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RESEARCH ARTICLE

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Finger coordination during discrete and oscillatory force production tasks

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Abstract We used the framework of the uncontrolled manifold (UCM) hypothesis to analyze the structure of finger force variability in discrete (ramp) and oscillatory force production tasks performed by the index and middle fingers of the right hand acting in parallel. Subjects performed the tasks at fast and slow rates, with and without a visual template presented on the screen. The variance of finger forces was partitioned into two components, compensated variance (V_{COMP}), which did not affect total force, and uncompensated variance (V_{UN}), which affected total force. Only minor effects of task (discrete or oscillatory) and of template (with or without) were seen on the variance profiles, leading us to conclude that the basic principles of synergy organization are common across discrete and oscillatory tasks. In contrast, the rate of force production had major effects on the structure of force variance. A modification of Goodman's model of motor variability was used to analyze the dependences V_{UN} and V_{COMP} on the magnitude of force and on the rate of force production. V_{UN} showed a strong relation to the rate of force production and only weak dependence on the magnitude of force. In contrast, V_{COMP} showed minimal effects of the rate of force production and strong effects of the force magnitude. The findings are interpreted as demonstrations of a limitation in the ability of the central nervous system to organize a two-finger synergy such that errors in the timing of individual finger force profiles are canceling each other's effects on the total force. In contrast, the synergy is efficiently intercompensating errors related to imprecise setting of force magnitudes of the two fingers.

Keywords Variability · Synergy · Redundancy · Finger · Human

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Introduction

The problem of coordinating several effectors in motor tasks has been known for a long time as the problem of motor redundancy or the Bernstein problem (Turvey 1990; Latash 1996). Following the famous Bernstein's formulation (Bernstein 1967), it has been commonly viewed as the problem of elimination of redundant degrees-of-freedom (DOFs, Newell 1991; Vereijken et al. 1992). Different methods have been used to generate unique solutions for such problems (reviewed in Rosenbaum et al. 1995; Latash 1993).

Recently, we have suggested an alternative approach to this problem consistent with the traditions set by Gelfand and Tsetlin (1966). According to this approach (Scholz and Schöner 1999; Latash et al. 2002), the central nervous system (CNS) does not eliminate DOFs. It creates task-specific subspaces within the state space of the elements whose purpose is to stabilize functionally important performance variables. Such subspaces have been addressed as "uncontrolled manifolds" (UCMs). The CNS has been assumed to structure the variability of elements such that it is mostly confined to a UCM, which does not affect a required value of a selected performance variable. As a result, individual elements can show relatively high variability while a functionally important variable shows high stability. The UCM hypothesis has been tested successfully in a variety of tasks ranging from whole body sit-to-stand tasks (Scholz and Schöner 1999; Scholz et al. 2001), single-limb shooting tasks (Scholz et al. 2000), two-limb pointing tasks (Domkin et al. 2002), and multifinger force production tasks (Latash et al. 2001; Scholz et al. 2002).

In many studies, the problem of motor redundancy has been addressed using the notion of motor synergies associated with coordinated changes in the outputs of a number of elements either over a realization of a task (correlated time profiles of the outputs of the elements) or over modifications in task parameters (correlated scaling of the outputs of the elements). The notion of synergy has been used in relation to coordinated outputs of muscles/joints in voluntary multijoint limb movements, force production tasks, quiet standing, locomotion, and other motor actions and reactions (Smith et al. 1985; Desmurget et al. 1995; Wang and Stelmach 1998; Santello and Soechting 2000; Pelz et al. 2001). In contrast, we focus on relations among dispersions in the outputs of elements of a synergy across several task realizations assuming that these relations are reflective of processes underlying the stabilization of performance variables by the synergy (see review in Latash et al. 2002).

In particular, we studied the structure of finger force variability across many trials at certain phases of a motor task that required the production of sine-like oscillatory total force profiles by pressing with two, three, or four fingers of a hand (Latash et al. 2001; Scholz et al. 2002; also reviewed in Latash et al. 2002). One finding was unexpected and even puzzling. Although the subjects were explicitly required to produce total force profiles and given feedback only on the total force, they stabilized the total moment produced by the involved set of fingers with respect to the longitudinal functional axis of the hand/forearm. Such moment stabilization was seen in tasks involving two, three, and four fingers. When only two fingers were involved, the stabilization of moment required positive covariations between finger forces across trials. For example, consider exerting equal downward forces on the two ends of a seesaw. If one of the two forces increases or decreases, it changes its moment with respect to the fulcrum. An equal change in the other force has to happen to balance the changed moment and keep the seesaw from rotating, i.e., a positive covariation between the forces is required to keep the net moment zero. Note that stabilization of total force produced by two fingers obviously requires a negative covariation between finger forces. Hence, stabilization of moment over most of the force cycle duration was accompanied by destabilization of force. Three fingers theoretically can stabilize both force and moment simultaneously. However, in three finger tasks, moment once again was stabilized and force was destabilized. Only when all four fingers participated in such tasks, the subjects were able to avoid force destabilization and stabilize it within a range of the force cycle corresponding to relatively high forces (Scholz et al. 2002).

These results were unexpected since the subjects had never been told anything about moment stabilization; neither were they provided any feedback about the moment. We interpreted this behavior as being biased by the lifetime experience which requires, in most everyday grasping and manipulation tasks, precise stabilization of total moment produced by the fingers with respect to the point of thumb contact, while total force only needs to be above the slipping threshold and below the crushing level. However, the result was observed in only one particular experimental condition: oscillatory force production at a relatively fast rate (2 Hz) with only the peak force levels shown to the subjects, but without an explicit template. It was, therefore, possible that particular experimental features brought about the counterintuitive observation of force destabilization.

In particular, it has been suggested that oscillatory tasks represent a special group of tasks that may be controlled differently from discrete tasks (Sternad et al. 2000). To perform an oscillation at a comfortable frequency, as in our earlier experiments, one can set a "pattern generator," or a limit cycle attractor that would produce the required task with minimal corrective actions from the controller. Such a system can function in a mostly feedforward, autonomous fashion with only infrequent episodes of corrections introduced if it deviates significantly from the prescribed set of parameters (such as central point, amplitude, and frequency). In contrast, a discrete, slow, tracking task requires continuous monitoring and correction of the output of the system.

To analyze whether our results could be affected by the specificity of the oscillatory force production task, we performed similar analysis for a set of tasks that varied in three major aspects. First, they were either oscillatory or discrete. Second, their typical time was either close to that of the first experiment or much slower to emphasize the importance of visual feedback during tracking. And, third, they either involved or did not involve a template presented on the screen that the subjects were supposed to track. All the tasks were performed with two fingers of a hand acting in parallel to contrast total force and total moment stabilization: As mentioned earlier, in two finger tasks, it is impossible to stabilize both force and moment simultaneously. If the subjects are indeed biased by the everyday experience in favor of moment stabilization, we expected to see this bias in all conditions. These expectations were not met, however, and we have been forced to reconsider our previous understanding of the two-finger coordination.

Materials and methods

Subjects

Seven unpaid healthy volunteers, four males and three females, took part as subjects in the experiments. All of them were right handed according to their preferential use of the right hand during writing and eating. The age of the subjects was 28.6±4.2 years. Their weight was 67.4±10.5 kg, and their height 1.73±0.07 m. All the subjects gave informed consent according to the procedures approved by the Office for Regulatory Compliance of the Pennsylvania State University.

Apparatus

During testing, the subject was seated 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. A wooden board supported the wrist and the forearm; two pairs of Velcro straps were used to prevent forearm or hand motion during the tests. A wooden piece shaped to fit comfortably under the subject's palm was placed underneath the palm to help maintain a constant configuration of the hand and fingers. The subject viewed the monitor, which displayed the sum of the forces produced by individual fingers (Fig. 1).

Four piezoelectric sensors (Model 208A03, Piezotronic, Inc.) were used for force measurement. Analog output signals from the sensors were connected to separate AC/DC conditioners (M482M66, Piezotronic, Inc.). The system was operating in a DC-coupled mode, utilizing the sensor's discharge time constant as established by the built-in microelectronic circuit within the sensor. As such, the sensor's time constant was theoretically infinite. Actually, each sensor gave approximately 1% error over the typical epoch of recording of a constant signal. Cotton covers were attached to the upper surface of the sensors to increase friction and prevent the influence of finger skin temperature on the measurements. The sensors were placed under each finger of the right hand.

The sensors were mounted inside a steel frame (140×90 mm, see Fig. 1). The position of the sensors could be adjusted in the forward-backwards direction within a range of 60 mm, to fit the individual subject's anatomy. The steel frame with sensors was placed inside a groove in the wooden board and positioned so that the subject could place his or her fingers comfortably on the sensors/posts while preserving the described arm configuration. A Gateway 450-MHz microcomputer was used for data acquisition and processing. The force measured by each sensor was sampled at 50 Hz.

Procedure

Each experiment started with a series of trials at maximal force production (maximal voluntary contraction, MVC). During MVC tests, the subjects were asked to produce maximal force by pressing on the sensors using each of the following finger combinations (I, M, R, L, IM, and IMRL). The computer generated two tones ("get ready"); then a trace showing the total force produced by the explicitly involved 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 then to relax. They were instructed to pay no attention to possible force generation by other, "uninvolved" fingers as long as the explicitly involved fingers generated their peak force. Each subject performed two trials using each finger combination. The trial with the highest force produced by the explicitly involved fingers was kept as a reference to adjust the target forces in the two others tests.

Then, Ramp tests were run. The purpose of the Ramp tests was to generate linear estimates of the relations between changes in individual finger forces and in the total force during a multifinger task. These relations are non-trivial because of the phenomenon of enslaving (Li et al. 1998). As demonstrated in previous studies, patterns of finger enslaving show nearly linear relations between the force produced by a master finger and forces produced by slave fingers within a large range of forces (Li et al. 1998; Zatsiorsky et al. 1998, 2000). To be conservative, we asked the subjects to produce ramp patterns of force from 0% to 40% of MVC by pressing with only one finger in each separate trial. An oblique red line was shown on the screen, and the subject's task was to trace this line in time with the cursor representing the sum of the I and M finger forces. All ramp tasks were performed twice, and the average of the two trials was used to estimate the effect of enslaving for further analysis.

There were eight main experimental conditions. In each condition, the subject was asked to produce a certain pattern of total force while pressing with the IM finger combination. Subjects were explicitly instructed not to lift the ring (R) and little (L) fingers off the sensors, as well as not to pay attention to possible force generation by these fingers. As a result, the R and L fingers produced forces, but, in all conditions, the total force displayed on the screen was the sum of the I and M finger forces.

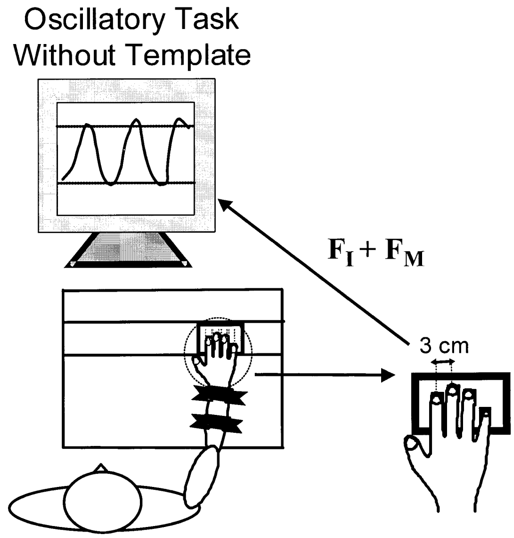

Fig. 1 Illustration of the experimental setup. All four fingers of the right hand rested on the force sensors. The task was to produce oscillatory force or discrete ramp force over short or long time intervals. The screen showed the subject the actual value of total force produced by the index and middle fingers and either a template curve or only peaks and troughs that the total force was supposed to reach

Three experimental factors were manipulated:

Task (oscillatory vs discrete). In oscillatory tasks, the subjects were required to produce a smooth sine-like curve on the monitor screen with the combined force of the two fingers (IM) such that the peaks of the curve were at 5% and 25% of the IM MVC. In discrete tasks, the subjects were required to produce ramps of force up from 5% to 25% and down from 25% to 5% of the IM MVC. Two red horizontal lines were used to show the required peak values of force in all trials.

Speed (fast vs slow). In oscillatory tasks, the frequency was either 1.25 Hz or 1/6 Hz corresponding to the cycle duration of 0.8 s or 6 s respectively. In discrete tasks, the time of ramp change was set at either 400 ms or 3 s.

Template (with vs without). In some trials, a template curve was drawn on the screen that the subjects were supposed to follow. In other trials, only points or horizontal line segments showing the extrema of the required force profiles were shown on the screen. During the discrete tasks, the subjects were asked to connect segments with straight lines. During the oscillatory task, they were asked to connect points with a smooth sine-like curve.

The three experimental factors were crossed with each other for a full design, leading to eight experimental conditions. The duration of each fast trial was 11 s, and the duration of each slow trial was 22 s. Within each discrete trial, the subject produced a sequence of up and down ramps separated with 2-s intervals of constant force production until the end of the trial. Within each oscillatory trial, the subjects produced a continuous force oscillation over the trial duration. The number of trials per condition was adjusted such that each subject performed the total of 45 ascending and descending ramps for each discrete task, and the total of 45 cycles for each oscillatory tasks. This required two visits by each subject to the laboratory. MVC and Ramp tests were run on each visit. Prior to each condition, the subjects had a few practice trials (typically, five trials) until they reported feeling comfortable with the task. The intervals between successive trials were about 15 s. The order of the tests as well as the order of the experimental conditions was pseudo-randomized among subjects. Subjects never reported fatigue.

Data processing

For MVC tests, the finger forces were measured at the moment when the maximal total force value was reached for the explicitly involved fingers. The highest value over the three trials was used as a reference for other tests.

For each Ramp-test trial, we performed linear regressions for the total force displayed on the screen during the experiment, and for the force produced by individual fingers. For Ramp-test trials performed with a particular finger serving as the master finger, the onset of the ramp and time at which 40% MVC was reached were determined. Although the target force in the actual experiments was 25% of MVC, we had subjects exert forces up to 40% MVC in these trials to ensure that the relations between individual finger forces and the total force were linear beyond the actual range of forces used in the experiments. The trials were then cut at these points and normalized to 100%, then averaged. The change of total force and of each individual finger force was determined. A 2-by-2 enslaving matrix (ENSL) was then constructed as follows:

$$\mathrm{ENSL} = \begin{bmatrix} \Delta fi, i/\Delta Fi & \Delta fi, m/\Delta Fm \\ \Delta fm, i/\Delta Fi & \Delta fm, m/\Delta Fm \end{bmatrix}, \tag{1}$$

where $\Delta f_{j,k}$ and ΔF_k are the changes of individual finger force j (j={index (i), middle (m)}) and the change of total force produced during the ramp when finger k (k={index (i), middle (m)}) was the instructed master finger. This matrix is a linear approximation of a matrix containing partial derivatives $\delta f_{j,k}/\delta F_k$ where $\delta f_{j,k}$ and δF_k are the infinitesimal changes of individual and total finger forces. We will use a term "force mode" for a combination of individual finger forces produced when the subject is asked to press with only one finger.

The data obtained in the main series were analyzed as follows. For oscillatory trials, individual cycles were cut such that each cycle started at the time of force minimum and ended at the time of the next force minimum. We applied the following exclusion criteria to individual cycles to eliminate obvious mistakes. The onsets of the ascending (or descending) limbs of the force increase (or decrease) were determined for all trials of each ramp or oscillatory condition. Each trial was then aligned at the onset sample and the remaining data plotted up to the force maximum. Horizontal bars were plotted at 20–30% (target peak force was 25%) and at 2–10% of the MVC (target valley force was 5%). In addition, the mean period of the force increase (or decrease) was obtained and vertical bars representing ±10% of the mean period were plotted. Individual trials were then replotted in a different color and selected or rejected by the user via an interactive Matlab program. Thus, the force peaks had to be within the range from 20% to 30% of MVC (target peak force was 25%), the force valleys had to be within the range from 2% to 10% of the MVC (target valley force was 5%) and the duration of the increase or decrease had to be within the range of ±10% of the mean duration (which was typically close to the intended duration). All the trials meeting these spatial and temporal criteria were kept for further analysis.

Each data point was expressed as a percentage of movement time. In further statistical analysis, the data were averaged over quartiles of the trajectory. For discrete trials, ramp-up and ramp-down trials were analyzed separately. For oscillatory trials, the ascending and descending limbs of each cycle were analyzed separately. All trials were aligned by the initiation of force increase or decrease. The number of excluded trials for each condition is reported in the "Results" section.

Ignoring the effects of enslaving, the following formulation of the relationship between variations in individual finger forces and changes in the total force (F_{TOT}) would apply.

$$d\mathrm{F_{TOT}} = \begin{bmatrix} 1 & 1 \end{bmatrix} * \begin{bmatrix} dfi \\ dfm \end{bmatrix} \tag{2}$$

The enslaving effect, however, may induce a structure in the variability of individual finger forces that may be unrelated to a particular task variable. To eliminate such enslaving-induced correlations, we transform the individual finger forces into a set of force modes, **m**:

$$\mathbf{m} = ENSL^{-1} * \begin{bmatrix} dfi \\ dfm \end{bmatrix}, \tag{3}$$

When, for instance, the instruction asks for only the index finger to be used, the corresponding mode is $[1\ 0]^T$, which leads to the observed patterns of finger forces through the inverse transformation:

$$\begin{bmatrix} df_i \\ df_m \end{bmatrix} = ENSL * \mathbf{m} \tag{4}$$

Change in total force can now be expressed as a function of these mode variables:

$$dF_{TOT} = \begin{bmatrix} 1 & 1 \end{bmatrix} * ENSL * \mathbf{m} \tag{5}$$

We tested a hypothesis that F_{TOT} is stabilized against fluctuations in finger forces. This hypothesis accounts for one degree of freedom, so that the two-dimensional space of the finger forces is redundant. The analysis was performed on all samples of the ascending and descending limbs of the force oscillation cycle, the period of which was defined as the time from one force minimum to the next, and of the force ramp, defined from the beginning to the end of the ramp. At each time, we assumed that the mean total force across all trials represented the value that the nervous system tries to stabilize. These values were calculated from the means of the individual finger forces (f^0) across all task repetitions. Thus, in Eqs. 2, 3 and 4, $df_j=(f-f^0)$. The mean values of the individual finger forces constitute the reference force configurations for each interval of analysis. The linearized model is described by Eq. 5 above when accounting for the effects of enslaving. Multiplying the vector of force deviations from the mean by the inverse of the enslaving matrix (i.e., $\mathrm{ENSL}^{-1}\times(f-f^0)$) yields deviations in force modes.

An uncontrolled manifold can be computed in the space of the mean-free finger force modes. It represents individual finger force mode combinations that are consistent with a stable value of total force ($dF_{TOT}=0$). The manifold is approximated linearly by the null-space spanned by basis vectors, $\mathbf{e}_i$, solving:

$$0 = \begin{bmatrix} 1 & 1 \end{bmatrix} * ENSL \cdot \mathbf{e}_i \tag{6}$$

There is one nullspace basis vector, so that the null space has one dimension. The basis, e_i, of the null space was computed numerically at each recorded sample using Matlab. The vector of individual mean-free finger force modes, obtained at each sample of the ascending and descending limbs of each force oscillation and force ramp, i.e., $\mathbf{m}=\mathrm{ENSL}^{-1}\times(f-f^0)$, was resolved into its projection onto the null space:

$$f_{||} = \sum_{i=1}^{n-d} (\mathbf{e}_i^T \cdot \mathbf{m})\mathbf{e}_i \tag{7}$$

and the component perpendicular to the null space:

$$f_{\perp} = \mathbf{m} - f_{||} \tag{8}$$

The amount of variance per DOF within the uncontrolled manifold was estimated as:

$$\sigma_{||}^2 = \sum_{trials} |f||^2 \Big/ (N_{trials}), \tag{9}$$

where $\left|f_{||}\right|^2$ is the squared length of the deviation vector lying within the linearized UCM. Analogously, the amount of variance per DOF perpendicular to the uncontrolled manifold was estimated as:

$$\sigma_{\perp}^2 = \sum_{trials} |f_{\perp}|^2 \Big/ (N_{trials}). \quad (10)$$

The primary dependent variables used in subsequent analyses are: $\sigma_{||}^2$ and $\sigma_{\perp}^2$, and are referred to, respectively, as variance per DOF that is compensated (V_{COMP}) and that is uncompensated (V_{UN}).

Statistical procedures

Standard descriptive statistics were used. Repeated measures ANOVAs were used with the factors Task, Speed, and Template described earlier. Certain analyses also used a repeated factor "quartile of the trajectory" (Q-Traj) to compare values averaged over the four quartiles. This factor was included because a previous study revealed differences in the control of force and moment at different phases of the force trajectory, reflected in the relative amounts of V_{COMP} and V_{UN} (Scholz et al. 2002). To simplify the analyses of variance, we used as the dependent variable the ratio of V_{UN} to V_{COMP}, or R_V. The ratio is, perhaps, a more appropriate dependent variable in this context because of the fact that force variability increases with total force (Newell et al. 1984), which increases across the factor Q-Traj. A large value of R_V indicates that V_{COMP}>>V_{UN}, consistent with force stabilization, while a value of R_V≤1 (V_{COMP}≤V_{UN}) indicates a lack of force stabilization. M-matrix contrasts in SPSS were used for post hoc comparisons.

Results

Typical patterns of force variance

All subjects performed all of the tasks without apparent difficulty. However, a substantial number of trials were rejected based on the acceptance criteria (see "Materials and methods"). The average across subjects percentage of rejected trials was 24.3±11.5% for the ascending limbs of movements, and it was 23.8±10.2% for the descending limbs of movements. Table 1 presents the average and range (across subjects) of the percentage of trials rejected for each condition and direction of movement. While the percentage of rejected trials did not differ significantly between the slow and fast ramp conditions (21.2±2.2% vs 22.6±3.1%), a significantly larger number of trials were rejected for the slow oscillatory conditions (33.8±2.9%) compared to the fast oscillatory conditions (17.8±2.0%; $F_{(1,5)}$=6.79, P<0.05).

All accepted trials were processed as described in "Materials and methods." The variance components, V_{UN} and V_{COMP}, were computed at every recorded sample value of the ascending and descending limbs of both the oscillatory task and of the ramp (discrete) task.

Two qualitatively different patterns of the observed behavior of V_{UN} and V_{COMP} are illustrated for a representative subject in Fig. 2. The left top panel shows variance profiles for a slow ramp task performed with the template, while the right top panel shows these profiles for a fast oscillatory task performed without a template. There were two major differences between the results of the two conditions. First, the increase in V_{COMP} (bold solid line) that occurred with increasing force (from 0% to 100% of the trajectory) was greater for the slow ramp trials compared to the fast oscillatory trials. Second, V_{UN} (dashed line) remained nearly constant as the force increased in the ramp task (Fig. 2, top left panel) while V_{UN} increased to a peak near the middle of the fast oscillatory force trajectory and then decreased thereafter. As a result, V_{UN} was significantly lower than V_{COMP}, corresponding to total force stabilization, throughout most of the trial for the slow ramp task. This was true only for the last half of the force trajectory in the fast oscillatory task.

Five of seven subjects showed a pattern of results similar to those illustrated in the top panels of Fig. 2. Further statistical analyses were run using their data. Two subjects showed a different control strategy for both the force ramps and force oscillations performed at fast speeds. An example of one subject's data is illustrated in the bottom panels of Fig. 2. First, these two subjects had a much lower overall variance (compare the different scales of the top and bottom panels), which was due, in part, to the fact that their MVC was substantially smaller (47.5±6.5 N) than for the other subjects (116.3±5.4 N). The relative amount of V_{COMP} and V_{UN} for these two subjects was similar to that of the other five subjects for the slow conditions, whether involving a force ramp or force oscillation (cf. left bottom and upper panels, Fig. 2). In contrast, for the fast oscillatory task without a template (bottom right panel, Fig. 2) and, indeed, for all ramp and oscillatory conditions performed at fast speeds, these two subjects showed little difference between the variance components, and both V_{COMP} and V_{UN} were quite low.

The results for the descending limb of the ramp and oscillatory trials differed somewhat quantitatively, but not qualitatively from those for the ascending limb of the

Table 1 Percentages of rejected trials for different tasks. Average (across seven subjects) percentages and range (*parentheses*) of recorded ramps or sinusoids (± SD) that were rejected based on the criteria described in the "Materials and methods." Criteria were applied separately for the ascending and descending limbs of the ramps or sinusoids

Speed of movement	Limb of trajectory	Slow with template	Slow without template	Fast with template	Fast without template
Ramp	Ascending	20±6.7% (13–30%)	21±9.8% (10–33%)	19±12.3% (0–40%)	18±14.7% (1–40%)
	Descending	21±8.5% (7–14%)	22.4±7.6% (13–33%)	33.8±9.9% (20–47%)	20.8±11.4% (0–37%)
Sine	Ascending	36.7±5.3% (31–46%)	35±10% (20–51%)	20±13.2% (1–47%)	24±19.7% (1–51%)
	Descending	40.4±6.3% (31–51%)	23.7±13.0% (9–43%)	13.3±13.8% (0–36%)	15±11.3% (0–34%)

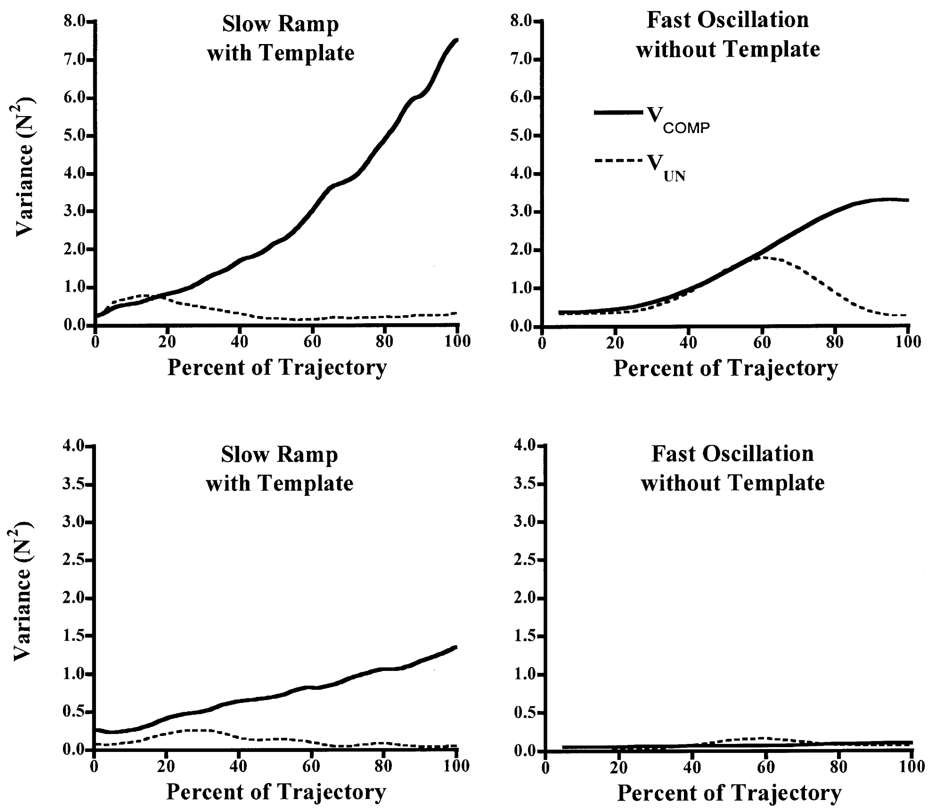

Fig. 2 Time profiles of the two components of variance V_{UN} (*dashed lines*) and V_{COMP} (*solid lines*), for a "typical subject" (the *top panels*) and for an "atypical subject" (the *bottom panels*). The subjects performed either a slow ramp force production task with the template profile shown on the monitor screen (the *left panels*) or a fast oscillatory force production task without a template profile (the *right panels*). Ascending limbs of the ramp and cyclic force profiles were analyzed

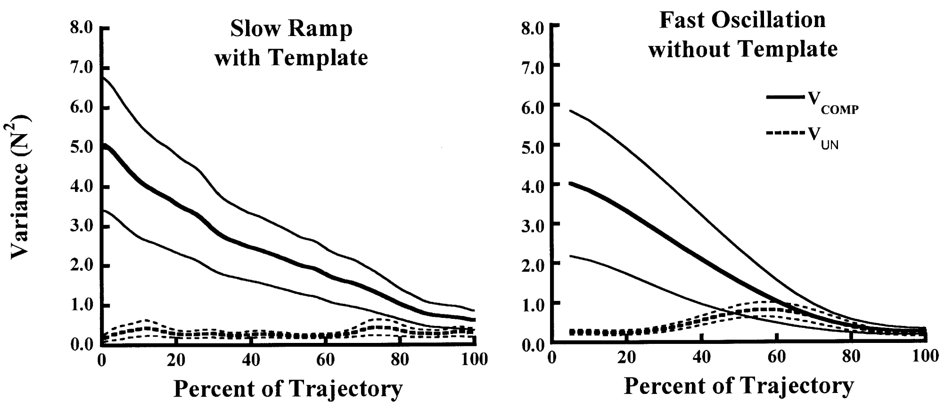

Fig. 3 Time profiles of the two components of variance V_{UN} (*dashed lines*) and V_{COMP} (*solid lines*), averaged across the five "typical subjects," performing either a slow ramp force production task with the template profile shown on the monitor screen (the *left panel*) or a fast oscillatory force production task without a template profile (the *right panel*). Descending limbs of the ramp and cyclic force profiles were analyzed. *Thin lines* show mean profiles ± 1 SE

force trajectories. These results are illustrated in Fig. 3, where the average variance components across the five subjects discussed above are presented for the same two conditions as in Fig. 2.

The two tasks illustrated in Fig. 2 differ in three major ways, rate of force change, type of force trajectory and visual information about the required trajectory. To analyze which of these three factors brought about the qualitative differences in the relations between V_{UN} and V_{COMP}, a complete 2×2×2 experimental design was run.

Effects of task, force rate, and visual feedback on profiles of V_{COMP} and V_{UN}

Figures 4 (slow conditions) and 5 (fast conditions) present the average values of V_{COMP} and V_{UN} for the ascending limb of each task of the five subjects exhibiting results similar to those illustrated by the top panels of Fig. 2. The top two panels in each figure present the results for the ramp tasks with (left) and without (right) a template. The bottom panels show the same results for the oscillatory

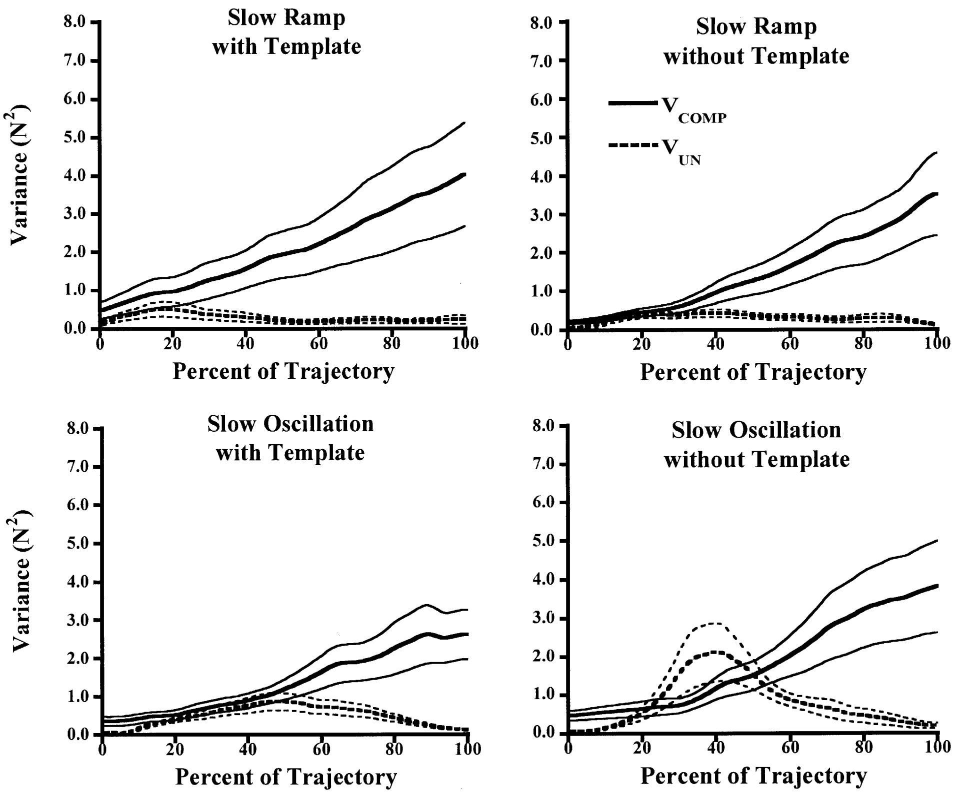

Fig. 4 Time profiles of the two components of variance V_{UN} (*dashed lines*) and V_{COMP} (*solid lines*), averaged across the five "typical subjects," performing either a slow ramp force production task (the *top panels*) or a slow oscillatory force production task (the *bottom panels*) with (the *left panels*) or without the template (the *right panels*). Ascending limbs of the ramp and cyclic force profiles were analyzed. *Thin lines* show mean profiles ± 1 SE

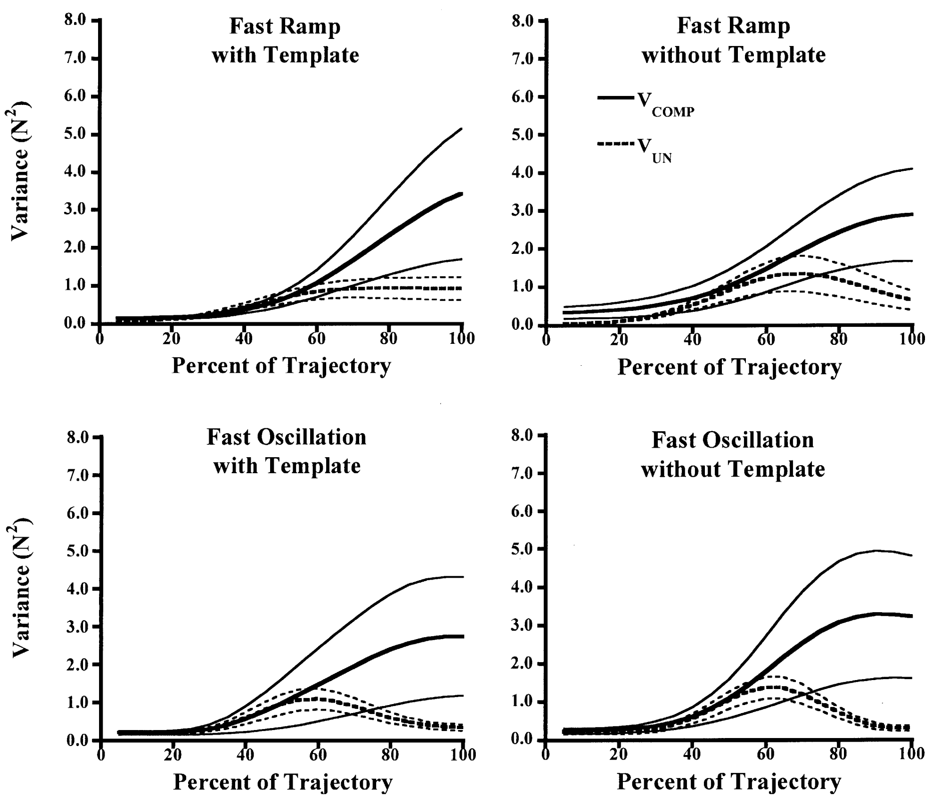

Fig. 5 Time profiles of the two components of variance V_{UN} (*dashed lines*) and V_{COMP} (*solid lines*), averaged across the five "typical subjects," performing either a fast ramp force production task (the *top panels*) or a fast oscillatory force production task (the *bottom panels*) with (the *left panels*) or without the template (the *right panels*). Ascending limbs of the ramp and cyclic force profiles were analyzed. *Thin lines* show mean profiles ± 1 SE

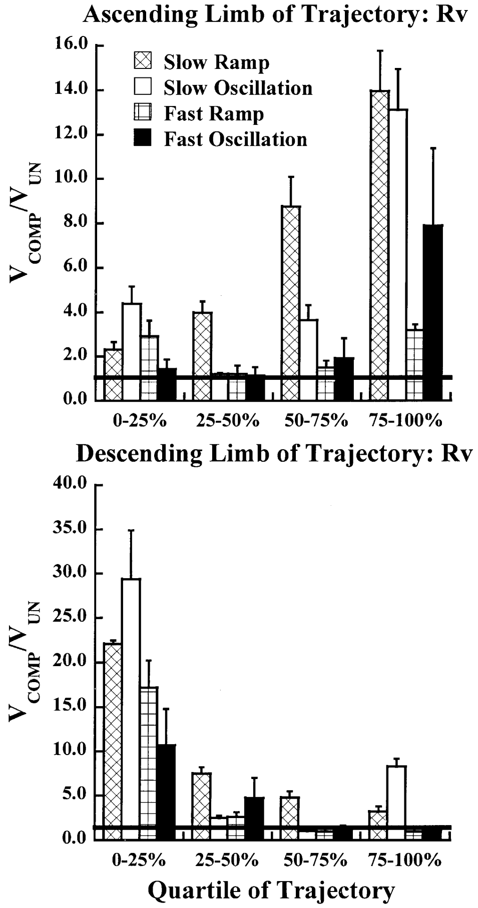

Fig. 6 The ratio between the two variance components ($R_V=V_{COMP}/V_{UN}$) was averaged over each of four quartiles of the force trajectory. Average values across the subjects are presented for the ramp force production tasks (*bars with patterned fill*) and oscillatory force production tasks (*open and black bars*) with standard error bars. The *two leftmost bars at each quartile* represent the slow force production conditions while the *two rightmost bars* represent the fast conditions. The results for the ascending (the *top panels*) and descending (the *bottom panels*) limbs of the force profiles are shown

tasks. The following qualitative observations can be made.

First, the presence of a template appeared to affect only V_{UN} in the slow oscillatory task (Fig. 4, bottom panels). Because there were no significant main effects or interactions involving template in the ANOVAs, we dropped this factor to further simplify the statistical analyses. Second, a comparison of the four panels of Figs. 4 and 5 suggests little qualitative difference in the variance structure between ramp and oscillatory force trajectories, especially when those trajectories there were performed at a fast speed. In each case, V_{COMP} increases with increasing force across the trajectory while V_{UN} increases toward the middle of the trajectory and then decreases thereafter. Thus, in these conditions total force was not stabilized very well, especially in the first part of the force trajectory, at lower forces. In contrast, for the slow ramp trials, V_{COMP} increased with force as for the other conditions, but V_{UN} remained relatively flat and lower than V_{COMP} throughout the force trajectory.

Figure 6 illustrates values of R_V (V_{COMP}/V_{UN}) averaged across subjects for different tasks at each quartile of the ascending (upper panel) and descending (bottom panel) limb of the force trajectories. The solid horizontal line in the figure indicates a ratio of 1 ($V_{COMP}=V_{UN}$). ANOVAs for both ascending and descending limbs revealed significant main effects for Q-Traj (Ascending: $F_{(3,12)}=29.4$, $P<0.001$; Descending: $F_{(3,12)}=75.95$, $P<0.001$) and Speed ($F_{(1,4)}=184.7$, $P<0.001$; $F_{(1,4)}=13.4$, $P<0.05$), as well as a significant Speed by Q-Traj interaction ($F_{(3,12)}=6.1$, $P<0.01$; $F_{(3,12)}=5.4$, $P<0.05$). The speed effect was due to the tendency for R_V to be higher (i.e., a greater difference between V_{COMP} and V_{UN}) when the tasks were performed slowly (the leftmost pair of bars at each quartile in Fig. 6), especially for the ascending limb. R_V was also largest at the highest forces (75–100% of the ascending limb and 0–25% of the descending limb; top and bottom panels of Fig. 6, respectively), indicating better force stabilization at the higher forces.

Post hoc contrasts largely confirmed the differences discussed above. R_V was significantly larger for the slow ramp compared to the slow oscillatory and both fast conditions in the middle quartiles of the force trajectory (for all comparisons, $F_{(1,4)}\geq 9.6$, $P<0.05$). This was due primarily to an increased V_{UN} component in the latter conditions during this period (e.g., Figs. 4, 5). No differences in R_V between the fast ramp and oscillatory conditions were found, even at the highest forces (Fig. 6; $P>0.22$ for all quartiles).

A linear model for the two components of variance

Patterns illustrated in Figs. 2, 3, 4, and 5 suggest that the two components of variance show different relations to the instantaneous values of total force (F_{TOT}) and its first time derivative (dF_{TOT}/dt). In both ramp and oscillatory tasks, both fast and slow, V_{COMP} changes parallel those of F_{TOT} and do not show any obvious changes with dF_{TOT}/dt. In contrast, V_{UN} shows little change with F_{TOT}, particularly obvious during the slow trials while it tends to show peaks near the time when dF_{TOT}/dt is maximum, particularly obvious for the fast trials.

To analyze further these relations, we used a simple linear model:

$$\begin{aligned} V_{COMP} &= a_1 * F_{TOT} + c_1 \\ V_{UN} &= a_2 * F_{TOT} + b_2 * dF_{TOT}/dt + c_2, \end{aligned} \quad (11)$$

where a, b, and c with subscripts 1 and 2 are constants.

Figure 7 shows averaged (across subjects) time profiles of V_{UN} (thick traces) and dF_{TOT}/dt (thin traces) with standard errors (dashed lines) for slow and fast, ramp and oscillatory tasks performed without a template. Since the presence of the template did not play a major role, we have decided to present illustrations only for these

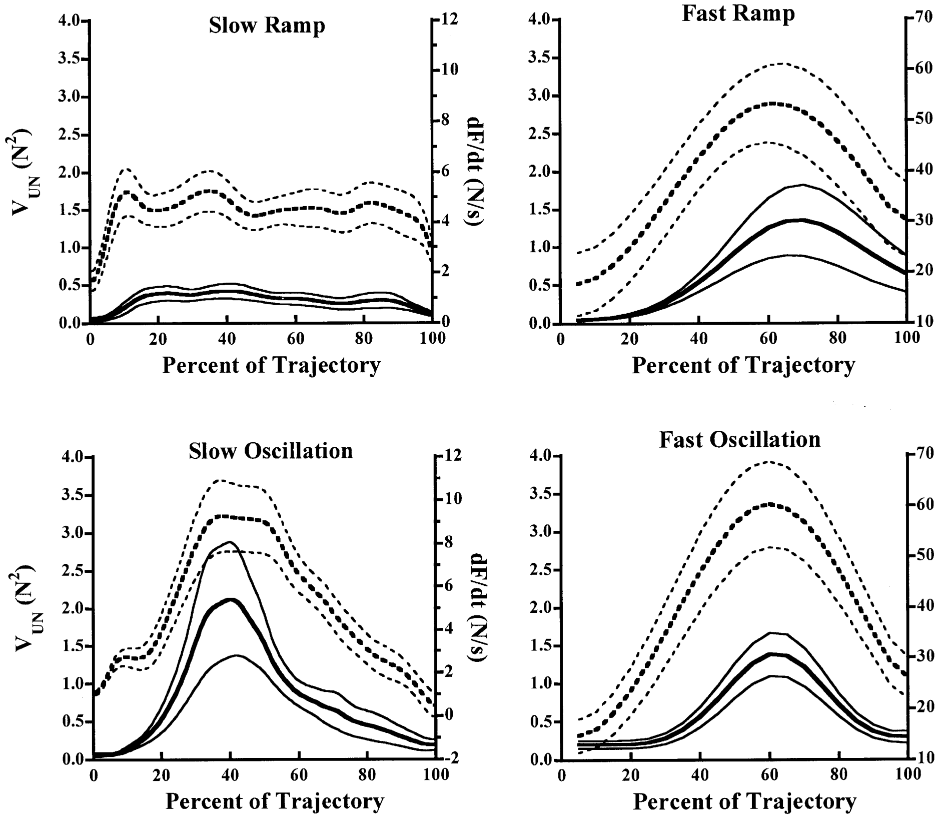

Fig. 7 Time profiles of the rate of force production (*dashed thick lines in the top of the graphs*) and of V_{UN} (*solid thick lines on the bottom of the graphs*), averaged across subjects, are shown for the slow (the *left panels*) and fast (the *right panels*) trials at the ramp (the *top panels*) and oscillatory (the *bottom panels*) tasks. *Thin lines* show mean profiles ± 1 SE. Note the similarities between the pair of time profiles

Table 2 Results of regressions of V_{UN} with total force and rate of force change. Results are shown for the ascending force trajectory. The first letter in the abbreviations in the upper row stands for the task (*R* ramp, *C* cyclic); the second letter shows the speed (*S* slow, *F* fast); and the third letter shows the presence (*T*) or absence (*N*) of the template

V_{UN} vs total force and dF/dt	RSN	RST	CSN	CST	RFN	RFT	CFN	CFT
R^2	0.713	0.558	0.711	0.775	0.661	0.814	0.840	0.815
P value	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
c_2	–0.124	–0.138	–0.396	–0.280	–0.442	–0.283	–0.347	–0.279
a_2	0.00144	–0.0054	0.00665	–0.0118	0.02175	0.02635	0.00517	0.00506
b_2	0.09088	0.112	0.226	0.125	0.02454	0.0207	0.02266	0.01972

Table 3 Results of regressions of V_{UN} with rate of force change. Results are shown for the ascending force trajectory. Abbreviations are the same as in Table 2

V_{UN} vs dF/dt	RSN	RSP	SSN	SSP	RFN	RFP	SFN	SFP
R^2	0.712	0.548	0.709	0.748	0.639	0.786	0.838	0.812
P value	0.0001	0.0001	0.0001	0.0001	0.001	0.001	0.001	0.001
c_2	–0.120	–0.153	–0.347	–0.218	–0.389	–0.263	–0.332	–0.264
b_2	0.0935	0.102	0.320	0.136	0.02871	0.0271	0.0236	0.02058

conditions. Figure 8 shows similarly organized curves for time profiles of V_{COMP} (thick traces) and F_{TOT} (thin traces). There are obvious similarities between the pairs of curves presented in each panel of both Figs. 7 and 8.

Results of linear regression analysis based on Eqs. 11 are presented in Table 2 for the relationship between V_{UN} and F_{TOT} and dF_{TOT}/dt. All the results were highly significant. In particular, the model accounted for 55–84% of the total variance of V_{UN}. The slower tasks typically had the worse fits, the poorest being for the slow ramp task with a template. We purposefully used both F_{TOT} and dF_{TOT}/dt in the model for V_{UN} to test possible relations of V_{UN} to F_{TOT} on top of the apparent relation to dF_{TOT}/dt. When a similar analysis was run using a model $V_{UN}=b_2 \times dF_{TOT}/dt+c_2$ (Table 3), the total amount of variance dropped only slightly, by 2.7% in the worst case. The results of regressing V_{COMP} on F_{TOT} are presented in Table 4. These relationships were highly

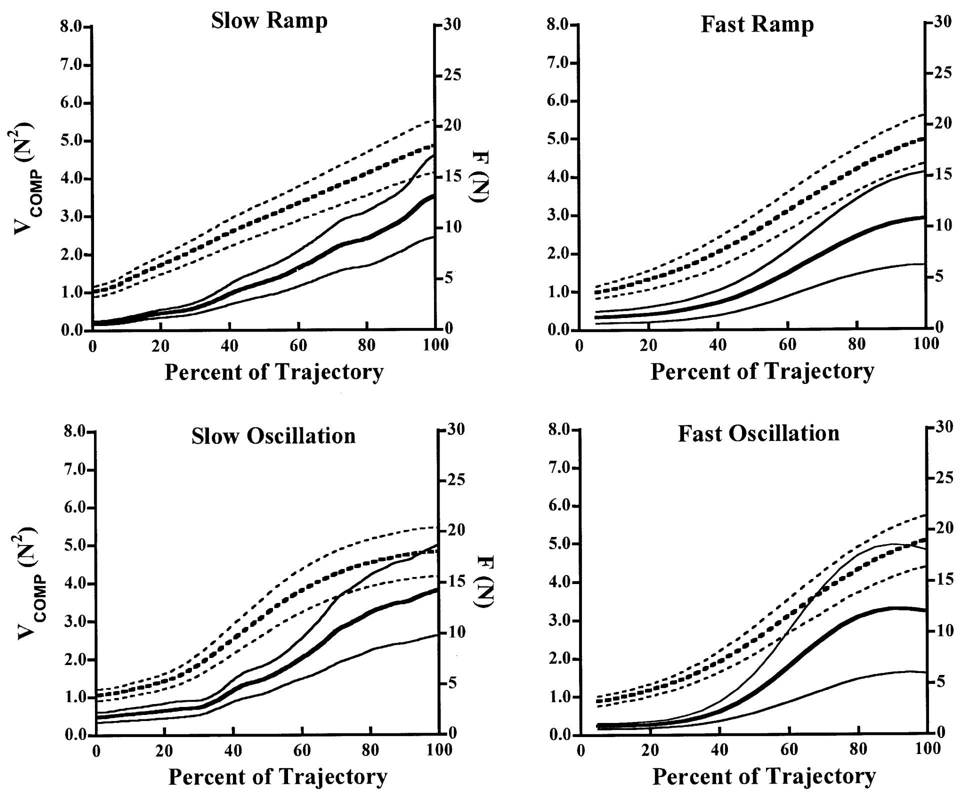

Fig. 8 Time profiles of the force (*dashed thick lines at the top of the graphs*) and of V_{COMP} (*solid thick lines at the bottom of the graphs*), averaged across subjects, are shown for the slow (the *left panels*) and fast (the *right panels*) trials at the ramp (the *top panels*) and oscillatory (the *bottom panels*) tasks. *Thin lines* show mean profiles ± 1 SE. Note the similarities between the pair of time profiles

Table 4 Results of regressions of V_{COMP} with total force. Results are shown for the ascending force trajectory. Abbreviations are the same as in Table 2

V_{COMP} vs total force	RSN	RSP	SSN	SSP	RFN	RFP	SFN	SFP
R^2	0.817	0.831	0.521	0.695	0.343	0.518	0.521	0.409
P value	0.0001	0.0001	0.0001	0.0001	0.001	0.0001	0.0001	0.0001
c_1	−1.127	−1.286	−0.418	−0.413	−0.326	−0.921	−1.174	−0.936
a_1	0.232	0.308	0.194	0.169	0.155	0.249	0.265	0.220

significant but generally somewhat weaker than for those between V_{UN} and dF_{TOT}/dt. The variance of F_{TOT} explained between 34% and 83% of the variance of V_{COMP}, the fits being largest for the slow ramp tasks.

Discussion

In the current study, the effects of three factors on the patterns of two components of finger force variability were investigated. Namely, subjects performed different tasks (a discrete ramp and an ongoing oscillation), at different speeds, and with or without an explicit template. Our analysis was based on the uncontrolled manifold (UCM) hypothesis, which assumes that the variance of outputs of elements participating in a multielement task is organized in such a way that significantly more variance lies within a manifold (UCM), which preserves a desired value of a functional output variable. We addressed this variance component as compensated variance (V_{COMP}) while the other component, which is orthogonal to the UCM, has been addressed as uncompensated variance (V_{UN}). Earlier studies have supported this approach within a variety of motor tasks (reviewed in Latash et al. 2002). Four results of this study are of particular interest.

Individual differences in control strategy

Two of the seven subjects appeared to use a different force control strategy during fast force production trials, regardless of whether they were discrete or oscillatory (Fig. 2, bottom right panel). They appear to have stabilized total force by keeping the variability of each finger's force low. Their data were similar to those of an "atypical subject" described in our earlier study of fast force production tasks (Latash et al. 2001). Observations of such "atypical" behaviors show that the UCM method is able to distinguish different strategies of coping with tasks involving an abundant set of effectors. During the slow ramp and oscillatory trials, these two subjects selectively channeled the individual finger force variance into V_{COMP}, although their variance components were still smaller than those of the other subjects matching their relatively low maximal finger forces.

Control of discrete vs oscillatory tasks

Although our study addressed only force production and not movement, the similarity of our findings for discrete and oscillatory tasks does not support the hypothesis that discrete and oscillatory movements represent two qualitatively different classes with qualitatively different control structures (cf. Sternad et al. 2000). Our analysis of the coordination of two finger forces revealed only one significant interaction effect involving the ramp and oscillatory tasks, namely a difference between slow ramp and slow oscillatory force production trials in the ratio $R_v=V_{COMP}/V_{UN}$ averaged over the middle quartiles of the force trajectory (Fig. 6). We should emphasize, however, that slow ramp trials were characterized by very irregular dF/dt profiles as compared to slow oscillatory trials (e.g., Fig. 7a). Since V_{UN} has shown a strong relation to the rate of force change (Fig. 7, Tables 2 and 3), the irregularities in the actual dF/dt profiles during slow ramp tasks were likely to bring about the mentioned differences in R_v. No differences were observed between the fast ramp and cyclic force production tasks. Our observations are more compatible with an earlier suggestion that discrete and oscillatory actions are products of similar central organizations and differ only in the timing of their initiation and/or termination (Schöner 1990). For example, according to the latter view, a discrete movement can be viewed as half a cycle of an oscillatory movement. This view also seems to us more parsimonious since it assumes the existence of a single control structure for all movements rather than two separate control structures. It remains to be seen, however, if our results can be generalized to tasks involving movement.

Force vs moment stabilization

When two fingers of a hand produce force on an object that can rotate about an axis located between the points of force application (for example about an axis passing through a point of thumb contact or through a point of contact with an external object), stabilization of their total moment with respect to this axis is incompatible with stabilization of their total force. The former requires a positive covariation of the forces produced by the fingers while the latter requires a negative covariation. Note that the phenomenon of finger enslaving, by itself, brings about an increase in the force of a finger when another finger shows an increase in its force (Zatsiorsky et al. 1998, 2000). As such, enslaving tends to bring about a positive covariation between the finger forces contributing to moment stabilization and acting against force stabilization.

Imagine now that a central controller tries to stabilize a time profile of total force (as it was required in our experiments) by selecting a particular sharing pattern between the two fingers, for example 50:50, and generating required individual finger force profiles with a certain error margin. Let us assume that control signals to the two fingers are not correlated. In this case, enslaving will bring about a positive covariation of finger forces measured in different trials at the same phase of the total force profile. This will produce what we would like to call a "spurious UCM effect," i.e., a result that can be interpreted as moment stabilization by the controller. Because we have been interested in control strategies and their adjustments to task modifications, we performed analysis of across trial variability using a different pair of variables, namely "force modes" (introduced in "Materials and methods"). This approach accounts for the enslaving effects, reducing the likelihood of such spurious effects.

The variance analyses performed in the current study using force modes have shown, for slow movements and particularly for slow force ramps, higher values of the component of variance that did not affect the total force (V_{COMP}) than the component that affected the total force (V_{UN}). In contrast, fast movements could show an equal or higher value of the variance component that was reflected in the total force, i.e., V_{UN}. The latter finding corroborates our previous observations of higher V_{UN} as compared to V_{COMP} over much of the force cycle duration during oscillatory force production by two fingers at a relatively high rate (Latash et al. 2001). The opposite finding during slow movements, however, requires a reconsideration of our earlier interpretation for the relation between V_{UN} and V_{COMP}. In the previous paper, we discussed the dominating $V_{UN}>V_{COMP}$ relation, calculated with respect to the force control hypothesis, as being conditioned by the lifetime experience with object manipulation that commonly imposes strict requirements on the stabilization of the total moment generated by the fingers with respect to the thumb contact while requirements for total force stabilization may not be as strict.

Findings of the current study suggest that the central controller actually tried to stabilize total force as required by the instruction but was successful only at low rates of force generation. At higher rates of force production, it failed to stabilize total force except at the highest force values and showed relations between the two variance components in some parts of the force trajectory that suggested stabilization of moment and destabilization of total force. In other words, the controller is characterized with a frequency bandwidth of changes in a performance variable (e.g., total force) within which it is able to stabilize the variable. While arguments about the higher ecological value of moment stabilization may be correct, these results point to another major factor that defines which of the two major kinetic variables, force or moment, is stabilized. This factor is related to the rate of force development, which leads us to the next topic of the "Discussion."

Speed related differences in the structure of variability

Simon Goodman/Gutman (Gutman and Gottlieb 1992; Gutman et al. 1993) was arguably the first to introduce a formal model of motor variability, which explicitly considered two sources of motor errors during single-joint movements, one related to an imprecise setting of a parameter related to planned movement amplitude and the other related to an imprecise setting of a parameter related to movement time. Within the model, motor errors are composed of two components, only one of which is related to movement velocity. In a recent paper (Latash et al. 2001), we have discussed this model with respect to finger force production data and reformulated Goodman's model as:

$$Var(F(t)) = F^2(t)\frac{Var_A}{A^2} + t^2(dF(t)/dt)^2\frac{Var_\tau}{\tau^2} \qquad (12)$$

where *F(t)* is the time varying force, and *Var* stands for variance. The first term in the right side of Eq. 12 depends on the precision of setting parameter A related to planned force magnitude; it predicts an increase in force variance with an increase in the average level of force (cf. Newell et al. 1984; Slifkin and Newell 1999). The second term depends on the precision of setting the timing parameter τ and predicts an increase in the force variance at high rates of force change.

To analyze the relative role of timing errors in each of the two variance components, V_{COMP} and V_{UN}, we have used a somewhat different, linear model, Eq. 11. This particular equation was suggested by the patterns of the experimentally measured time profiles of V_{COMP} and V_{UN} (Figs. 4, 5). Both Goodman's model, Eq. 12, and the model used in the current study, Eq. 11, have been able to account for the experimental findings with high accuracy with no statistically significant differences between the percentages of variance they accounted for. The striking feature of the model represented by Eq. 11 is the lack of the velocity related term in V_{COMP} while this term plays a major role in V_{UN}. Note that, by definition, V_{UN} affects variability of the total force, while V_{COMP} reflects finger force variance that has no effect on the total force. Equation 12 was introduced by Goodman to address the variance of the total output of a single-element system; the fact that a similar model accounts well for the variance component that is reflected in the total force output of a set of effectors (V_{UN}) confirms the validity of the model. It is, however, unexpected that the complementary component of variance shows no dependence on the term that depends on the accuracy in setting the timing parameter τ.

To analyze this phenomenon, let us consider sources of variance within a hierarchical system involving two levels, a higher one (the timing level according to Schöner 1995) that sets a required time course of a task variable (total force), and a lower one (the synergy level), where the time pattern of the task variable gets distributed among the elements (fingers). At the timing level, Eq. 12 describes two sources of variance in total force reflected in V_{UN}. Total force variance can also get contribution from the synergy level, i.e., from variance in the behavior of individual fingers.

Two types of interactions at the synergy level may occur that would contribute to V_{COMP}. First, there may be variance in sharing patterns across trials leading to different finger forces for a given total force magnitude. By definition, this variance will contribute only to V_{COMP}. Second, if a task variable shows an error originating at the timing level, elements at the synergy level may have an ability to perceive this error and to change their outputs in order to reduce it. Our observations suggest that this ability is limited to compensating for errors related to imprecise setting of A but not of τ in Eq. 12. Third, if an error is introduced by an element at the synergy level, other elements may be able to perceive it and change their outputs such that the task variable remains relatively unaffected (cf. principle of minimal interaction in Gelfand and Tsetlin 1966 and error compensation in Latash et al. 1998).

The strong relation in our experiments of V_{UN} to dF/dt without an apparent relation to F, and the strong relation between V_{COMP} and F without an apparent relation to dF/dt, suggest the action of at least three mutually non-exclusive factors: (1) variability in the sharing pattern is a major contributor to V_{COMP}; (2) an error in setting the magnitude of the task variable, i.e., total force (A in Eq. 12) is either relatively small or is effectively compensated for at the synergy level; and (3) errors that may occur spontaneously in outputs of individual elements (finger forces) are quickly and effectively corrected by changes in the activity of other elements.

This quantitative analysis suggests that the controller can use a superposition of two strategies in producing a required mechanical output of a set of fingers. The first one we will call a "rigid strategy" or a "fork strategy" (cf. Latash et al. 2002). Imagine that you have a fork in your hand and press with each prong on a force sensor. Any error generated by the hand will be reflected in the forces produced by each prong such that a positive covariation of individual prong forces will be seen. Such a covariation can be interpreted as total moment stabilization and total force destabilization. The second strategy we will call a "flexible strategy." Within this strategy, each finger can be controlled independently, and multifinger synergies unite the neural structures related to individual finger force production to assure stabilization of a selected mechanical variable (total force in our experiments). Apparently, at low rates of force production, the controller is able to take full advantage of the "flexible strategy," while at high rates the "fork strategy" dominates. One interpretation is that using the "flexible strategy" requires corrections of individual finger forces based on visual or proprioceptive feedback which can be efficiently used during slow trials but not during fast force production tasks. Typical delays for a mechanically effective correction of force in the course of force production have been reported in the range between 150 ms and 250 ms (Evarts and Granit 1976; Strick 1978;

Latash and Gottlieb 1991). One would expect, therefore, very fast force production actions to be performed largely in a feed-forward (pre-programmed) manner. Slower actions may make use of the afferent information for comparison of current force signals with the desired force pattern. If so, the desired pattern can apparently be specified visually or by memorized information, because the presence of an explicit template in the present study did not affect the subjects' performance in this study.

According to our model (see Eq. 11 and Tables 2, 3), variance of total force, expressed as V_{UN}, has only a weak relation to force magnitude and is defined mostly by the rate of force production. This result is quite different from the well-established relations between force and force variability (for review see Newell et al. 1984). Those studies have shown a close to linear relation between the magnitude of force and its standard deviation across a series of trials. More recent studies have shown a close to exponential relation between the two (Slifkin and Newell 1999) for steady force production trials. Note, however, that the contradiction between these reports and our findings may be only apparent. In those experiments, measurements were performed at steady levels of force, i.e., when the rate of force change was zero. According to Eq. 12, the component of variance related to imprecise setting of τ also becomes zero when dF/dt is zero. Therefore, measurements at steady state reflected the residual relation of the total force variance to the magnitude of force (the first term in the right side in Eq. 12). Besides, in experiments with fast force production, the peak value of dF/dt is typically proportional to the peak magnitude of force (Gordon and Ghez 1987; Corcos et al. 1990). The trend to show larger errors for larger rates of force production has also been confirmed in a recent study of a ramp tracking task (Blank et al. 2000). Hence, if a τ-related error can accumulate during a trial (cf. Gutman et al. 1993), one may expect a relation of the total force variance measured at a steady state to force magnitude.

Concluding comments

One of the major outcomes of the present study is the demonstration of a limitation in the ability of the central nervous system to organize a two-finger synergy such that errors in the timing of total force profiles are cancelled. Apparently, error correction between the outputs of the two fingers involves time delays that may be too long to allow an efficient stabilization of the total force during fast rates of the force production. In contrast, intercompensation of errors related to imprecise setting of force magnitudes of the two fingers was rather efficient such that much of this variance got into V_{COMP} and was not reflected in the variance of the total force. Analysis of the structure of motor variability using the UCM approach allows one to address questions related to the efficacy and limitations of motor synergies. The UCM approach also offers a powerful toolbox to address, in an indirect way, issues of control of different types of motor tasks, discrete and oscillatory, fast and slow, with and without visual feedback, etc.

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