaged over those time intervals. Prior to running this analysis, M_I_PR and M_L_SU percentage values were converted into *z*-scores. There were main effects of *Time* for both M_I_PR and M_L_SU ($F_{[1,11]} = 40.3$, $P < 0.001$; and $F_{[1,11]} = 5.99$, $P < 0.05$, respectively).

UCM analysis

To remind (see the Methods), this analysis quantifies two components of the total variance, V_{UCM} and V_{ORT}, in the space of hypothetical command signals to fingers (finger modes). The V_{UCM} component reflects co-varied changes in signals to fingers across trials that keep an average value of a performance variable, either total force or total moment, constant. The V_{ORT} component reflects variations in signals to fingers that change the performance variable. We performed analysis with respect to two performance variables, F_{TOT} and M_{TOT} at each time sample for each of the two tasks. A normalized index (ΔV) of the difference between V_{UCM} and V_{ORT} was computed in such a way that its positive values could be interpreted as multi-finger synergies stabilizing that particular performance variable.

Figure 8 illustrates ΔV indices computed for F_{TOT} (ΔV_F) and for M_{TOT} (ΔV_M) across all the subjects with standard error bars. The corresponding task templates are shown with dashed lines. Figure 8a, b shows ΔV_F and ΔV_M indices for the M-Ramp task while Fig. 8c, d shows these indices for the M-Sine task. All the subjects were able to stabilize the time profile of the total moment as reflected by positive ΔV_M values over the full duration of both tasks (Fig. 8b, d). In contrast, the index of total force stabilization tended to be positive early in each task but then dropped close to zero or even into negative values (Fig. 8a, c).

For statistical analysis, we used a three-way, *Index* (levels, ΔV_F and ΔV_M) × *Task* × *Time* ANOVA with repeated measures on ΔV. In order to do comparisons across the two tasks, the *Time* factor had five levels corresponding to five 1-s intervals. Two of them were over the steady-state PR moment production at the beginning and at the end of moment changes, two more were centered about the times when the moment changed direction (PR–SU and SU–PR), and the fifth was centered about the middle of the SU moment production interval. The ANOVA showed a main effect of *Index* ($F_{[1,11]} = 16.8$, $P < 0.01$) and a main effect of *Task* ($F_{[1,11]} = 6.04$, $P < 0.05$). These effects corresponded to significantly smaller ΔV_F as compared to ΔV_M and significantly smaller ΔV indices in the M-Sine task as compared to the M-Ramp task. Besides, there was also a main effect of *Time* ($F_{[3.7,11]} = 12.3$, $P < 0.01$; the sphericity assumption was not met so the Huynh-Feldt correction was applied). Post hoc Tukey's tests show that ΔV over the early interval of steady-state PR moment production was significantly higher than over the two intervals when the moment changed its direction ($P < 0.05$). There was also a significant *Index* × *Task* interaction ($F_{[1,44]} = 8.75$, $P < 0.001$) reflecting higher ΔV_F and somewhat smaller ΔV_M in the M-Sine task as compared to the M-Ramp task.

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Discussion

The results of the experiments allow addressing a number of issues related to the coordination of finger action in the production of time patterns of the total moment of force. Our main hypothesis has been supported by the finding of strong multi-finger synergies (as reflected by the positive ΔV values, see Latash et al. 2002a, b; Shim et al. 2005) that stabilized the total moment across trials in both tasks and at all phases of the moment production. In contrast, no strong synergies stabilized the time profile of the total force produced by the fingers, particularly in the task with the production of a smooth time profile of the total moment (M-Sine task). Taken together, these findings extend the earlier observations of moment-stabilizing synergies in tasks that did not require the subjects to produce particular moment time profiles but instead focused their attention on the production of certain time profiles of the total force (Latash et al. 2001, 2002a; Scholz et al. 2002).

The current study differs from the previous ones in several aspects. First, this is the first study of motor variability during purposeful accurate production of a time profile of the moment of force by a set of fingers. The significance of accurate moment production for everyday hand actions has been emphasized in the Introduction; this factor, by itself, makes the current results important. Second, the earlier studies focused on indices of multi-finger synergies without analyzing factors that could potentially contribute to these indices as well as to the overall performance. Here we analyzed such essential issues as antagonist moment production, the role of mechanical advantage, differences between pronation and supination moment production, and the general patterns of relations between moment magnitude and its variability.

In support of our secondary hypothesis on the lack of proportionality between the magnitude of the performance variables and their variability in the multi-finger tasks, the results have shown no linear (even stronger, —no monotonic) change in variability of the total moment with the magnitude of the moment. These observations suggest that the established relationships between the magnitude of force and its variability (Newell et al. 1984; Slifkin and Newell 1999) may not be valid for actions that involve several effectors united into a synergy. This conclusion is in a good correspondence with the study by Rearick et al. (2003) who suggest that relations between force and force variability may be task-dependent. They also provide indirect support for the general view on the apparently redundant design of the human motor apparatus (including the hand, Zatsiorsky and Latash 2004) not as a source of computational problems for the central nervous system but as a source of abundance that allows to assure stable performance with respect to important variables in the presence of relatively high variability in the outputs of elements (fingers in our study).

In the remainder of the Discussion, we address these and other issues relevant to the control of multi-digit rotational actions in more detail.

Moment of force of its variability

The two tasks used in the experiment were selected for the following reasons: first, the M-Ramp task was similar to the tasks used in earlier studies that required the subjects to produce ramp time profiles of the total force with several fingers pressing in parallel (Latash et al. 2001, 2002a, b; Scholz et al. 2002; Shim et al. 2005). As such, it allows direct comparison with those results. On the other hand, the well-known low-pass filtering properties of human muscles (reviewed in Zajac 1989) make it impossible to produce abrupt changes in the force (moment) when a steady-state segment of the task turns into a ramp and then a ramp turns into another steady-state segment (the derivative in the inflection points in both cases is infinite). This is the reason we used another task that required smooth changes in the total moment that could be seen as easier to produce given the mentioned muscle properties. The results were very similar across the two tasks, and we have not seen a single index that would point at an

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advantage of the “easier” M-Sine task. Actually, the only significant differences that we could detect were in favor of the M-Ramp task. In particular, indices of multi-digit synergies stabilizing the total force profile were larger for the M-Ramp task as compared to the M-Sine task (Fig. 8).

In both tasks, the subjects were capable of producing, on average, the required time profiles of the total moment (Figs. 2, 3). The time profiles of the moment variance were also similar (Fig. 4). Note that each task started with a relatively easy segment that required the subjects to produce a steady-state comfortable level of the total moment into pronation. Not surprisingly, most subjects did this mostly by pressing with the index finger (Fig. 7). A change in the total moment was associated with a quick increase in the variability of the total moment, which stabilized after 1–2 s and remained unchanged until the end of the trial despite the changes in both the magnitude and the direction of the total moment (Fig. 4). A drop in the variability of the total moment by the end of the trial when the subjects returned to the initial level of PR moment suggests that the production of accurate SU moments may be more challenging.

Several papers report differences in the ability of humans to produce high magnitudes of pronation and supination moments. In particular, Salter and Darcus (1952) report higher peak pronation torque magnitudes at some elbow flexion angles but not at others. A more recent study (Shim et al. 2004b) reported somewhat higher torque magnitudes during supination efforts. To our knowledge, no study compared indices of variability in torque production tasks into pronation and supination.

We see as the most important finding the rather high indices of variability of the total moment during time intervals when it changed direction and the moment magnitude was very low (time intervals 5 and 10 s in the M-Ramp task and time intervals 5 and 8 s in the M-Sine task; Fig. 4). These findings illustrate the lack of a monotonic relation between the magnitude of the total moment and its variability. They may be compared to the earlier observations of an initial increase in the total force variability and its relatively minor changes with the total force level in tasks that required the production of a ramp profile of the total force (Shinohara et al. 2003,2004). Also, a recent study of static prehensile tasks has shown a V-shaped relation between the variability of the tangential force and that force's magnitude (Shim et al. 2003). In other words, similar to the present study, the variability of the tangential force was maximal when the force was minimal.

These observations contrast the well-known force magnitude–force variability relation investigated by Newell and his colleagues (reviewed in Newell et al. 1984). Earlier studies of this group suggested that standard deviation of force increased linearly with the force magnitude, while more recent publications have suggested that this relation may be non-linear and closer to exponential (Slifkin and Newell 1999). However, in all studies an increase in indices of force variability with force magnitude was described (for more recent reports see Sternad et al. 2000; Sosnoff et al. 2006). Those studies also involved grasping tasks with several digits (Sosnoff et al. 2005). Such monotonic relations were also described for other variables characterizing human motor behavior including indices of muscle activation (Carlton et al. 1985) and were used in several computational models of human movement (Gutman and Gottlieb 1992; Plamondon and Alimi 1997).

Higher indices of moment variability at low magnitudes of the moment, in particular during PR–SU and SU–PR transitions, could get contributions from several factors. One of them is a timing error, which may represent a variable lag across trials or a variable timing parameter specifying the moment time profile. A timing error may be expected to lead to higher indices of variability when the first derivative of the variable is high. For single-joint actions, this has been formalized in a model by Goodman/Gutman and colleagues (Gutman and Gottlieb

1992; Gutman et al. 1993). More recently, the model has been generalized for multi-finger force production tasks (Goodman et al. 2005). The model has shown, in particular, that timing errors contribute significantly to the overall variability indices and that multi-finger synergies fail to reduce this component of variability (Latash et al. 2002a). As such, the results fit a hierarchical scheme of control of multi-element systems advocated by Schoöner (1995).

Indeed, the index of moment-stabilizing synergy (ΔV_M) showed a transient drop about the times when the direction of the moment changed but only for the M-Sine task (Fig. 8). Even in that task, ΔV remained positive corresponding to stabilization of the total moment across trials by co-varied changes in individual finger actions. There were no visible changes in ΔV_M during the M-Ramp task although the variability of the moment of force showed a visible increase when the moment magnitude was close to zero (Fig. 5). These observations cast doubt on a major role played by timing errors in the observed relations between moment variability and its magnitude.

The most earlier studies considered actions by single apparent elements, such as single-joint torque production or single-digit force production. Such simple systems could not potentially benefit from multi-element neural organizations (synergies) that are assumed to play a major role in assuring low-variability performance of multi-digit action (Latash et al. 2002b, 2004). We are going to discuss potential role of multi-digit synergies in bringing down variability in the total moment production tasks in the next subsection.

Multi-digit synergies stabilizing the total moment

Multi-element actions such as multi-joint movements, multi-digit prehensile actions, and multi-muscle actions have frequently been described using the notion of a synergy (reviewed in Latash et al. 2004). Recently, this notion has been defined operationally and a particular computational approach to it has been developed, the UCM hypothesis (Scholz and Schoöner 1999; Scholz et al. 2000; see the Introduction). According to the UCM hypothesis, the purpose of synergies is to bring variability down along particular directions in the space of elemental variables (finger modes in our study) while allowing variability in other directions. For example, if the controller tries to assure accurate production of a particular value of the total moment produced by the fingers, it is expected to keep the variability mostly confined to a sub-space (a UCM) in the finger mode space that does not lead to changes in that value. The index of synergy we used in this study (ΔV, see also Shinohara et al. 2004; Shim et al. 2005) was computed in such a way that its positive values corresponded to proportionally more variability computed across a series of trials within the corresponding UCM, which can be interpreted as a multi-finger synergy stabilizing the value of the total moment. In both tasks, ΔV remained positive over the whole trial duration supporting a hypothesis that the total moment was indeed stabilized across trials by co-varied changes in commands to individual fingers.

In several earlier studies, subjects required to produce an accurate profile of the total force by a set of fingers showed stabilization of the total moment that persisted even when it led to destabilization of the total force (Latash et al. 2001, 2002a; Scholz et al. 2002). In other words, a performance variable produced by a set of digits, which was not mentioned as part of the task and was not displayed to the subjects, was stabilized at the expense of another performance variable, which was an explicit part of the task. This somewhat surprising result led to the formulation of a hypothesis that stabilization of the rotational hand action is conditioned by everyday experience with such tasks as drinking from the glass, eating with the spoon, and handwriting (Latash et al. 2004).

In the current study, the task was switched: The subjects got feedback and instruction with respect to the total moment but not with respect to the total force. The result, however, remained the same. The total moment was stabilized over the trial duration for both tasks while the total

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force was stabilized to a lesser degree in the M-Ramp task and was not stabilized at all in the M-Sine task. Note that total force and total moment stabilization may be viewed as partly competitive. The former requires predominance of negative covariation among changes in individual finger forces. The latter requires positive covariation between the weighted sums of forces produced by the IM pair and the RL pair. In the M-Ramp task, the controller was apparently able to stabilize both variables simultaneously. The M-Sine task, originally viewed as “more natural” failed to show total force stabilization. Taken together, the results corroborate the hypothesis that stabilization of the total moment dominates in multi-finger tasks and can happen with or without total force stabilization.

The decoupling of total force and total moment stabilization also supports the principle of superposition suggested originally in robotics (Arimoto et al. 2000, 2001). According to this principle, some actions by manipulators may benefit from having separate controllers for components of the action such as gripping (force production) and rotation action (moment production). The principle of superposition has also been supported in recent studies of human prehensile actions (Shim et al. 2003, 2005; Zatsiorsky et al. 2003).

Why is antagonist moment produced?

Over the duration of each task, there was a steady increase in the total force produced by the four fingers. This happened despite the fact that the last interval of each task was exactly the same as its initial interval: the steady-state production of a certain value of PR moment was required in both cases. The increase of the total force while producing the same moment was accompanied by a steady increase in the magnitude of moments produced by fingers that acted against the required moment direction. During the task intervals that required the production of PR moments, forces generated by the R and L fingers produced moments into SU, antagonist moments (M_{ANT}). Similarly, during the intervals that required the production of SU moments, M_{ANT} into PR were produced by forces generated by the fingers I and M. The production of M_{ANT} was not required by the task and was apparently wasteful. Why did it happen?

Several earlier studies described the production of antagonist moments (Zatsiorsky et al. 2002a,b; Shim et al. 2004a). It has been suggested, in particular, that this phenomenon originates from the mentioned phenomenon of enslaving: When a person sends commands (modes) to the fingers acting in the required direction, enslaving leads to force production by the other two fingers, which generate M_{ANT}. This idea was successfully used to model finger forces in prehensile static tasks (Zatsiorsky et al. 2002b). However, if one assumes that enslaving does not change with time, an increase in the M_{ANT} magnitude over the trial duration remains unexplained: If the subjects produced the same moments by the I and M fingers at the end of each trial as they did at the beginning of the trial, M_{ANT} would have remained unchanged.

The relative magnitude of M_{ANT} was particularly large when the direction of the moment switched (Fig. 6). At that time, agonist moment, M_{AG} (for example, into PR) became M_{ANT} since the task turned into the production of SU moment. It is obvious that at the time of switch, M_{ANT} and M_{AG} were equal to produce a zero total moment. Hence, the task required an increase in the relative magnitude of M_{ANT}; however, it did not require a steady growth in its absolute magnitude.

Another reason for production of M_{ANT} suggested in an earlier study was to assure rotational stability of the hand-held object by stiffening the system to possible rotational perturbations (Shim et al. 2005). In particular, the mentioned study showed higher M_{ANT} in elderly and associated this apparently less frugal strategy with a desire to assure rotational equilibrium of the handle in the presence of age-related higher variability in individual finger forces (Galganski et al. 1993; Enoka et al. 2003; Shinohara et al. 2003; Vaillancourt and Newell

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2003). However, the current study involved a task performed against a fixed set of sensors in isometric conditions and was not associated with a possibility of rotational perturbations.

Apparently, there is another reason for the observed increase in M_{ANT} beyond the two mentioned hypotheses. It may be related to the mentioned necessity to have M_{ANT} and M_{AG} of the same magnitude when the direction of the total moment changed coupled with a deliberate strategy to keep all finger forces over a certain threshold that would assure their accurate detection by sensory mechanisms to help stabilize the overall output of the hand. Such a system would be compatible with several feedback-based control schemes (Todorov and Jordan 2002; Latash et al. 2005).

The mechanical advantage hypothesis

When several effectors contribute to a common mechanical effect while acting in the same direction, sharing patterns among the elements may be defined by optimization rules. In particular, a mechanical advantage hypothesis has been suggested as a principle that defines sharing patterns for multi-muscle and muscle-digit actions (Buchanan et al. 1989; Prilutsky 2000). This hypothesis is based on a general idea that effectors with larger lever arms should produce larger shares of the total moment because they have to produce relatively smaller forces per unit of total moment.

In our study, PR moments were shared by the I and M fingers with the I finger having the lever arm three times longer than that of the M finger (4.5 vs. 1.5 cm). Similarly, for SU moment production, the L finger had a lever arm that was three times longer than that of the R finger. One could expect, therefore, I finger to produce a larger percentage of the total moment into PR and L finger to produce a larger percentage of the total moment into SU. This was true when the finger pairs produced M_{AG} but not necessarily when they produced M_{ANT}. Figure 7 shows that I finger produced about 80% of the total PR moment when the task required PR moment production; this share dropped to about 50% in the M-Ramp task and to about 65% in the M-Sine task during time intervals when the production of SU moment was required (PR moments were M_{ANT}). The contrast is somewhat less dramatic for the L finger share of the SU moment. However, during M_{AG} production, L finger generated over 70% of the total SU moment; this share was considerably lower in the M-Ramp task when the total moment was in the PR direction.

The modulation of the shares of the fingers with longer lever arms suggests that the principle of mechanical advantage may have limitations (also see Shim et al. 2004a). It may be applicable to sets of effectors that produce action in a required direction (agonists) but not for sets of effectors that oppose the required action (antagonists). This conclusion suggests different control processes defining how action of a group of effectors is shared among them depending on whether the group acts as an agonist or as an antagonist.

Concluding comments

Some of the findings in the experiments inspire more questions than they answer. In particular, the increase in the total force produced by the fingers over the duration of the task suggests that we analyzed a non-stationary process. If our subjects were asked to continue producing moment patterns (M-Ramp or M-Sine) without an interruption over several cycles, it would be unrealistic to expect the increase in the total force to continue indefinitely. Likely, the force level would stabilize about a certain level and be modulated about that level within each cycle. This might be accompanied with better stabilization of the force profile across cycles as compared to the results of the current study. Whether these expectations are true is to be seen in a future experiment.

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Along similar lines, indices of multi-finger synergies stabilizing the total force and total moment of force may be expected to be sensitive to task parameters, for example to changes in the hand/forearm position, changes in the pivot point about which the moment is produced (cf. Shim et al. 2004b), and involvement of the thumb (Olatsdottir et al. 2005). We would like to note, however, that at least one study reported high indices of moment-stabilizing synergies during more natural grasping tasks (Shim et al. 2004a).

Although qualitatively the two tasks showed similar main results, there were differences between the tasks that are not easy to interpret. We expected the M-Sine task to be more natural and easy because it did not involve physiologically impossible requirements of infinite moment derivatives that were present in the M-Ramp task. However, indices of multi-finger synergies stabilizing the total force were higher for the M-Ramp task (Fig. 8). Besides, the overall modulation of the shares of the I and L finger forces in the production of PR and SU moments respectively was substantially larger in the M-Ramp task as compared to the M-Sine task (Fig. 7). Apparently, our simplistic assumption of one task being harder than the other was not supported.

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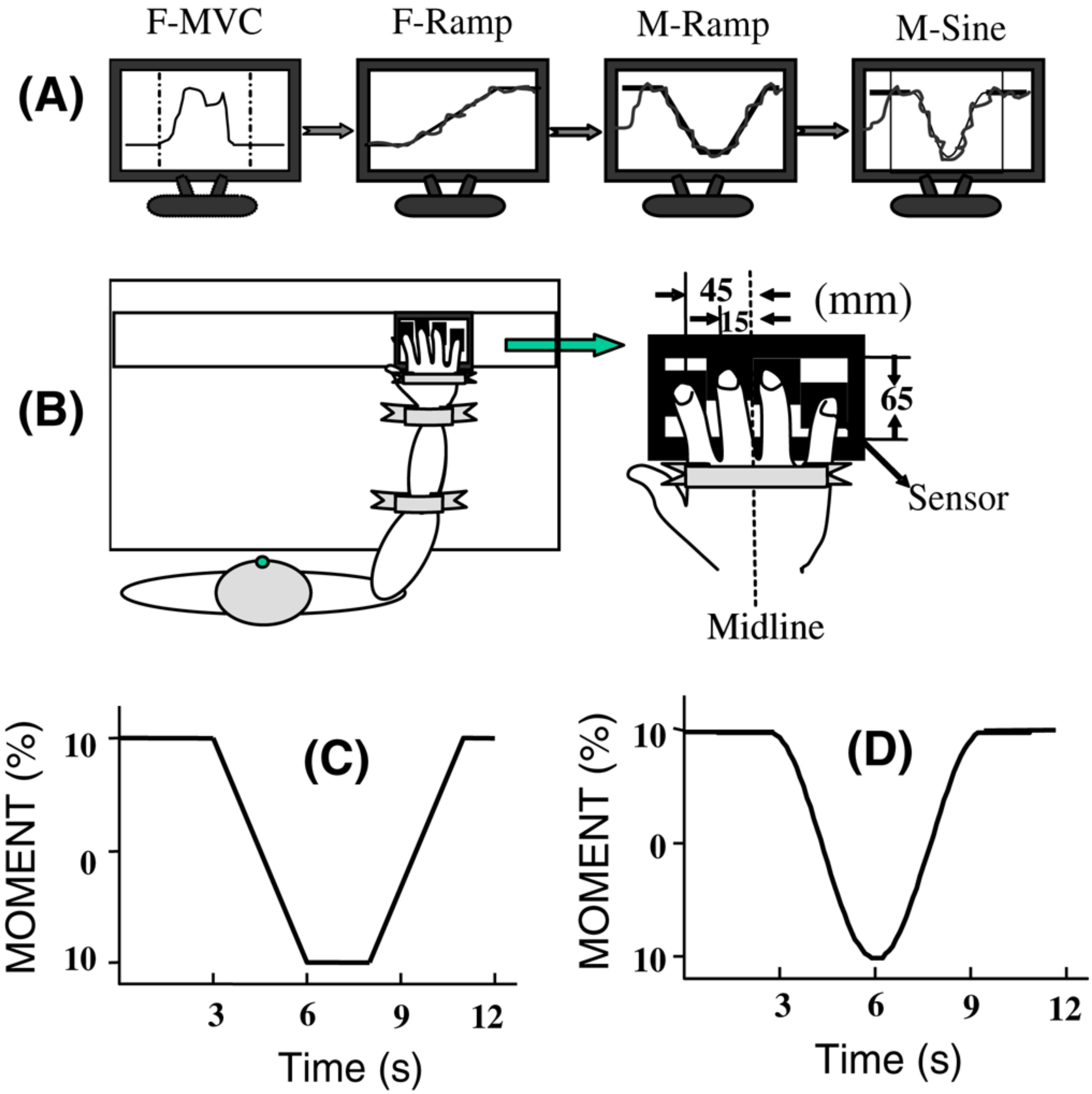

Fig. 1.

a The experiment set-up showing the main tasks: F-MVC, F-Ramp, M-Ramp and M-Sine. **b** The subject and hand positions. During the experiment, the subject sat comfortably, with forearm fixed on the table. The hand position, sensor arrangement and frame size (65 × 120 mm) are shown on the right panel. Moment arms with respect to hand midline of index and little fingers are 45 mm, and that of middle and ring fingers are 15 mm. **c** The target line showed on the screen during M-Ramp task. **d** The target line showed on the screen during M-Sine task. **c, d** Moment axes in percent of the product of individual subject's index finger MVC by its moment arm

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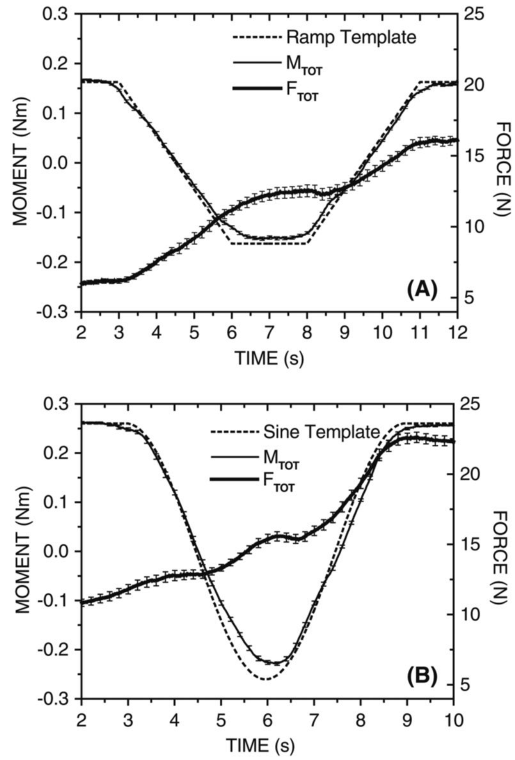

Fig. 2.

Typical subject performance in the M-Ramp (**a**) and M-Sine (**b**) tasks. Averaged F_{TOT} and M_{TOT} time profiles with standard error bars across 25 trials produced by two representative subjects in the M-Ramp task (**a**) and in the M-Sine task (**b**). *Thick solid lines* represent F_{TOT} (right *y*-axis), *thin solid lines* represent M_{TOT} (left *y*-axis), and *dashed lines* show the task template in each task

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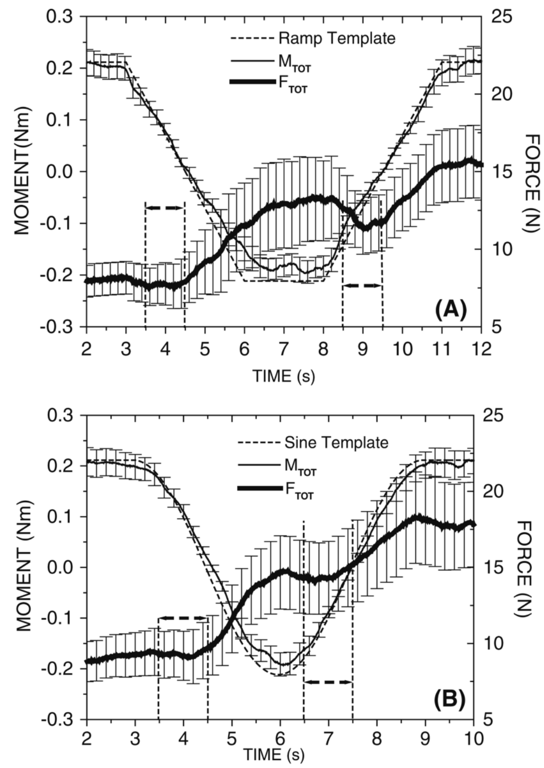

Fig. 3.

Averaged M_{TOT} and F_{TOT} across 12 subjects with standard error bars in the M-Ramp (**a**) and M-Sine (**b**) tasks. The *dashed lines* show the task template displayed on the screen in each task, the *thin solid lines* around the dashed line represent M_{TOT}, and the thick solid lines represent F_{TOT} in each panel. The *two-end arrows* indicate the time intervals where the local minima of F_{TOT} happened

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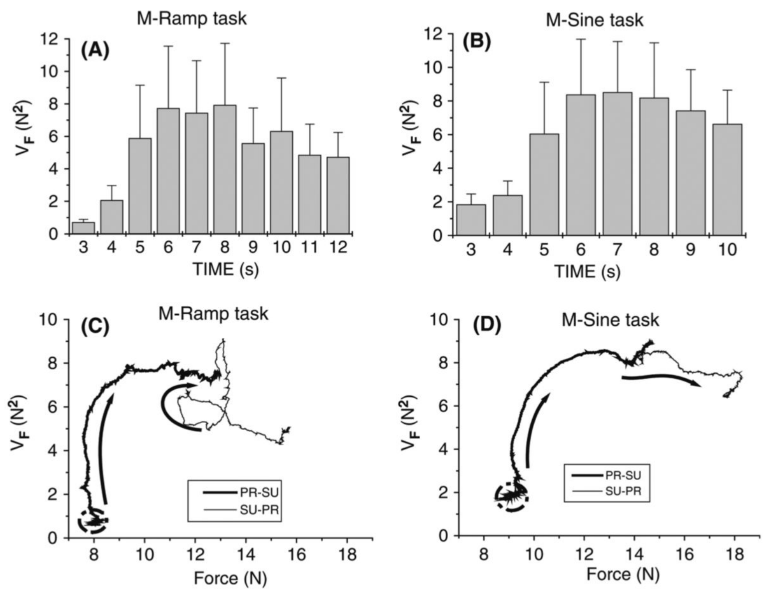

Fig. 4.

a, **b** Time profiles of the variance (V_F) with standard error bars of the total finger force (F_{TOT}) averaged over each one-second interval and further across subjects in the M-Ramp (**a**) and in the M-Sine tasks (**b**). **c**, **d** The relations between F_{TOT} and V_F in the M-Ramp (**c**) and M-Sine (**d**) tasks. *Thick solid lines* show V_F over the PR–SU interval, and *thin solid lines* show V_F over the SU–PR interval. *Dashed circle* and *arrows* indicate the onset of the task and real time changes of V_F

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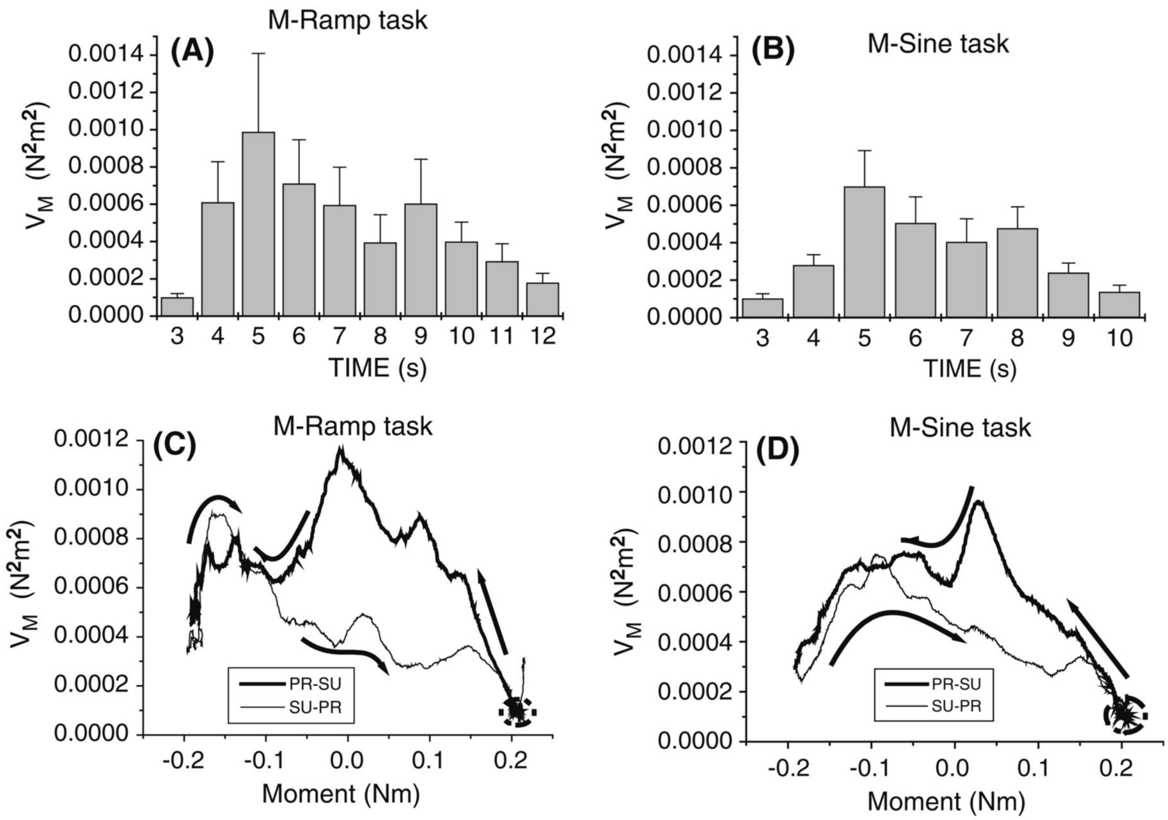

Fig. 5.

a, **b** Time profiles of the variance (V_M) with standard error bars of the total moment (M_{TOT}) averaged over each 1-s interval and further across subjects in the M-Ramp (**a**) and in the M-Sine tasks (**b**). **c**, **d** The relations between M_{TOT} and V_M in the M-Ramp (**c**) and M-Sine (**d**) tasks. *Thick solid lines* indicate V_M over the PR–SU interval, and the *thin solid lines* show V_M over the SU–PR interval. *Dashed circle* and *arrows* indicate the onset of the task and real time changes of V_M

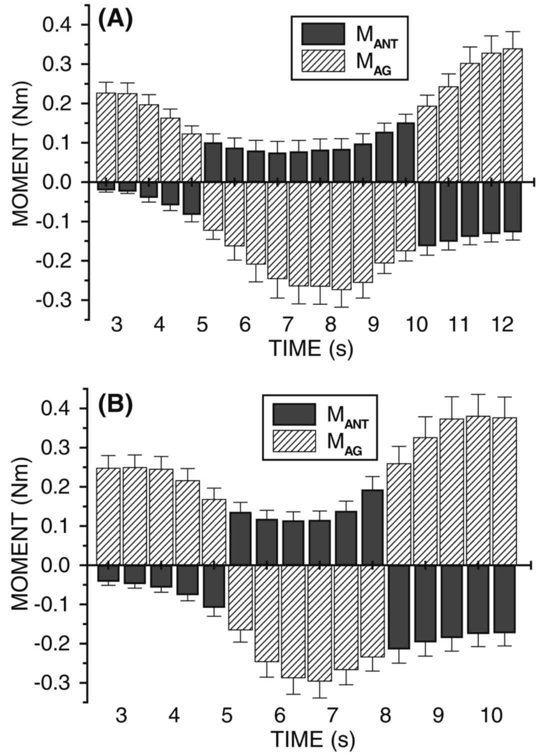

Fig. 6.

Time profiles of the agonist moment (M_{AG}, *striped bars*) and antagonist moment (M_{ANT}, *dark bars*) with standard error bars averaged over half-second intervals and further across subjects for the M-Ramp (**a**) and M-Sine (**b**) tasks

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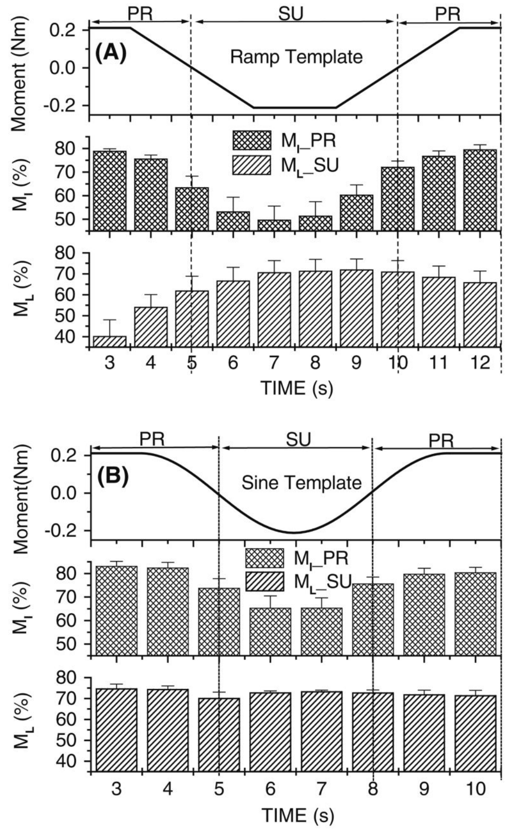

Fig. 7.

Top panels: task template shown on the screen to the subject in each task; *medium panels*: average percentage contribution of the index finger force to the total PR moment (M_I_PR) with standard error bars over each one-second interval and over the 12 subjects; *bottom panels*: Averaged percentage contribution of the little finger force to the total SU moment (M_I_SU) with standard error bars over each one-second interval and over the 12 subjects. **a, b** M-Ramp and M-Sine tasks, respectively

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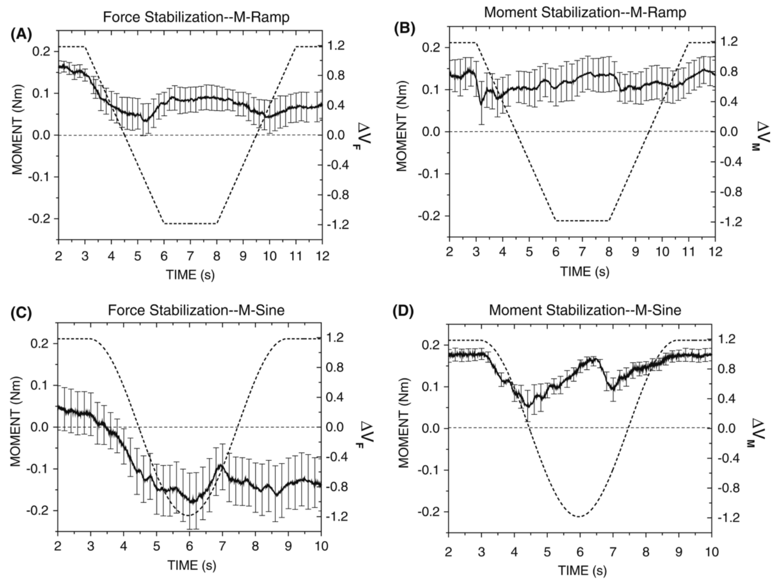

Fig. 8.

Time profiles of ΔV indices computed for the total force and total moment stabilization at each time sample (ΔV_F and ΔV_M, respectively). Averaged across subjects data are shown with standard error bars. a, **b** Indices ΔV_F and ΔV_M for the M-Ramp task; **c, d** ΔV indices for the M-Sine task. *Dashed lines* in each panel refer to task templates. Note the positive values of ΔV_M and lower, sometimes negative values of ΔV_F