Fatigue and Motor Redundancy: Adaptive Increase in Finger Force Variance in Multi-Finger Tasks

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Singh T, SKM V, Zatsiorsky VM, Latash ML. Fatigue and motor redundancy: adaptive increase in finger force variance in multi-finger tasks. *J Neurophysiol* 103: 2990–3000, 2010. First published March 31, 2010; doi:10.1152/jn.00077.2010. We studied the effects of fatigue of the index finger on indices of force variability in discrete and rhythmic accurate force production tasks performed by the index finger and by all four fingers pressing in parallel. An increase in the variance of the force produced by the fatigued index finger was expected. We hypothesized that the other fingers would also show increased variance of their forces, which would be accompanied by co-variation among the finger forces resulting in relatively preserved accuracy of performance. The subjects performed isometric tasks including maximal voluntary contraction (MVC) and accurate force production before and after a 1-min MVC fatiguing exercise by the index finger. During fatigue, there was a significant increase in the root mean square index of force variability during accurate force production by the index finger. In the four-finger tasks, the variance of the individual finger force increased for all four fingers, while the total force variance showed only a modest change. We quantified two components of variance in the space of hypothetical commands to fingers, finger modes. There was a large increase in the variance component that did not affect total force and a much smaller increase in the component that did. The results suggest an adaptive increase in force variance by nonfatigued elements as a strategy to attenuate effects of fatigue on accuracy of multi-element performance. These effects were unlikely to originate at the level of synchronization of motor units across muscle compartments but rather involved higher control levels.

INTRODUCTION

The term muscle fatigue is used to denote a transient decrease in the capacity to perform physical actions. This general definition implies not only a drop in voluntary muscle force but also a decline in accuracy of performance (for review, see Enoka and Duchateau 2008). Several studies have shown, however, that if a motor task involves a redundant set of elements, goal-relevant features of performance are relatively preserved during fatigue of one (or a few) of the elements (Côté et al. 2002, 2008; Forestier and Nougier 1998; Gates and Dingwell 2008; Huffenus et al. 2006). Until recently, however, no methods were available to explore how the CNS manages to protect important features of performance from the seemingly unavoidable fatigue-induced increase in motor variability.

The recent developments of the notion of motor synergies (reviewed in Latash 2008; Latash et al. 2007) and of the uncontrolled manifold (UCM) hypothesis (Scholz and Schöner 1999) allow approaching this problem with quantitative indices reflecting how well elements within a mechanically redundant system interact to provide stability of their combined functionally important output. In line with our earlier studies, we are going to use the term "synergy" to imply co-varied (across trials) adjustments of elemental variables (variables produced by elements) that result in lower variability of an important performance variable produced by all the elements as compared with what one could have expected in the absence of such co-variation. The UCM hypothesis implies that the CNS acts in a space of elemental variables, creates in this space a subspace (UCM) corresponding to a desired value of a performance variable, and then limits variance of the elemental variables to that subspace. In other words, variance of elemental variables is viewed as the sum of two components, "good variance" along the UCM (V_{UCM}) that does not affect performance, and "bad variance" orthogonal to the UCM (V_{ORT}) that does. Having a synergy implies that variance along the UCM is larger than variance along the orthogonal subspace, $V_{\text{UCM}} > V_{\text{ORT}}$ (properly quantified).

The notion of synergies has been used for many years to address the famous problem of motor redundancy (Bernstein 1967; for recent reviews, see Latash 2008; Latash et al. 2007; Ting and McKay 2007; Tresch and Jarc 2009). The most common approach views synergies as a means of reducing the number of variables the hypothetical controller manipulates. This is achieved by uniting elements (for example, muscles) into groups; further, the controller uses just one variable to scale the outputs of the elements in parallel. In line with this definition, various matrix factorization techniques have been used to identify and quantify synergies. Note that the definition used in our study does not necessarily imply a change in the number of variables manipulated by a hypothetical controller but relates the notion of synergy to stability of potentially important characteristics of performance.

This framework has been used in several studies of multi-finger synergies in accurate force production tasks (Friedman et al. 2009; Latash et al. 2001, 2002a,b; Scholz et al. 2002; Shim et al. 2005). These studies used finger modes (hypothetical commands to individual fingers) (Danion et al. 2003; Zatsiorsky et al. 1998) as elemental variables to avoid spurious effects resulting from unintentional force adjustments of finger forces when one finger of the hand changes its force (enslaving or lack of individuation) (Kilbreath and Gandevia 1994; Li et al. 1998; Zatsiorsky et al. 2000).

A few studies addressed effects of fatigue on indices of finger interaction, such as enslaving and force deficit (Li et al. 1998; Ohtsuki 1981), using maximal force production (MVC) tasks (Danion et al. 2000, 2001). They showed, in particular, that if only one finger performed the fatiguing exercise, indices of interaction between this finger and other fingers of the hand

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decreased while there were no such effects on indices of finger interaction among the nonfatigued fingers. Note that these studies did not quantify multi-finger synergies in accurate force production tasks. Those results led the authors to a "weak-link" hypothesis: if a redundant set of effectors performs a task, interactions between relatively well performing elements and poorly performing elements ("weak links") are reduced.

In a series of studies of multi-joint movements by kinematically redundant effectors, Côté et al. (2002, 2008) have shown that the CNS takes advantage of motor redundancy during fatigue and involves to a larger degree less affected elements during such actions as sawing and hammering. This view suggests an adaptive strategy, which looks similar to the mentioned "weak-link" idea: the relatively unaffected elements take care of the task with decreased involvement of the fatigued elements.

The notion of a multi-element synergy as a means of reducing variability of the combined output of a set of elements allows offering another hypothesis. During fatigue, an increase in the variance of variables produced by the affected element(s) is expected. If the less affected (nonaffected) elements also show increased variance of their output variables accompanied by stronger co-variation among the outputs of the affected and nonaffected elements, relatively preserved accuracy of performance may be achieved.

This hypothesis was tested in experiments with four-finger accurate force production before and after a fatiguing exercise performed by the index finger. We decided to induce fatigue in the index finger because its force production is accompanied by relatively low unintentional forces by other fingers (Zatsiorsky et al. 2000).

In recent studies, we have shown qualitative differences between discrete and cyclic tasks in the relationships between a component of variance that affects performance (V_{ORT}) and action characteristics (such as force derivative) (Friedman et al. 2009; Latash et al. 2002a). That is why, in this study, we explored both discrete and cyclic actions (cf. Hogan and Sternad 2007; Schaal et al. 2004; Sternad and Dean 2003).

METHODS

Participants

Ten right-hand dominant participants, seven males and three females [age: 27.5 ± 4.0 (SD) yr, mass: 73.1 ± 12.94 kg, height: 1.75 ± 0.08 m, hand width: 8.10 ± 0.63 cm, hand length: 18.64 ± 1.08 cm] participated in the experiment. All the participants were healthy with no known history of neurological or motor disorders. Hand length was measured as the distance from the tip of the distal phalanx of digit three to the distal crease of the wrist with the hand in a neutral flexion extension pose. Hand width was measured between the lateral aspects of the index and little finger metacarpophalangeal (MCP) joints. None of the participants had a history of long-term involvement in hand or finger activities such as typing and playing musical instruments. All participants gave informed consent according to the procedures approved by the Office for the Research Protections of the Pennsylvania State University.

Experimental setup

Four unidirectional piezoelectric force sensors (Model No. 208C02; PCB Piezotronic, Depew, NY) were used to measure vertical forces produced by the individual fingers of the right hand. The sensors were placed under the index, middle, ring, and little fingers. Each sensor was covered with a cotton pad to increase friction and prevent the influence of finger skin temperature on the force measurements. The four force sensors were placed within aluminum frames (140 × 90 mm each) in a groove on a wooden board (see Fig. 1). The sensors were mediolaterally spaced 30 mm apart from each other. The position of the sensors in the sagittal plane could be adjusted within 60 mm to fit individual subject hand anatomy. The signals from the sensors were amplified using signal conditioning units (M482M66, PCB Piezotronic). The signals were then sampled at 200 Hz using a 12-bit data acquisition card (National Instruments) and a Labview program running on a PC.
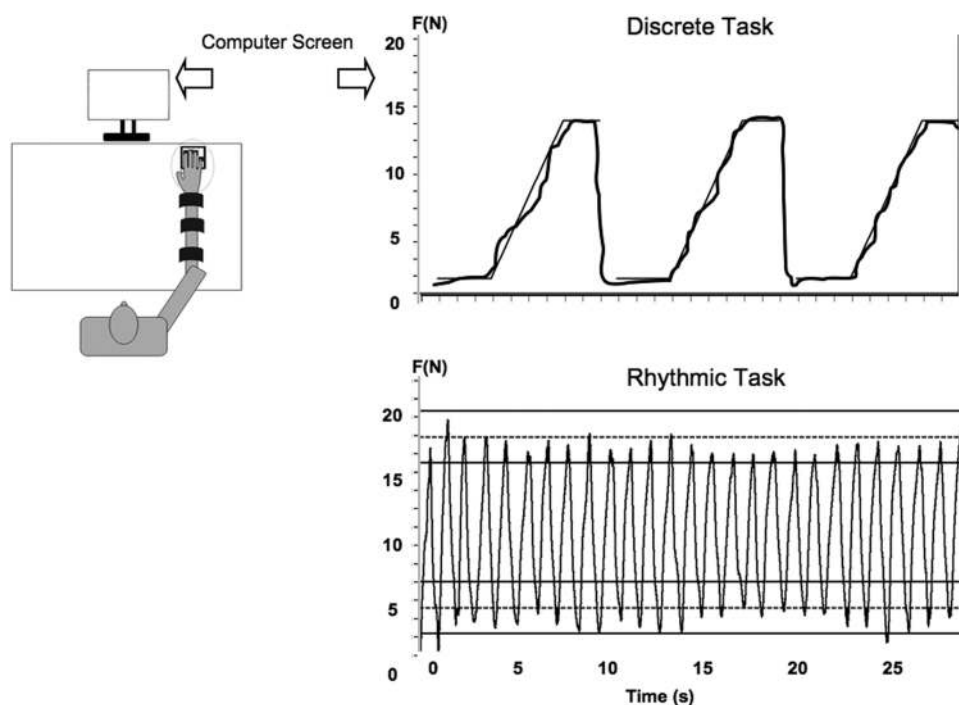

FIG. 1. Experimental setup with the feedback for the discrete experiment and for the rhythmic experiment. Examples of typical subject performance (single trials, 4-finger tasks, before fatigue) are shown together with the presentation of the task on the screen. Note that the discrete task involved several episodes of force ramp changes within a trial. - - - and — (in the rhythmic task), the target force values and the permissible error margins.

During the experiment, the participants sat in a chair facing the test table with his/her upper arms at ~45° of abduction in the coronal plane and ~45° of flexion in the sagittal plane. The elbow was flexed at ~135°. The participants were allowed to either keep their left arm on their lap or on the table but not to use it for any kind of force application. The right forearm rested on the wooden board that housed the sensors. The forearm was strapped to the wooden board with three sets of Velcro straps. A custom-fit support object was placed underneath the palms to help maintain a constant configuration of the hand and fingers. The subject's hand formed a dome-like structure with the MCP joint flexed at 20° and all interphalangeal joints slightly flexed as well. Participants selected comfortable thumb positions during the experiment. A computer monitor was located 0.65 m away from the participant. The monitor displayed the task (described in the next section).

Data Collection

DAY 1. The experiment was run over two successive days. On the first day, the participants were familiarized with the experimental protocol. The familiarization exercise was done to minimize effects due to learning during the main experiment on the second day. For the familiarization exercise, the participants completed all the trials in the actual experimental protocol that they were supposed to do on day 2. In all the tests, the participants were given feedback on the force produced by the instructed finger(s), by a constantly updating plot of the force magnitude (*y* axis) against time (*x* axis).

DAY 2: PREFATIGUE TRIALS. There were four kinds of tests including: MVC tasks, one-finger ramp tasks, rhythmic force production tasks, and discrete force production tasks.

MVC trials. After the familiarization part, on the second day of the experiment, the participants were required to produce MVCs by each of the four fingers, index (I), middle (M), ring (R), little (L), and all four fingers together (IMRL). Initially (for the 1st 10 s) the subjects rested their fingers on the sensors. Then after the cursor passed a vertical line (at 10 s), in a self-paced manner they were instructed to press as hard as they can with the instructed finger(s) without lifting any of the fingers from the sensors. The subjects were told that after they reached their maximum force, they could relax. The subjects got feedback on the amount of force they produced. For the IMRL trial, the total force produced by the I, M, R, and L fingers was displayed on the screen as feedback. Two trials were recorded for each finger or finger combination. The greater of the two force values was used for later analysis. The total duration of each MVC trial was 20 s. The order of the five MVC trials was randomized across participants. There was a one-minute interval between trials.

One-finger ramp tasks. In these trials, the participants were shown a template on the screen that had zero force for the first 5 s and then a slanted line from 0 to 40% MVC over the next 10 s. In each trial, the participants were asked to produce a force profile matching the template on the screen by trying to press with one of the fingers. Feedback on force produced by that finger was shown on the screen. The participants were instructed to keep the other three fingers on the sensors. Participants were instructed not to pay attention to any force production by the other three fingers and no feedback on forces produced by these fingers was provided. The data from these trials was used to compute the enslaving matrix **E** (described in *Data Processing*). There was one trial for each finger, as the instructed finger, and the order of these trials was randomized. There was a 5-s interval between trials.

Discrete and rhythmic force production tasks. The next several experimental series involved one-finger (I) and four-finger (IMRL) accurate force production tasks. The tasks involved discrete or rhythmic force production. In the discrete tasks (I_D and $IMRL_D$), the screen showed a template corresponding to a flat profile at 5% MVC for 2 s, followed by a 5–25% MVC ramp over 5 s and then a 3-s flat profile at 25% MVC (see Fig. 1). The task was to follow the template as

accurately as possible by a signal corresponding to the force produced by the task finger(s). One trial was 30 s long; it contained three such ramps. Four trials were recorded in a row resulting in a total of 12 ramps. In the rhythmic tasks (I_R and $IMRL_R$), the screen showed two horizontal targets placed at 5 and 25% of MVC. The task was to change force profile in a smooth, sine-like fashion in such a way that the crests and troughs lied within the target range specified by two horizontal lines at 5 ± 3 and $25 \pm 3\%$ of MVC. The participants were also required to do this at a pace set by a metronome that produced audible "ticks" at a frequency of 0.9 Hz. This frequency was set based on earlier studies as comfortable for all participants (Friedman et al. 2009). Examples of typical discrete and rhythmic accurate force production trials performed by four finger before fatigue can be found in Fig. 1. The order of the four series, (I_D, $IMRL_D$, I_R, and $IMRL_R$) was randomized across participants. There were 5-s intervals between trials within a series and 2-min intervals between series.

DAY 2: FATIGUE PROTOCOL AND DURING-FATIGUE TRIALS. There was a 5-min break after the completion of the prefatigue set of trials. We chose a fatiguing protocol based on a pilot study with seven subjects that compared two protocols: 1-min MVC force production and 30%MVC force production until task failure. This comparison showed a significantly larger force drop after the 1-min MVC test (by 40% for the 1-min MVC protocol as compared with 28% for the 30% MVC protocol) with similar force restoration curves over 3 min. Besides, the 1-min fatiguing exercise, followed by 20-s exercises to maintain fatigue level was used in earlier studies by our group (Danion et al. 2000, 2001). Therefore we chose the 1-min MVC fatiguing protocol as the first fatigue trial for our study. All subsequent fatigue trials were of 20-s duration each. These 20-s trials were done after each trial in testing during fatigue (MVC, 1-finger ramp, discrete, and rhythmic) to prevent index finger force recovery. During the fatiguing exercise, the subjects were always reminded to try not to involve other fingers of the hand and to avoid excessive muscle co-contraction (stiffening the hand). For each participant, the during-fatigue trials were conducted in the same order as the prefatigue trials.

Data Processing

The data were processed using Matlab (The MathWorks, Natick, MA). The data were filtered using a second-order zero-lag Butterworth filter with a cutoff frequency of 10 Hz.

Peak force (MVC) was measured at the time when the force produced by the task finger(s) peaked.

The difference between the peak force of a finger in its single-finger MVC trial ($F_{i,i}$) and its peak force at the peak of the IMRL force in the four-finger MVC task ($F_{i,IMRL}$) was expressed in percent to the former value: $FD_i = 100\%*(F_{i,I} - F_{i,IMRL})/F_{i,i}$. Total force deficit across the four fingers was computed as the difference between the sum of the peak forces of individual fingers in their single-finger tasks ($\Sigma F_{i,i}$) and their combined peak force during the IMRL task expressed in percent to the former value.

The enslaving matrices (**E**) were computed for each subject by using the single-finger ramp trials. For each trial, a linear regression of the forces produced by individual fingers against the total force produced by all the four fingers over the 10-s ramp time interval was computed. The regression coefficients were used to construct **E** as follows

$$\mathbf{E} = \begin{bmatrix} \Delta M_{i,i} & \Delta M_{i,m} & \Delta M_{i,r} & \Delta M_{i,l} \\ \Delta M_{m,i} & \Delta M_{m,m} & \Delta M_{m,r} & \Delta M_{m,l} \\ \Delta M_{r,i} & \Delta M_{r,m} & \Delta M_{r,r} & \Delta M_{r,l} \\ \Delta M_{l,i} & \Delta M_{l,m} & \Delta M_{l,r} & \Delta M_{l,l} \end{bmatrix} \quad (1)$$

where $\Delta M_{i,j}$ is the slope of the regression equation when finger *i* force was regressed on the sum of all four finger forces, where finger *j* is the task finger. All the regression equations had R^2 values of over 0.9. Typical examples of 95% confidence intervals for M_{ij} were (0.183,

0.1843); (0.4852, 0.489); (0.271, 0.2745), and so on. Computation of the enslaving matrix $\mathbf{E}$, allowed for a conversion of the force data $\mathbf{f}$ into finger modes by using the equation $\mathbf{m} = \mathbf{E}^{-1}\mathbf{f}$, where $\mathbf{m}$ is the mode vector. Finger mode is a hypothetical command reflecting the desire of a person to involve a finger (Danion et al. 2003; Zatsiorsky et al. 1998). We assume that these commands may be varied independently of each other and therefore finger modes can be changed by the neural controller one at a time. Each mode leads to force generation by all four fingers of the hand. The order of the fingers was randomized across participants. The index of enslaving $|\mathbf{E}|$, was computed as the sum of all the off-diagonal entries of $\mathbf{E}$.

The RMS error for the discrete task was computed with respect to the task template ($RMSE_{task}$) and with respect to the actual average (across trials) performance ($RMSE_{mean}$). Because there was no force template for the rhythmic task, only $RMSE_{mean}$ was computed. For the rhythmic task, the quasi-sinusoidal force profiles were aligned and averaged (described in detail later). For both cases, the RMS error was normalized to 15% MVC (mean value of the ramp range).

For the IMRL trials, the variance of the forces produced by the I, M, R, and L fingers over the trials was computed for each phase of the action. For the discrete task, the variance was computed at each time sample over the ramp and then averaged over the ramp time for each subject separately. For the rhythmic IMRL task, the force variance at each of the 100 resampled points was computed and then averaged across the points. The mean of the variances of the force produced by each finger were normalized to the MVC squared of the particular finger.

Analysis of multi-finger synergies (UCM analysis)

The analysis of multi-finger synergies stabilizing the force profile in the IMRL tasks was performed in the framework of the UCM hypothesis (Scholz and Schöner 1999; reviewed in Latash et al. 2002b, 2007). The hypothesis assumes that the controller organizes covariation among elemental variables to stabilize a certain value of a performance variable. Individual finger forces may co-vary because of the phenomenon of enslaving, i.e., unintended force production by fingers when other fingers of the hand produce force (Kilbreath and Gandevia 1994; Li et al. 1998; Ohtsuki 1981; Zatsiorsky et al. 1998, 2000). Therefore instead of using the finger forces $\mathbf{f}$, we used the force modes, $\mathbf{m}$ as elemental variables. The total force, F_{TOT}, is viewed as the performance variable. According to the UCM hypothesis, the neural controller works in a space of elemental variables and creates in that space a subspace corresponding to a desired value of a particular performance variable. The four-dimensional space of finger modes can be divided into two subspaces, one corresponding to a fixed value of the total force (the UCM, 3-dimensional space) and the other leading to changes in the total force (orthogonal to the UCM, 1 dimensional). Variance across trials was computed for each time sample (each phase) and compared within the two subspaces, V_{UCM} (or V_{GOOD}) and V_{ORT} (or V_{BAD}) after normalization per degree-of-freedom. We interpret $V_{UCM} > V_{ORT}$ as a sign of a multi-finger synergy stabilizing the total force.

A synergy index, ΔV was computed reflecting the relative amount of V_{UCM} in the total variance (V_{TOT})

$$\Delta V = \frac{V_{UCM} - V_{ORT}}{V_{TOT}} \qquad (2)$$

where all variance indices are computed per degree of freedom. Given the number of degrees-of-freedom in each space, $4V_{TOT} = 3V_{UCM} + V_{ORT}$. Hence the index of synergy ΔV ranges between $+1.33$ (all variance is within the UCM) and -4 (all variance is in the orthogonal subspace). For statistical analysis, the ΔV values were transformed using a Fisher's z-transformation adapted to the boundaries of ΔV

$$z_{\Delta V} = 0.5\log\left(\frac{4 + \Delta V}{1.33 - \Delta V}\right) \qquad (3)$$

For the discrete force production tasks, only the force data over the ramp portion were used for analysis. The first and last 20 data points were rejected to minimize end effects.

For the rhythmic task, the force data were segmented into the periods of force increase and force decrease. The segmentation was done as described in our earlier publication (Friedman et al. 2009). Briefly, force rate was computed by using a five-point derivative on filtered data (using a 2nd-order low-pass Butterworth filter at 6 Hz). Force data were selected between consecutive peaks in dF/dt. Start of each segment was defined as a local minimum of the force between a peak dF/dt and the previous peak dF/dt (or 1st sample, as the case may be). End of a segment was defined as local maximum between a peak dF/dt and the next dF/dt, (or last sample, as the case may be). Only those segments where the force crossed the midline were considered for analysis. In addition, we rejected segments where the start or end of segment was >15% MVC away from the target or <20% of a cycle away from the metronome tick. The accepted segments were then resampled into 100 points using cubic spline interpolation. We then converted the forces into modes as described earlier. Then, at each of these 100 points, we decomposed the mode variance into V_{UCM} and V_{ORT} as described earlier. To compare between the discrete and rhythmic tasks, only the data from the force increase part was used.

Statistics

Standard descriptive statistics were used (means $\pm$ SE). Repeated measures ANOVA was run on outcome variables of interest. Tukey's pairwise contrasts were used to analyze significant effects at $P < 0.05$. A two-way ANOVA was run on MVC with *fingers* (I, M, R, L, and IMRL) and *fatigue-condition* (fatigue and no-fatigue) as factors. To compute if there were any significant differences for the indices of enslaving $|\mathbf{E}|$, a paired *t*-test was performed. All statistical analysis was done using Minitab 15.

To analyze fatigue-induced changes in the error index ($RMSE_{mean}$) across the discrete and rhythmic tasks, ANOVA with factors *task* (discrete and rhythmic), and *finger-combination* (I and IMRL) was performed. To analyze the $RMSE_{task}$ for the discrete task only, a two-way ANOVA with factors *fatigue-condition* and *finger-combination* (I and IMRL) was performed.

To analyze effects of fatigue of variance of the individual finger forces, an ANOVA was run on force variance data with *fingers* (I, M, R, and L), *task*, and *fatigue-condition* as factors. Note that in this case the factor *fingers* has only four levels unlike when we had *fingers* as a factor for MVC where it had five levels. To analyze effects of fatigue on the two variance component (V_{UCM} and V_{ORT}), an ANOVA was run on changes in the two variance components induced by fatigue with factors *variance-type* (V_{UCM} and V_{ORT}) and *task*.

RESULTS

Effects of fatigue on maximal force, force deficit, and enslaving

Performance of our subjects in all the tests was typical of similar tasks used in earlier studies (Danion et al. 2001; Friedman et al. 2009; Latash et al. 2001, 2002a; Li et al. 1998); examples of typical performance in the rhythmic and discrete accurate force production tasks are shown in Fig. 1. One-minute MVC exercise by the index (I) finger led to a significant drop in the maximal finger forces (MVC) in both one- and four-finger tasks. On average, the force of the I finger dropped by 33.5%. The prefatigue MVC produced by the I finger was 35.30 ± 2.69 N while during fatigue, MVC was 23.47 ± 2.31 N. The prefatigue MVC of the M, R, L, and IMRL fingers were 30.33 ± 4.42, 28.67 ± 2.50, 22.94 ± 3.90, and 88.73 ± 10.48, respectively. During fatigue, the MVC of the M, R, L, and
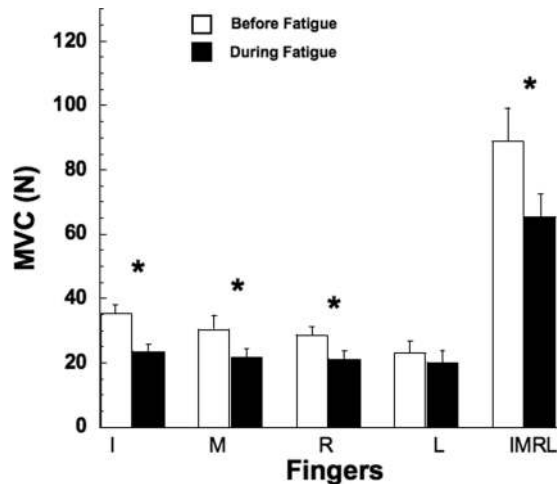
FIG. 2. Maximal voluntary contraction force before (□) and during fatigue (■). *, significant differences ($P < 0.05$) between the prefatigue and during-fatigue conditions. Mean data across the subjects are shown with SE bars. I, index; M, middle; R, ring; L, little finger.

IMRL fingers decreased to 21.95 ± 2.83, 21.32 ± 2.49, 20.17 ± 3.74, and 65.77 ± 7.35. The drop in the average MVC of the M, R, and L fingers was smaller than the I finger (middle, M – 27.7%; ring, R – 25.9%, and little, L – 12.1%). The four-finger (IMRL) MVC dropped, on average, by 25.8%. Figure 2 illustrates these results with the MVC data averaged across subjects; significant changes from preexercise (□) to postexercise (■) conditions are marked (*).

The changes in MVC with fatigue were significant according to an ANOVA with fingers and fatigue-condition as factors. The ANOVA showed main effects of both fingers [$F_{(4,81)} = 102.57$, $P < 0.001$] and fatigue-condition [$F_{(1,81)} = 28.25$, $P < 0.001$]. The interaction effect was also significant [$F_{(4,81)} = 1.07$, $P < 0.05$]. Pair-wise contrasts showed that fatigue significantly decreased MVC for the I [$F_{(1,9)} = 66.33$, $P < 0.001$], M [$F_{(1,9)} = 18.83$, $P < 0.01$], and R [$F_{(1,9)} = 16.49$, $P < 0.01$] fingers, and for the IMRL combination [$F_{(1,9)} = 35.21$, $P < 0.001$] but not for the L finger [$F_{(1,9)} = 3.49$, $P > 0.05$].

There was a trend for unintentional force production by nontask fingers (enslaving) to increase during fatigue (on average, by ~10%). The mean of the enslaving index |E| (computed as the sum of the off-diagonal terms in the enslaving matrix E, see METHODS), for the postexercise tests was higher (1.66 ± 0.14) than before the exercise (1.51 ± 0.14),

but this difference was under the significance level [$F_{(1,9)} = 3.72$, $P = 0.09$]. Force deficit (FD) did not change during fatigue. On average, FD before fatigue was $23.84 \pm 2.20\%$ and during fatigue it was $23.83 \pm 2.35\%$.

Effects of fatigue on accuracy of task performance

We estimated variability of performance using root mean square error indices ($RMSE_{mean}$) computed over the task duration with respect to the mean performance. Further, the index was normalized by the average force value over the task (15% of the MVC). Overall, fatigue led to an increase in $RMSE_{mean}$ from 0.080 ± 0.007 to 0.095 ± 0.007.

Subjects performed more accurately in the discrete tasks as compared with the rhythmic tasks and with all four fingers together (IMRL) than with the I finger alone. Fatigue led to lower accuracy in one-finger (I) tasks, both discrete and rhythmic, while its effects of the four-finger (IMRL) tasks were smaller. Figure 3A shows the RMS indices for the I finger in the discrete and rhythmic tasks. Fatigue led to an increase in the RMS error by 47% for the discrete task and by 18% for the rhythmic task. Figure 3B presents the RMS data for the tasks performed by the four fingers (IMRL). Fatigue led to smaller changes in the RMS, by 21.5% for the discrete task and by 7% for the rhythmic task.

Changes in the performance accuracy with fatigue were confirmed with a two-way ANOVA (task × finger-combination) on the relative changes in $RMSE_{mean}$ with fatigue. The ANOVA showed significant effects of task [$F_{(1,27)} = 5.76$, $P < 0.05$] and finger-combination [$F_{(1,27)} = 4.41$, $P < 0.05$] without a significant interaction.

A two-way ANOVA on absolute $RMSE_{mean}$ values for the I task (fatigue-condition × task) showed a significant main effect for both fatigue-condition [$F_{(1,27)} = 12.06$, $P < 0.01$] and task [$F_{(1,27)} = 188.0$, $P < 0.001$] without an interaction. A similar ANOVA for the IMRL condition showed only a significant main effect of task [$F_{(1,27)} = 271.78$, $P < 0.001$] without a significant effect of fatigue-condition.

Because the discrete task involved a visual template, we also analyzed the RMS index computed with respect to the template ($RMSE_{task}$). Fatigue significantly increased the RMS_{task} index. In particular, the normalized $RMSE_{task}$ computed for the I finger was 0.053 ± 0.003 before fatigue and it increased to 0.074 ± 0.005 during fatigue. The $RMSE_{task}$ for the IMRL condition, before fatigue was 0.049 ± 0.003 and for during fatigue it was 0.060 ± 0.004. In other words, fatigue led to a
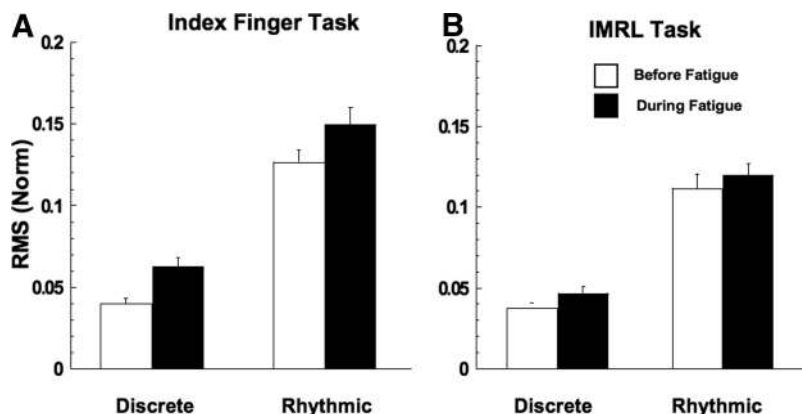

FIG. 3. Indices of performance (root mean square, RMS) error in the index (I) finger and 4-finger (IMRL) tasks, discrete and rhythmic, before (□) and during fatigue (■). Note the significant increase in force RMS during fatigue for the I tasks but not for the IMRL tasks.
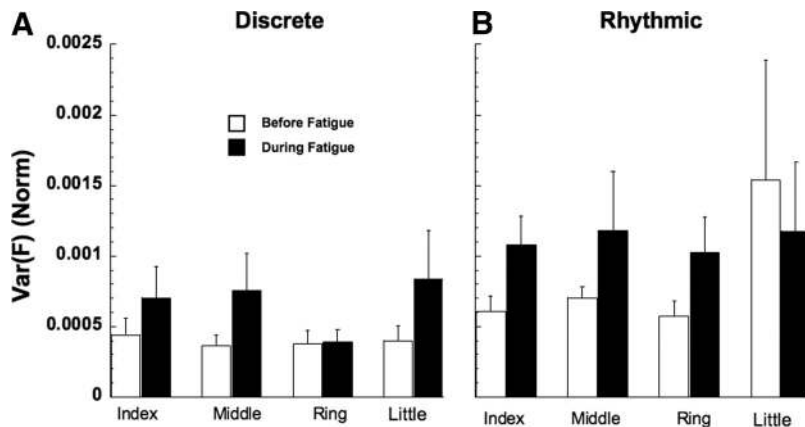
FIG. 4. Force variance [normalized to squared maximal voluntary contraction (MVC) of individual fingers] of individual fingers, averaged over the task interval, for the discrete (A) and rhythmic (B) tasks. Note that fatigue induced approximately equal changes in the force variance in all 4 fingers (□, before fatigue; ■, during fatigue).

42% increase in RMS_{task} for the I task and only to a 22% increase for the IMRL task. These results were confirmed with a two-way ANOVA with fatigue-condition and finger-combination (I and IMRL) as factors, which showed a significant main effect for both fatigue-condition [$F(1,27) = 65.52$, $P < 0.001$] and finger-combination [$F(1,27) = 18.02$, $P < 0.001$] with a significant fatigue conditions $\times$ finger-combination interaction [$F(1,9) = 37.85$, $P < 0.05$] reflecting a larger increase in $RMSE_{task}$ with fatigue for the I task as compared with the IMRL task.

Effects of fatigue on variance of finger forces in the four-finger tasks

Variance in the force produced by individual fingers was normalized to the MVC squared of the particular fingers. Fatigue significantly increased the variance of the force produced by the individual fingers in the four-finger tasks. Figure 4 shows the effects of fatigue on normalized indices of force variance for the discrete (A) and rhythmic (B) tasks. On average, the variance increased by ~50%. The variance increased more for the discrete task than for the rhythmic task, but this difference did not reach significance. There were differences between the tasks in the amount of variance increase in individual fingers, but, on average, all fingers showed comparable changes in force variance. A three-factor ANOVA showed a main effect for fatigue-condition [$F(1,135) = 4.28$, $P < 0.05$] and task [$F(1,135) = 11.5$, $P < 0.001$] but not for fingers. These effects reflected the higher overall variance for the rhythmic task. We did not find a significant interaction between fatigue-condition and task.

Effects of fatigue on multi-finger synergies

We used the framework of the UCM hypothesis (Scholz and Schöner 1999) to analyze patterns of co-variation among hypothetical commands to fingers (finger modes); we address such co-variation patterns as force-stabilizing synergies. Briefly, variance in the finger mode space was computed across trials (cycles) for each data point and represented as the sum of two components, one that did not affect total force values (V_{UCM}) and the other that did (V_{ORT}). Both indices, V_{UCM} and V_{ORT}, were quantified per dimension in the corresponding spaces.

Fatigue significantly increased total variance, $V_{TOT} = (3V_{UCM} + V_{ORT})/4$. On average, V_{UCM} was an order of magnitude higher than V_{ORT} for both tasks corresponding to a strong force stabilizing synergy. All the variance indices were higher for the rhythmic task as compared with the discrete task, both before and during fatigue. These results are illustrated in Fig. 5 that show both variance indices for both tasks, before and after the fatiguing exercise.

Fatigue led to an increase in both variance indices for both tasks (Fig. 5). However, V_{UCM} increased significantly more than V_{ORT}. In particular, V_{UCM} increased by ~130% for the discrete task and by ~46% for the rhythmic task (A), while the V_{ORT} increase was much smaller in magnitude (B).

The mentioned differences between the fatigue-induced changes in V_{ORT} and V_{UCM} were tested with a two-way ANOVA with task and variance-type as factors run on the relative changes in the variance indices induced by fatigue. The ANOVA showed a main effects of variance-type [$F(1,27) = 5.21$, $P < 0.05$] without other effects.
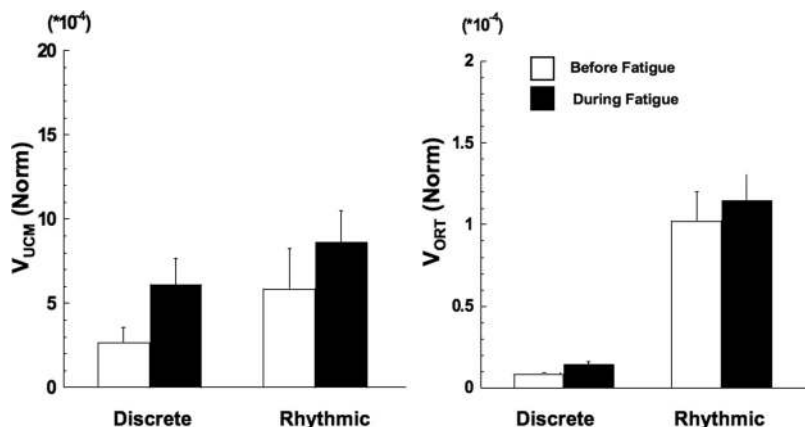

FIG. 5. Two components of variance in the finger mode space computed over the discrete and rhythmic 4-finger (IMRL) tasks. A: V_{UCM} reflects the amount of variance that did not affect total force. B: V_{ORT} reflects the amount of variance that affected total force. Note the larger increase in V_{UCM} during fatigue. Note the 10-fold difference in the scales of the y axes in A and B.

We also used two-way ANOVAs with fatigue-condition and task as factors run separately on the absolute values of the two variance indices, V_{UCM} and V_{ORT}. ANOVA on V_{UCM} showed main effects for fatigue-condition [$F(1,27) = 3.93$, $P < 0.01$] and task [$F(1,27) = 6.95$, $P < 0.05$] without an interaction. In contrast, ANOVA on V_{ORT} showed a main effect for task [$F(1,27) = 92.42$, $P < 0.001$] but not for fatigue-condition [$F(1,27) = 0.83$, $P = 0.37$] and no interaction. Taken together, the analyses show that fatigue led to a significant increase in V_{UCM} in the absence of a significant increase in V_{ORT} across the two tasks.

The normalized difference between the two variance indices was used as an index of a force stabilizing synergy (ΔV). For statistical comparisons, this index was z-transformed ($Z_{\Delta V}$, see METHODS for details). The mentioned disproportionate changes in V_{UCM} and V_{ORT} with fatigue led to an increase in ΔV in both tasks. For the discrete and rhythmic tasks, $Z_{\Delta V}$ increased by ~10% and by ~35%, respectively, during fatigue. The $Z_{\Delta V}$ index for the discrete task was 0.91 ± 0.13, and it increased to 0.99 ± 0.12; $Z_{\Delta V}$ for the rhythmic task was 0.45 ± 0.12, and it increased to 0.61 ± 0.14. These results are illustrated in Fig. 6. The results were confirmed by a two-way ANOVA on $Z_{\Delta V}$ with fatigue-condition and task as factors. There were main effects of both fatigue-condition [$F(1,27) = 7.59$, $P < 0.05$] and task [$F(1,27) = 78.61$, $P < 0.001$] without an interaction effect.

DISCUSSION

The most important outcome of our study is providing support for the main hypothesis offered in the Introduction. Indeed fatigue of the index finger resulted in an increase in force variance of all four fingers during four-finger accurate force production tasks. However, total force variance in the four-finger task showed only minor changes during fatigue, which was due to an increase in co-variation among finger modes (commands to fingers) (Danion et al. 2003l Zatsiorsky et al. 1998). In the framework of the UCM hypothesis (Scholz and Schöner 1999), fatigue led to disproportionate changes in the two components of variance, one that affected total force (V_{ORT}) and the other that did not (V_{UCM}): V_{UCM} increased more during fatigue corresponding to a significant increase in the index of

FIG. 6.   Z-transformed index ($Z_{\Delta V}$) of the force-stabilizing synergy before (□) and during fatigue (■) for the discrete and rhythmic 4-finger task. Note the increase in $Z_{\Delta V}$ during fatigue.

force-stabilizing synergy (ΔV). These results were common across the studied discrete and rhythmic force production tasks. Further in this section, we discuss implications of these findings for the notion of motor synergies and adaptive neural strategies to local fatigue.

Local, nonlocal, and adaptive effects of fatigue

We will discuss three types of effects of fatigue (for review, see Enoka and Duchateau 2008). First, local effects are those limited to the effector that performed the fatiguing exercise. Second, nonlocal effects are those seen in other effectors that were not explicitly involved in the exercise and produced relatively small forces that, by themselves, were not expected to induce fatigue. Both local and nonlocal effects are expected to be detrimental for such indices of performance as maximal force production, time to task failure, and accuracy. Effects of the third type are those that mitigate effects of fatigue on performance. We have been particularly interested in possible adjustments in indices of multi-element synergies during fatigue of one of the elements.

As expected from previous studies, the fatiguing exercise by the index finger led to a drop in its MVC force (cf. Danion et al. 2000, 2001) and worse performance in accurate force production tasks. The latter finding is in line with several reports on detrimental effects of fatigue on motor variability (Allen and Proske 2006; Carpentier et al. 2001; Contessa et al. 2009; Evans et al. 2003; Missenard et al. 2008, 2009). We did not observe differences between effects of fatigue on accuracy of performance of discrete and rhythmic accurate force production tasks.

Nonlocal effects of fatigue were reflected, in particular, in reduced MVC of the other fingers of the hand. These MVC changes were smaller than those observed in the I finger. The strongest effects were seen in the M finger, which is the closest neighbor of the I finger, while the most remote, L finger, showed minimal MVC changes (similar to results reported by Danion et al. 2001). These effects were unlikely due to unintentional involvement of the nontask fingers in the fatiguing exercise (enslaving). Based on the indices of enslaving measured in our subjects, the forces of the nontask fingers during the MVC production by the I finger were always under 25% of their MVC forces (see also Zatsiorsky et al. 2000). One-minute force production at such low force levels is not expected to induce fatigue. Over the exercise time, enslaving could increase, but this increase was modest (~10%) and under the level of significance (in an earlier study, the enslaving index was reported to drop during fatigue, Danion et al. 2001). Hence we conclude that the drop in the MVC forces by the nontask fingers was predominantly of a neural origin.

The presence of adaptive changes in finger coordination during fatigue was reflected in relatively small changes in the accuracy of force production by all four fingers acting together. This was an expected result, in line with several studies showing that goal-relevant features of performance are relatively preserved during fatigue in tasks involving redundant sets of elements (Sjogaard et al. 1988: multi-muscle torque production; Forestier and Nougier 1998: throwing a ball; Huffenus et al. 2006: multi-joint throwing; Kruger et al. 2007: multi-finger pushing; Selen et al. 2007: target tracking; Gates and Dingwell 2008: repetitive push-
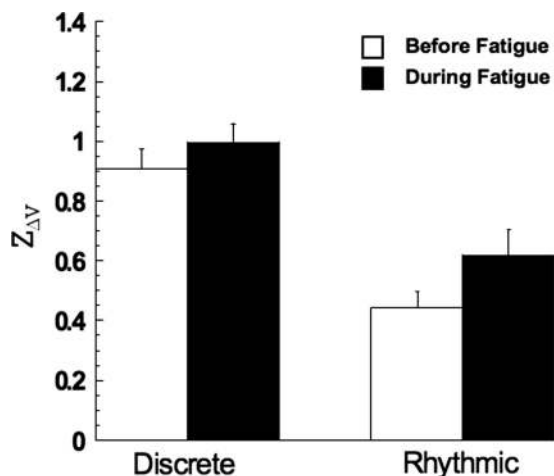
ing). Along similar lines, Strang et al. (2009) showed adaptive adjustments to fatigue of anticipatory postural adjustments (early changes in the activation of apparently postural muscles) (reviewed in Massion 1992). Other reported adaptive changes involved slowing down to maintain accuracy (Missenard et al. 2009).

Adaptive adjustments to fatigue in the four-finger accurate force production tasks involved two components. First, all four fingers showed an increase in force variance (except for the L finger in the rhythmic task, which showed a slight, nonsignificant decrease) computed over consecutive trials (cycles). This increase did not correlate with fatigue-induced MVC force changes; in particular, it was similar in the exercised finger (I) that showed the largest drop in the MVC force (by >33%) and in the L finger that showed small, nonsignificant effects of exercise on its MVC force. Second, there was a change in co-variation of finger forces that channeled most of the finger force variance into a sub-space (the UCM) where finger force variation had no effects on total force. Let us illustrate this adaptive strategy with the following metaphorical example.

Imagine that you carry a heavy object (a piano) with a few friends. The weight of the load has to be shared among all the participants. If one of the persons gets tired and starts to apply highly varied load-resisting force, all other participants have two strategies to keep the object from jumping up and down: *1*) to ask that person to step away and do the task without him/her (in line with the "weak-link" hypothesis) (Danion et al. 2001; also see Côté et al. 2002, 2008); *2*) to increase variance in their contribution to the load-resisting force and co-vary it with the force applied by the tired partner. Our current results suggest that the human CNS uses the latter strategy.

There is an apparent discrepancy between the main conclusions drawn from the current findings and results of our earlier studies of the effects of fatigue on finger interaction (Danion et al. 2000, 2001) supporting the "weak-link" hypothesis. We would like to emphasize that the studies by Danion and colleagues used only MVC tasks, not accurate force production tasks, and quantified finger interaction using such indices as enslaving and force deficit (Li et al. 1998; Zatsiorsky et al. 1998). A drop in the magnitude of enslaving between a fatigued finger and other fingers of the hand is compatible with increased, decreased, and unchanged index of multi-finger synergies in accurate force production tasks. Changes in force deficit, by themselves, have no direct effect on indices of finger force (and finger mode) co-variation. So the results of the current study are not in conflict with our earlier studies of fatigue.

What is the purpose of multi-finger synergies?

This question has been discussed in several earlier studies (reviewed in Latash et al. 2002b, 2007). Several models have been suggested accounting for such patterns of co-variation. These include a model using central back-coupling loops within the CNS (Latash et al. 2005), a feed-forward model (Goodman and Latash 2006), a model based on ideas of dynamical systems (Martin et al. 2009), and a hypothesis that links the idea of synergies directly to control with referent body configurations (Latash et al. 2010). The most common inter-

pretation of co-variation patterns that stabilize performance variables produced by redundant sets of elements has been that this is a strategy of optimizing accuracy of performance given the irreducible signal-dependent neuromotor "noise" (cf. Harris and Wolpert 1998). This interpretation is also in line with the optimal feedback control hypothesis for human motor actions (Todorov and Jordan 2002).

This latter interpretation, however, has been challenged in several recent publications. First, two studies have shown that relative accuracy of performance does not differ between multi- and single-finger accurate force production tasks (Gorniak et al. 2008; Shapkova et al. 2008). In multi-finger tasks, individual fingers show much higher variance in their force outputs, as compared with single-finger tasks, while their forces co-vary resulting in basically unchanged indices of performance accuracy. This strategy does not easily fit optimal control ideas. Indeed if the purpose of optimal control is to achieve high accuracy given the irreducible noise in the elements, allowing this noise to increase in multi-element tasks does not look like a productive strategy. Second, the component of variance (V_{UCM}) that has no effect on performance has been shown to increase with practice in an unusual force field (Yang et al. 2007) and in conditions of target uncertainty (Freitas and Scholz 2009).

These studies led to an alternative hypothesis on the purpose of synergies. According to this hypothesis, synergies are organized by the CNS to allow performing several tasks simultaneously by the same set of elements without an interference between the tasks (Gera et al. 2010; Zhang et al. 2008) and to handle possible perturbations of individual elements by intrinsic and extrinsic factors (Gorniak et al. 2009). In particular, multi-joint synergies allow a person to open a door by pressing on the handle with the elbow while carrying in the hand a full mug of hot coffee.

If one views local effects of fatigue as an intrinsic perturbations into the ability of a finger to produce accurate force, strengthening the multi-finger force stabilizing synergy allows to avoid major detrimental effects of fatigue on the accuracy of force production in four-finger tasks. Note, however, that strengthening a synergy (that is, increasing the relative amount of V_{UCM} in total variance) requires parallel changes in the variances of individual elements.

Figure 7 illustrates this idea for a simpler, two-finger force production task. Within this figure, one finger may be viewed as representing combined action of fatigued digits, and the other finger representing combined action of nonfatigued fingers. Ellipses in Fig. 7 show hypothetical data point distributions for finger forces across trials or cycles. In Fig. 7*A*, prior to fatigue, both fingers, on average, share the total force equally and produce similar amounts of force variance. There is negative co-variation between finger forces across trials corresponding to a force stabilizing synergy ($V_{UCM} > V_{ORT}$). In Fig. 7*B*, during fatigue, variance of one of the finger forces (F_1) is increased. If the nonfatigued finger continues to perform with unchanged force variance, V_{ORT} (a component that affects total force variance) will increase resulting in worse performance (the white ellipse has a larger projection on the ORT direction). To avoid this, force variance of the nonfatigued finger has to increase with a simultaneous increase in co-variation (the dark ellipse). This is the strategy we observed in our experiment.
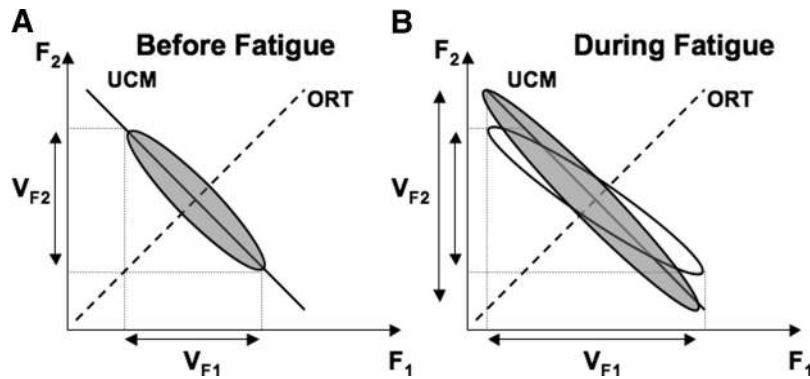
FIG. 7. An illustration of hypothetical data point distributions for the task of accurate total force production with 2 fingers. *A*: before fatigue, there is a strong negative co-variation between the 2 finger forces corresponding to a force-stabilizing synergy (the ellipse of data point distribution is elongated along the uncontrolled manifold, UCM). *B*: the fatigued finger (F_1) shows increased force variance (V_{F1}). If the other finger shows an unchanged force variance (white ellipse), the projections of force variance on the direction orthogonal to the UCM (V_{ORT}) is expected to increase thus leading to larger variance in the total force. To avoid this effect, variance of the 2nd finger force (V_{F2}) also has to increase with a simultaneous increase in the index of force co-variation (the darker ellipse).

Possible physiological mechanisms

There is growing evidence suggesting that multi-digit finger flexors, flexor digitorum profundus (FDP), and flexor digitorum superficialis (FDS), are subdivided into functional and anatomical compartments serving individual fingers (Bickerton et al. 1997; Fleckenstein et al. 1992; Jeneson et al. 1992; Serlin and Schieber 1993). A compartment is defined as a group of muscle fibers innervated by a subpool of alpha-motoneurons (α-MN) that produce muscle contraction leading to force production exclusively or predominantly by only one of the fingers. A study of finger responses to transcranial magnetic stimulation applied over the contralateral M1 cortical area has suggested that there is a strong degree of physiological independence across the FDP compartments (Danion et al. 2003).

Fatigue is known to produce additional motor unit recruitment (Bigland-Ritchie et al. 1981; Maton and Gamet 1989), changes in discharge rate (DeLuca et al. 1996), and motor unit substitution (Westgaard and DeLuca 2001). There are also neural contributions to fatigue-induced changes that may be of a supraspinal origin (Danion et al. 2000, 2001; Graven-Nielsen et al. 2002). A recent series of studies (Missenard et al. 2008, 2009) has suggested that the fatigue-induced increase in force variability may be related to the documented increase in motor unit synchronization in fatigued muscles (Bigland and Lippold 1954; Kadefors et al. 1968). On the other hand, strong motor unit synchronization has been documented among FDP compartments (Reilly et al. 2004), possibly contributing to the lack of perfect finger independence. In addition, a simulation study by Santello and Fuglevand (2004) has shown that across-muscles motor unit synchronization may play a functional role in the coordination of grip forces (Bickerton et al. 1997).

In our study, motor unit synchronization across FDP compartments could contribute to the increased force variance in the relatively nonfatigued fingers. However, such a synchronization would be expected to lead to predominantly positive co-variation among individual finger forces, which is opposite to our results. As illustrated in Fig. 7, there are two components of changes in characteristics of finger force variability, an increase in variance of commands to individual fingers and an increase in their negative co-variation. The former could get contribution from higher motor unit synchronization across FDP compartments, while the latter requires an explanation at a different level, possibly at a hierarchically higher level of the organization of multi-digit synergies (for reviews, see Latash 2008, 2010).

Motor variability and fatigue

In tasks that require accuracy, motor variability at the level of important performance variables is obviously undesirable. This is, however, less obvious when one considers variability within a redundant set of elements that contribute to the performance. A recent study has documented an increase in variability of the outputs of individual elements when a task was produced by a redundant set of elements as compared with a similar task produced by one element at a time (Shapkova et al. 2008). Why would the controller facilitate larger motor variability when an element participates in a task within a redundant set of elements?

A number of recent studies has emphasized positive effects on motor variability on aspects of motor performance associated with repetitive actions. In particular, more experienced workers show larger variability and smaller localized muscle fatigue (Granata et al. 1999; Kadefors et al. 1976; Madelaine and Madson 2009; Madelaine et al. 2008). Along similar lines, longer endurance is associated with more heterogenous muscle activation maps (Falla and Farina 2007; Madeleine and Farina 2008; van Dieën et al. 1993). Studies of work-related chronic and acute pain have also shown a decrease in motor variability (Madelaine et al. 2008). Based on these and other studies, it has been suggested that an increase in motor variability may play an important adaptive role to work related pain (Madelaine and Madson 2009; see also Lipsitz 2002; Mathiassen 2006; Slifkin and Newell 1999).

Our study goes a step further and suggests how an increase in variability of individual effectors can prevent fatigue from having adverse effects on the combined output of a redundant set of elements. To achieve this goal, both individual element variability and negative co-variation of commands to the elements have to be increased (see Fig. 7), and this is exactly what was observed in our experiments.

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