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The emergence and disappearance of multi-digit synergies during force-production tasks

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Abstract

We analyzed patterns of covariation among forces produced by the five digits of the human hand during tasks that required the production of a pattern of the total force consisting of ramp-up, constant force, and ramp-down segments with the time of the ramps ranging from 0 to 3000 ms. Patterns of the variance of the total force and the sum of the variances of individual digit forces were compared over sets of 12 trials at each task. The initiation of the ramp-up segment was associated with positive covariation of digit forces. Negative covariation among digit forces (force-stabilizing synergies) emerged after a critical time of 600–800 ms, which was only weakly dependent on the ramp time. These synergies persisted over the steady-state phase. A quantitative index of digit force covariation was introduced; it showed a drop about 100 ms before initiation of the ramp-down phase; we termed this phenomenon "anticipatory covariation" (ACV). The ramp-down phase was associated with rapid disappearance of the force-stabilizing synergy over a time period that ranged from 0 to 600 ms and scaled strongly with the duration of the force ramp. Thumb-virtual finger synergies showed qualitatively similar behavior to the multi-finger synergies (virtual finger is an imagined digit whose action is mechanically equivalent to the action of the four fingers). We conclude that abrupt changes in a time profile of total force are associated with transient destabilization of the total force. Changes in force-stabilizing synergies may occur in preparation to changes in the total force.

Keywords

Finger; Thumb; Force; Coordination; Human

Introduction

Recent series of studies have addressed the emergence of multi-finger synergies in isometric ramp force production tasks (Shim et al. 2003; Shinohara et al. 2003, 2004). Within those studies, synergies were defined as covariations of forces produced by individual fingers that reduced the variance of the total force across repetitive attempts at the task. Operationally, this definition was based on comparing the variance of the total force (Var F_{TOT}) with the sum of the variances of individual finger forces (ΣVar F_i), both computed over several repetitions at a task. A conclusion of predominance of negative covariations among finger forces, i.e. a multi-finger synergy stabilizing the total force, was drawn when $\Delta V = (\Sigma \text{Var } F_i - \text{Var } F_{TOT}) > 0$ (cf. Bienaymé equality theorem, Loeve 1977). We use the term "force-stabilizing synergy" in this paper to mean "covariation of finger forces that keeps the variation of the total force low across repetitive attempts at a task".

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All the mentioned studies described positive covariation among finger forces early in the ramp force production, which turned into negative covariation after a certain critical time (t_{CR}) that ranged between 150 and 850 ms. A conclusion has been drawn that the central nervous system (CNS) needs a certain time to establish a force-stabilizing multi-finger synergy and this time has only minor dependence on the rate of force increase (Shim et al. 2003). All these studies analyzed force production by the four fingers pressing in parallel; the thumb was not involved.

In another study, indices of interaction among the fingers and between the fingers and the thumb of the human hand were compared during maximum force production (maximum voluntary contraction, MVC) tasks (Olatsdottir et al. 2005). The study has shown that indices of thumb–finger interactions were similar to those of finger–finger interactions, particularly when the thumb pressed in parallel to the fingers. The authors concluded that the thumb behaves as a “fifth finger” in respect of the studied indices.

In the current paper we address the following main question: if the CNS needs time to assemble a force-stabilizing synergy during a ramp force increase, does this process have a counterpart during the phase of force decrease? Will ramp-up and ramp-down profiles of the total force over the same time intervals show symmetric patterns of variance reflecting symmetry of the processes of synergy emergence and disappearance? To answer this question we studied the digit force variance profiles during the task of producing a trapezoidal total force profile consisting of a ramp-up, steady-state, and ramp-down phases with different times of the ramp phases, which were always kept symmetrical within a task.

A secondary question addressed in the study was: do finger–thumb synergies that stabilize the total force show similar behavior to multi-finger synergies? To address this issue, we used the notion of the virtual finger (VF, Arbib et al. 1985; MacKenzie and Iberall 1994; Santello and Soechting 2000; Baud-Bovy and Soechting 2001; Zatsiorsky et al. 2004) as an imagined digit whose mechanical action is equivalent to that of the four fingers.

Methods

Subjects

Twelve healthy volunteers participated in the experiment, six males and six females. All subjects were right-handed according to preferential hand use during writing and eating. The age of the subjects ranged from 22 to 30 years. Their average weight was 66±12 kg; their average height was 1.69±0.07 m. All subjects gave informed consent according to procedures approved by the Office for Research Protection of the Pennsylvania State University.

Apparatus

Five piezoelectric sensors (Model 208A03, Piezotronic, USA) amplified by AC/DC conditioners (M482M66) were used for force measurement. 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 four finger sensors were medio-laterally distributed 30 mm apart (Fig. 1c). The position of these four sensors could be adjusted in the forward–backward direction within 60 mm to fit an individual subject's hand anatomy. The sensors were placed inside the groove in the wooden board so that the subject could place his or her fingers comfortably on the sensors. The fifth sensor measured the force produced by the thumb. It was placed on the top of a horizontal extension to the wooden board. The extension was 25 mm below the level of the board to create a comfortable configuration for all five digits. The thumb was abducted 45° relative to the index finger. Double-sided tape was used to keep sensors in place once their positions had been determined.

During the experiment, the subject sat 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 elbows at approximately 45° of flexion (Fig. 1a). A wooden board supported the wrist and the forearm. A wooden piece, shaped to fit comfortably under the subject's palm, helped maintain a constant configuration of the hand and fingers. Metacarpophalangeal joints were all flexed about 20° and all interphalangeal joints were slightly flexed, such that the hand formed a dome. A 17″ computer monitor was located about 0.8 m away from the subject. It displayed the task (see later) and also the current actual total force produced by all the digits. A customized LabVIEW program was used for data acquisition, and a MATLAB program was written for data processing. The data were sampled at 1000 Hz.

Procedure

Before each trial the subject sat relaxed with the digits of the right hand on the sensors. The computer generated two beeps (get ready), and a cursor showing the total force produced by all five digits started to move along the screen. The screen also showed the required total force profile (Fig. 1b), and the task was to try to follow the shown profile with the cursor. Each profile started with a 2 s interval when the force was supposed to be zero. Then, a slanted straight line went from 0 to a target force over a certain time (ramp time, t_{RAMP}). Further, a horizontal straight line followed for 5 s, and then another slanted line went back to zero level over the same t_{RAMP}. Four values of t_{RAMP} were used in a balanced order, 0, 500, 1500, and 3000 ms. The target force was always set at 20 N.

For each t_{RAMP}, the subjects performed 12 trials with 10 s intervals between consecutive trials. There were 3 min intervals between the 12-trial series. Before each series, three practice trials were given.

Data analysis

The force data were digitally low-pass-filtered with a second order, zero-lag Butterworth filter at 25 Hz. For the twelve ramp force production trials within each series, the following variables were computed at each point in time for each subject:

1. The average total force time profile ($F_{TOT}(t)$), its standard deviation (SD) and variance (Var);
2. The average time profiles of individual digit forces ($F_i(t)$, where i = {thumb-T, index-I, middle-M, ring-R, and little-L fingers) and their variances;
3. The time profile of the sum of the variances of individual finger forces [$\Sigma \mathrm{Var}\ F_i(t)$]; and
4. The difference between $\Sigma \mathrm{Var}\ F_i(t)$ and $\mathrm{Var}\ F_{TOT}(t)$: $\Delta V(t) = (\Sigma \mathrm{Var}\ F_i(t) - \mathrm{Var}\ F_{TOT}(t))$.

Note that when $\Delta V(t) < 0$, positive covariations among $F_i(t)$ dominate, and when $\Delta V(t) > 0$, negative covariations prevail.

Similar analysis was performed at the level of forces produced by the thumb and the VF. The force of the VF was computed as the sum of all four finger forces: $F_{VF}(t) = \Sigma F_k(t)$, where k = I, M, R, and L fingers. The difference between the sum of the variances of forces produced by the thumb and the VF and the variance of the total force was computed: $\Delta V_{VF}(t) = (\Sigma \mathrm{Var}\ F_j(t) - \mathrm{Var}\ F_{TOT}(\mathrm{t}))$, where j = T and VF. This index was used to reflect across-trials covariation of finger forces, which may not necessarily reflect within-a-trial finger force covariation (Scholz et al. 2003; Latash et al. 2003).

The following time indices were computed. Critical time (t_{CR}) was defined as the time when $\Delta V(t)$ became positive during the ramp-up phase (t^{+}_{CR}) and when it turned negative for the first time during the ramp-down phase (t^{-}_{R}). The times of the initiation of changes in the total force (t_F) during the two ramp phases were defined as the times when the first derivative of the total force reached 5% of its peak level observed during the ramp-up and ramp-down phases respectively. Similarly, the time of the initiation of changes in $\Delta V(t)$ during the ramp-down phase ($t_{\Delta V}$) was defined as the time when the first derivative of $\Delta V(t)$ reached 5% of its peak level observed during that phase. Figure 2 shows the introduced time indices for a typical data set performed by a representative subject for t_{RAMP} = 1500 ms.

Statistics

The data are presented in the text as means and standard deviations while standard errors of the mean are shown in some of the figures. Repeated-measures and mixed-effects ANOVA were used with factors *Ramp-time* (four levels, 0, 500, 1500, and 3000), *Digit* (five levels, T, I, M, R, and L), *Digit-group* (two levels, all digits versus T–VF), and *Interval* (three levels, ramp-up, steady-state, and ramp-down). Appropriate contrasts (pairwise comparisons) and post-hoc (Tukey's Honest Significant Difference, HSD test) were used to analyze significant effects. The level of significance was set at $P = 0.05$.

Results

General patterns of force and force variability

All the subjects were able to perform the task with relatively low variability of the total force. Figure 3 shows total force and SD time profiles computed over 12 trials performed for each of the tasks by a representative subject. It was certainly impossible for the subjects to match the ramp-up and ramp-down lines with $t_{RAMP} = 0$ (panel A in Fig. 3). This task implied producing the force ramps as quickly as possible. An overshoot was commonly seen during the ramp-up phase for $t_{RAMP} = 0$. The variability of the total force assessed as its SD (dashed lines in Fig. 3) showed pronounced peaks during the ramp phases and relatively low levels during the steady-state phase.

An increase in t_{RAMP} was associated with a decrease in the variability peaks during the ramp phases (compare the four panels in Fig. 3). It also showed a change in the relative magnitude of the peaks of force variability during the ramp-up and ramp-down phases: For $t_{RAMP} = 0$, the ramp-up phase showed higher variability, while for slower ramps the ramp-down phase showed higher variability. Figure 4 shows the average force variance in different phases of the task over all subjects. For $t_{RAMP} = 0$, variance indices were computed over the first 300 ms after the initiation of the ramp-up and ramp-down phases. It is obvious from Fig. 4, that the ramp phases were characterized by much higher variability compared with the steady-state (small white bars) and that the relationship between the average variance over the ramp-up and ramp-down phases reversed with an increase in t_{RAMP}. Repeated-measures ANOVA with factors *Ramp-time* and *Interval* (see Methods) confirmed these results with significant main effects of each of the factors ($F_{(3,33)} = 25.2$; $P < 0.001$ and $F_{(2,22)} = 45.8$; $P < 0.001$, respectively) and a significant interaction ($F_{(6,66)} = 15.9$; $P < 0.001$).

Relationships among digit force variance profiles

To analyze covariation of individual digit force profiles, variances of each of the digit forces (Var F_i) and the variance of the total force (Var F_{TOT}) were computed over 12 trials at a task. The sum of the variances over all the digits ($\Sigma\mathrm{Var}(F_i)$) is the total amount of variance in the digit force space. Figure 5 shows the time profiles of $\Sigma\mathrm{Var}(Fi)$ (thin solid lines), Var F_{TOT} (dashed lines), and the difference between the two, $\Delta V(t) = \Sigma\mathrm{Var}\,F_i(t) - \mathrm{Var}\,F_{TOT}(t)$ (see Methods; thick lines in Fig. 5) for each of the four tasks performed by a representative subject.

Note that $\Delta V(t) > 0$ correspond to negative covariation among digit forces stabilizing the total force whereas $\Delta V(t) < 0$ corresponds to predominantly positive digit force covariation.

During the steady-state phase of each task, Var F_{TOT} was much smaller than ΣVar(F_i) such that the lines for ΣVar(F_i) and for ΔV nearly overlap. Very different patterns are seen during the ramp phases. The ramp-up phase starts with $\Delta V(t)$ going into negative values and remaining negative for some time, which we are going to address as "ramp-up critical time", t^{+}_{CR}. At the initiation of the ramp-down phase, the typically positive values of ΔV drop and become negative after a "ramp-down critical time", t^{-}_{CR}. Panels C and D of Fig. 5 shows typical cyclic behavior of each of the variance profiles. It was associated with a few discernible steps during the drop in the total force (also see panel D in Fig. 3).

Critical time (t_{CR}) and its changes with the task were evaluated with respect to three criteria. First, t_{CR} was measured from the required time of the ramp-up or ramp-down initiation shown on the screen. These "theoretical" t_{CR} values averaged across subjects are shown in Fig. 6 (panel A). Note that an increase in the duration of the ramp was associated with longer t_{CR} for both ramp-up and ramp-down phases. During ramp-up tasks, there were relatively minor changes in the magnitude of t^{+}_{CR}, from 600 to 850 ms (black columns in panel A of Fig. 6). In contrast, during the ramp-down tasks, t^{-}_{CR} was close to zero for $t_{RAMP} = 0$ and it increased to over 650 ms for $t_{RAMP} = 3000$ ms (white columns in panel A of Fig. 6). Two-way repeated-measures ANOVA confirmed these results by showing significant main effects of both *Ramp-time* and *Interval* ($F_{(3,33)} = 11.9$; $P < 0.001$ and $F_{(1,11)} = 36.8$; $P < 0.001$, respectively).

A change in the sign of $\Delta V(t)$ was also analyzed with respect to actual total force produced by the digits at t_{CR}. This value, addressed as *critical force* (F_{CR}) is illustrated in panel C of Fig. 6. Note a substantial drop in F_{CR} with t_{RAMP} for the ramp-up phase and much less pronounced changes for the ramp-down phase. Significant effects of both *Ramp-time* and *Interval* ($F_{(3,33)} = 65.4$; $P < 0.001$ and $F_{(1,11)} = 54.0$; $P < 0.001$, respectively) and a significant interaction effect ($F_{(3,33)} = 32.5$; $P < 0.001$) were confirmed by repeated-measures ANOVA.

Actual changes in digit forces could start not exactly at the times prescribed by the task: In some trials the subjects started to change the digit forces in preparation to the required change in the total force. This was particularly pronounced for the ramp-down phase and for short t_{RAMP}. Hence, we analyzed critical times for the ramp-down phase with respect to two other times, the time (t_F) of the initiation of a change in the total force and the time ($t_{\Delta V}$) of the initiation of a change in $\Delta V(t)$. Both times were defined when the rate of change in the selected variable (F or ΔV) reached 5% of its peak values during the selected phase. This analysis was done only for the ramp-down phase, because before ramp-up all digit forces were zero and ΔV could not be defined.

Figure 7 shows the results of these analyses with filled bars showing the ($t_{CR}-t_F$) data and empty bars showing the ($t_{CR}-t_{\Delta V}$) data. The data in Fig. 7 show qualitatively similar patterns to those in panel A of Fig. 6 (empty columns), i.e. an increase in both indices with t_{RAMP}. Two-way, repeated-measures ANOVA confirmed the main effects of both *Ramp-time* and *Interval* factors on both indices ($F_{(3,33)} > 7.4$; $P < 0.01$ and $F_{(1,11)} > 40.0$; $P < 0.001$, respectively). On average, t_F started very close to the required time of force changes; over the four t_{RAMP} conditions, the average t_F was +15 ms, i.e. the total force started to change about 15 ms after the required time. This seeming delay probably originated from the criterion used, which gave somewhat delayed t_F values for relatively slow changes in the total force (long t_{RAMP}).

Figure 7 shows that ($t_{CR}-t_{\Delta V}$) was consistently larger than ($t_{CR}-t_F$). This implies that changes in the ΔV index started before initiation of the force ramp-down. Such anticipatory covariation (ACV) of the total force was seen across ramp durations. Figure 8a shows typical time profiles of $F_{TOT}(t)$ and $\Delta V(t)$ for a representative subject performing the ramp-down phase with t_{RAMP} = 1500 ms. Note that changes in $\Delta V(t)$ start earlier than changes in the total force. Panel B of Fig. 8 shows the time delays between $t_{\Delta V}$ and t_F for all five t_{RAMP} averaged across all subjects. These values are all negative. They range between 60 and 100 ms and show an increase with an increase in the duration of the ramp. All the average values shown in Fig. 8b were significantly different from zero ($P < 0.01$) according to one-group *t*-tests with Bonferroni corrections.

To further analyze the time changes of $\Delta V(t)$ during the ramp-up and ramp-down segments, time derivatives of $\Delta V(t)$ were computed for each task and each subject. Then, the times to peak $d\Delta V(t)/d\,t$ and to its first zero crossing were computed and analyzed, Fig. 9. In general, both time indices showed an increase with t_{RAMP} for both ramp-up and ramp-down phases of the task. This means that $\Delta V(t)$ changed quicker for tasks that required a quicker change in the total force. Both time indices showed significant effects of *Ramp-time* and *Interval* in two-way repeated-measures ANOVA ($F_{(3,33)} > 22.6$; $P < 0.001$ and $F_{(1,11)} > 9.2$; $P < 0.05$, respectively). A significant *Ramp-time*×*Interval* interaction was also found for both indices ($F_{(3,33)} > 5.4$; $P < 0.01$).

The differences in the rates of changes of the total force and of $\Delta V(t)$ were also analyzed using their peak values. Figure 10a shows that there was a close linear relationship between $d\,F(t)/d\,t$ and $d\Delta V(t)/d\,t$, while panels B and C of the same figure illustrate changes in these peak values with t_{RAMP}.

Analysis at the virtual finger versus thumb level

Analysis of force covariation at the level of the thumb and VF forces produced results qualitatively similar to those described for all five digit forces. Variances of the forces produced by the VF and by the thumb were computed over the 12 trials of each series. The index of the thumb-VF force covariation was computed as $\Delta V(t) = \mathrm{Var}\,F_{VF}(t) + \mathrm{Var}\,F_T(t) - \mathrm{Var}\,F_{TOT}(t)$.

Figure 11 shows typical examples of the variance time profiles for the four tasks. Note the similarity between the time profiles in Figs. 11 and 5. All the qualitative features of changes in $\Delta V(t)$ and t_{CR} indices described in the previous sections were also observed when similar analyses were run at the VF versus thumb level. In particular, $\Delta V(t)$ turned negative early in the ramp-up phase and changed its sign after a critical time t^{+}_{CR}. During the ramp-down phase, $\Delta V(t)$ dropped to negative values at a critical time t^{-}_{CR}. Panels B and D in Fig. 6 shows averaged-across-subjects t_{CR} and F_{CR} values for the ramp-up and ramp-down phases (black and white columns, respectively) and for the different t_{RAMP} values. Note the similarity of the data in these two panels and the data in panels A and C in the same figure. All the significant statistical effects observed at the level of individual finger forces were also observed at the level of the thumb and VF.

Discussion

All subjects that participated in the studies with ramp force production (Latash et al. 2001, 2002; Shim et al. 2003; Shinohara et al. 2003, 2004), including the authors of this paper, noticed that it was relatively easy to keep the total force constant or changing at a constant rate. In contrast, a change between these two regimes, e.g. starting a ramp force profile from a relaxed state, required concentration and practice, and was commonly associated with significant errors. The results of the current study suggest that these subjectively perceived difficulties were associated with processes of synergy formation and destruction.

Our experiments have shown that multi-digit synergies during accurate force production tasks depend strongly on the required pattern of the total force. In particular, changes in the total force were associated with transient changes in an index of digit force covariation (ΔV) suggesting that multi-digit force-stabilizing synergies emerged and disappeared over time in a task-specific manner. Special behavior of the multi-digit synergies was observed at times when changes in the rate of force production were required. In the following sections, we address implications of these findings for issues of stability of motor performance. We also introduce a new notion, that of anticipatory covariation, as a mechanism that prepares a multi-element system for a change in its performance regime.

Emergence and disappearance of multi-finger synergies

During the production of a constant force, individual finger forces have been shown to co-vary negatively such that an increase in the force of a finger is nearly perfectly compensated for by changes in other finger's forces (Shim et al. 2004). As a result, the relatively high variance in the finger force space results in a much lower variance of the total force. As in earlier studies (Scholz et al. 2002; Shinohara et al. 2003; Shim et al. 2003), we quantified this effect with an index ΔV reflecting the difference between the sum of the variances of individual digit forces and the variance of the total force; ΔV showed reproducibly high values over the steady-state phase of the task. The ramp-phases, however, presented a strikingly different picture.

When the subjects started a task, ΔV was undefined, because all digit forces were zero. At the start of the ramp-up phase, digit forces showed positive covariation reflected in negative values of ΔV for a time period of between 600 and 800 ms (cf. Shim et al. 2003). Then, ΔV turned positive and rose to a level which persisted over the steady-state phase. The beginning of the ramp-down phase, however, did not mirror the end of the ramp-up phase: There was a rapid drop in ΔV, faster for quicker ramp tasks.

The delayed emergence of negative digit force covariation ($\Delta V > 0$) during the ramp-up phase has been interpreted as a sign of a critical time required by the controller to assemble a force stabilizing synergy (Shim et al. 2003; Shinohara et al. 2004). In the current study, we also saw relatively small changes in t_{CR} with the ramp duration. Note that for the two shortest t_{RAMP} conditions, this time was sufficient for the subjects to reach the required plateau of the total force, while for the slowest condition (t_{RAMP} = 3000 ms) the total force was only about 30% of that value. Hence, we can conclude that the creation of a synergy did not depend crucially on reaching a critical force, for example to provide sensory feedback necessary for total force stabilization (e.g., Todorov and Jordan 2002).

The $\Delta V(t)$ patterns observed during the ramp-down phase show that the force-stabilizing synergy was quickly destroyed. The process of synergy destruction started close to the time of the initiation of the total force change and was much faster for the shorter ramp durations, nearly instantaneous for $t_{RAMP} = 0$. We will discuss these results in more detail later.

Synergies at the level of interaction between the thumb and VF

The thumb has a separate and mostly independent muscular apparatus in contrast to the four fingers that share external multi-tendon muscles (Moore 1992). The thumb also has a larger and more separate brain representation in the cortical primary motor area (Penfield and Rassmussen 1950), which may be responsible for its different susceptibility to neural injury (Lang and Schieber 2003). According to one of the influential theories, control of prehension is organized in an hierarchical manner: The upper level of the hierarchy defines motor outputs of the thumb and a VF, and the lower level distributes the VF action among the individual digits (MacKenzie and Iberall 1994; Baud-Bovy and Soechting 2001).

However, more recent studies have questioned the traditional homunculus view on the M1 cortical projections in favor of a more fragmented and mixed pattern (Schieber 2001). Besides, indices of finger interaction, such as enslaving and force deficit (reviewed in Zatsiorsky et al. 1998), have been shown to be similar to the indices quantified for finger-thumb interactions (Olatsdottir et al. 2005). The current study shows that digit interaction is organized similarly when it is analyzed at the level of individual digits and at the thumb-VF level. At both levels, force outputs of the digits are organized in synergies stabilizing the total force output over much of the task duration. At both levels, however, the early fragments of the ramp-up and ramp-down phases were characterized by large transient changes in the ΔV index, which we have interpreted as the processes of emergence and disappearance of force-stabilizing synergies. These findings suggest that the CNS may not control the thumb as a special digit but rather as one of the fingers.

Purposeful destabilization of performance variables

Stability of performance has commonly been viewed as an important feature of multi-element motor actions (reviewed in Saltzman and Kelso 1987; Kugler and Turvey 1987). This view has its roots in engineering where performance stability is one of the most important goals. It is achieved by a variety of means ranging from continuous feedback-based control to implementing redundant parallel controllers and to finding regimes that are characterized by high dynamic stability. Studies of stability of motor performance have been particularly active within the dynamic systems approach to movement studies (reviewed in Turvey 1990; Kelso 1995). This approach implies, in particular, that the system for production of voluntary movements typically functions in regimes close to those that can induce loss of stability of motor performance (Schoner 1990). Many of the studies within this line of research analyzed the relative phase of actions performed by two effectors (Kelso 1984; reviewed in Kelso 1995). It has been shown, in particular, that a change in the relative phase is characterized by an increase in the variability of the performance (Kelso 1984; Haken et al. 1985).

Our results show that stability may be an overvalued notion with respect to motor performance; in particular, multi-digit performance was destabilized when a change in the total force was required by the task. In his classical book “On Dexterity and Its Development”, Bernstein (1996) suggested a definition for dexterity that involved both stability of performance and its maneuverability if a quick change in performance is required. To change quickly a variable stabilized by a synergy, one needs to destabilize it: Our observations show that a change in the regime of performance of a multi-digit system is indeed associated with transient destabilization of its output. The importance of such transient episodes of destabilization of the motor output is exemplified by the phenomenon of anticipatory covariation (ACV).

Anticipatory covariation—a novel mechanism of adjustments in motor synergies

Anticipatory behavior of the motor control system has been known for many years (Bernstein 1935; Belenkiy et al. 1967). One of the first and best studied examples of anticipatory control is the anticipatory postural adjustments (APA; Belenkiy et al. 1967, reviewed in Massion 1992). APA are changes in the activity of muscles involved in a postural component of a task in anticipation of mechanical consequences of a voluntary action that may potentially destabilize posture. APA typically start about 100 ms before the initiation of a “focal” voluntary action and induce forces acting against the expected postural perturbation (Cordo and Nasher 1982; Bouisset and Zattara 1987, 1990).

Anticipatory changes in the index of digit force covariation (ΔV)—anticipatory covariation (ACV)—have features that are similar to those described for APA. During the ramp-down phase of the task, ACV started about 100 ms before the change in the total force. During ACV, its index (ΔV) changed faster for the planned faster changes in the total force. APA also typically start about 100 ms before the focal motor action; during APA that accompany fast voluntary movements, changes in the levels of muscle activity are earlier and larger for faster movements (Horak et al. 1984; Lee et al. 1987). While both APA and ACV represent anticipatory (feed-forward) mechanisms of motor control, the purpose of ACV seems to be rather different from that of APA: ACV may be viewed as a means of destabilizing the total output of a multi-element system to enable its quick change.

Concluding comments and limitations of the study

A major novel finding in the study is a change in the index of across-trials covariation of finger forces without a change in the total force, in anticipation of its required future change. These subtle preparatory changes apparently helped the subjects to shift from a pattern of finger force covariation that stabilized the total force at a required level to a pattern that facilitated a change in the total force. Preparation for an action is of a major importance for various everyday actions. It has been shown to suffer in certain neurological conditions such as Parkinson's disease (Bazalgette et al. 1986; Viallet et al. 1987) and during normal aging (Woollacott et al. 1988). We believe that studies of anticipatory covariation in different subpopulations can reveal changes that may be causally related to impairments in motor synergies.

There are several features of the design of the study that may be modified to further test our conclusions. First, to produce a perfect ramp profile of the total force starting from a constant zero force level, the subjects were required to show an infinite first derivative of the force at the instant of the ramp initiation. This is hardly compatible with the known properties of the human muscles (Zajac 1989). Some of the results may reflect a strategy the subjects adopted to handle this impossible task. We plan in future to confirm the findings using more natural sigmoid force profiles. Second, to provide a more complete description of this behavior, subjects may be asked to produce ramp-up force profiles starting not from zero force but from a non-zero constant force level. Actually, we performed such experiments in an unpublished study and observed virtually no changes in the index of force covariation at the time of the ramp-up initiation in contrast with the findings of major changes in this index at the initiation of a ramp-down phase in the current study. It was practically impossible to add all these conditions to the current experimental design; hence, this is a challenge for a future study.

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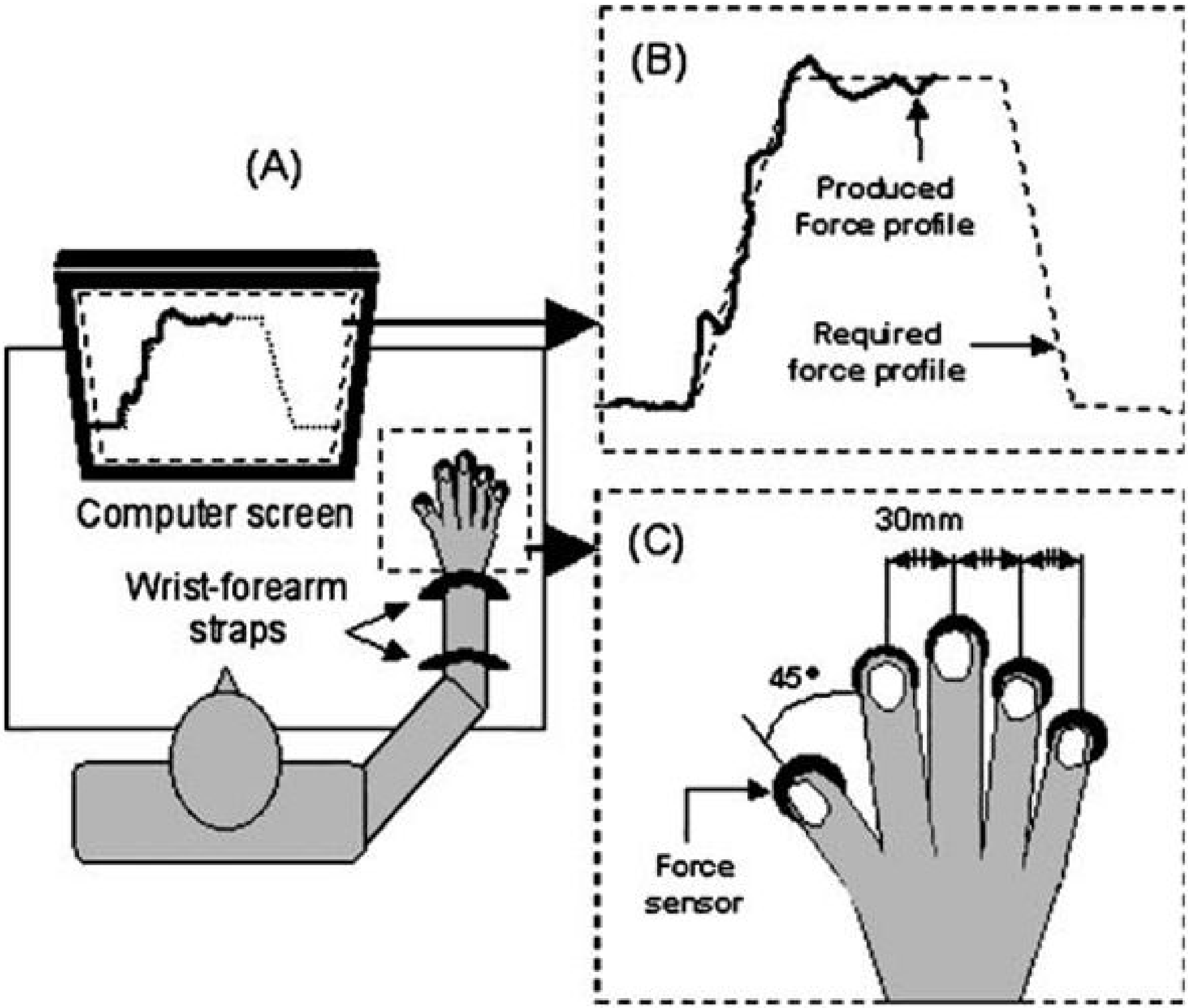

Fig. 1.

A Schematic illustration of the experimental setup. **B** The required total force pattern and the total force produced by a subject shown on the monitor screen. **C** The configuration of force sensors and digits

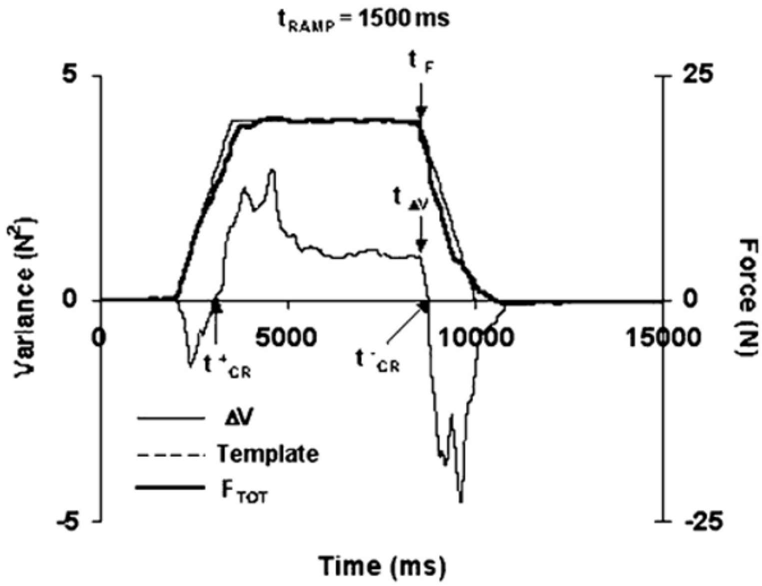

Fig. 2.

Typical time profiles of the difference ($\Delta V(t)$) between the sum of the variances of individual digit forces and the total force variance computed over 12 trials [$\Delta V(t) = \Sigma \mathrm{Var}\, F_j(t) - \mathrm{Var}\, F_{TOT}(t)$], and of the total digit force, $F_{TOT}(t)$, for the task with the ramp duration of 1500 ms. Critical times, t^{+}_{CR} and t^{-}_{CR}, are the times of ΔV turning positive during ramp-up and negative during ramp-down, respectively; t_F and $t_{\Delta V}$ are the times of the initiation of F_{TOT} and ΔV changes, respectively, at the beginning of the ramp-down phase. Data from a representative subject are shown

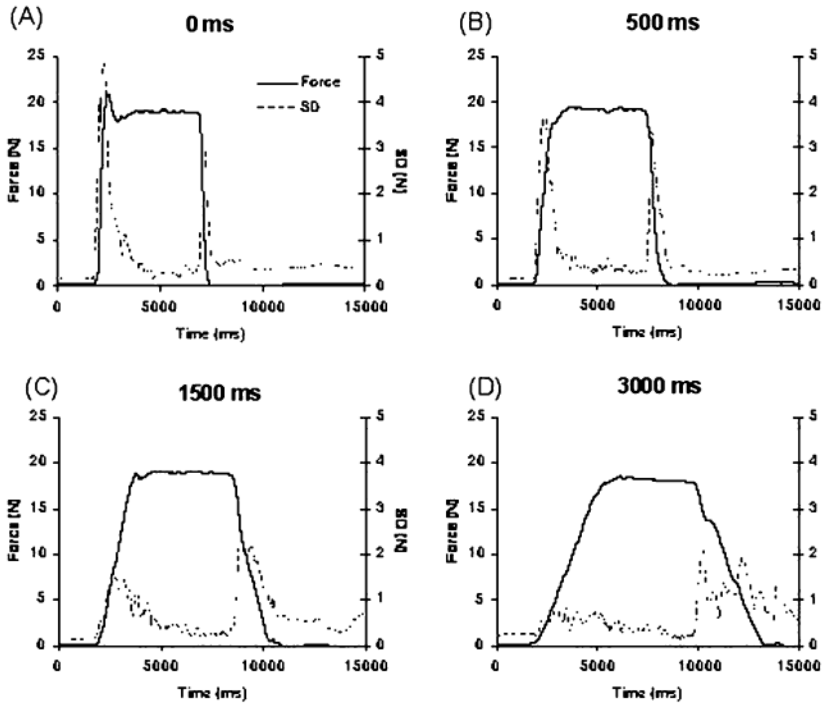

Fig. 3.
Typical time profiles of the average and standard deviation of the total digit force computed over 12 trials for a representative subject. Data for **A** 0 ms, **B** 500 ms, **C** 1500 ms, and **D** 3000 ms ramp durations are shown

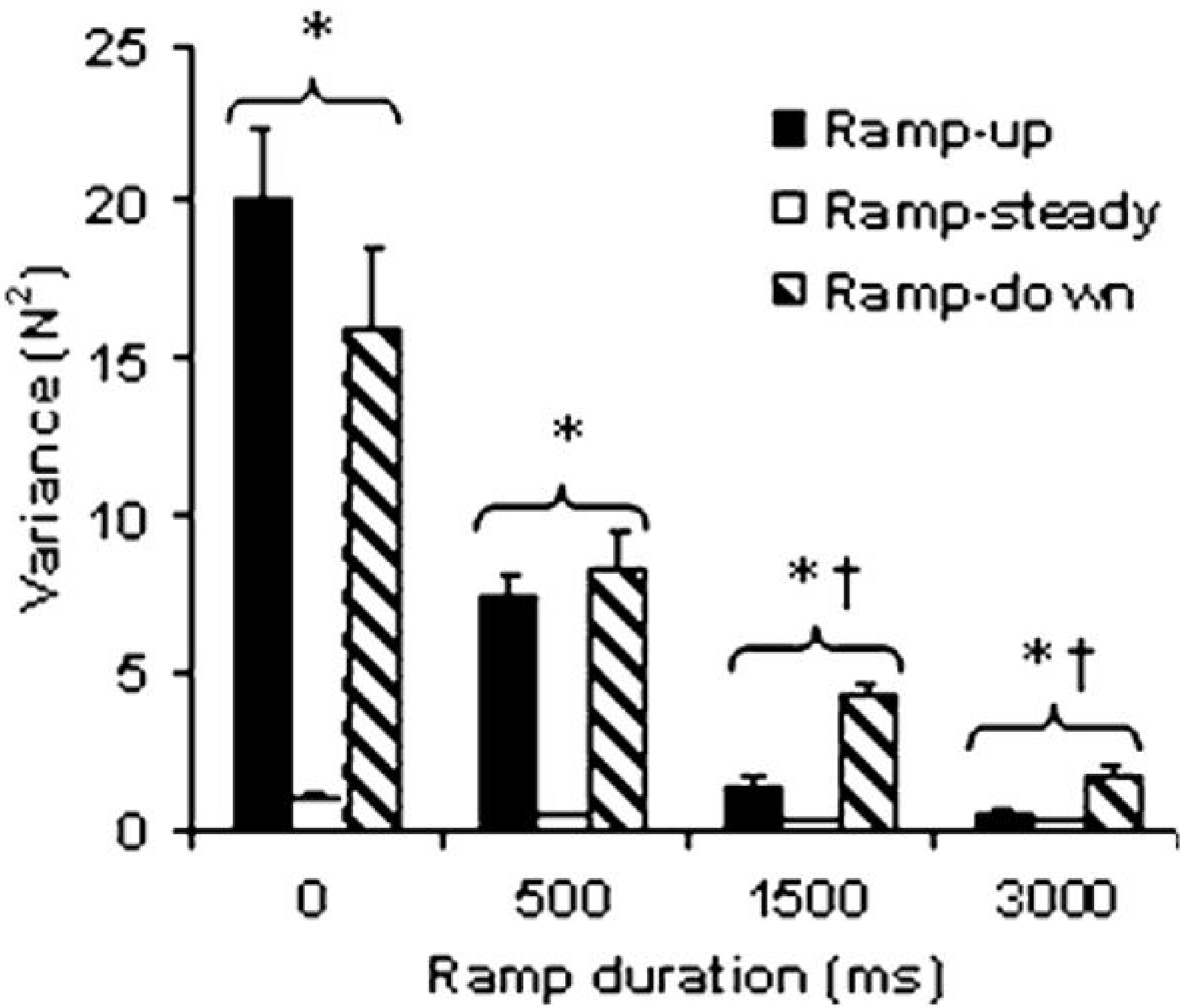

Fig. 4.

The total force variance during ramp-up, steady-state, and ramp-down phases computed over sets of 12 trials performed by each subject at each task. Averaged group data are presented with standard error bars. * and †, respectively, signify significant ($P < 0.05$) differences between the steady force production phase and the ramp phases (ramp-up and ramp-down) and differences between the ramp-up and ramp-down phases. A significant effect of ramp duration was found

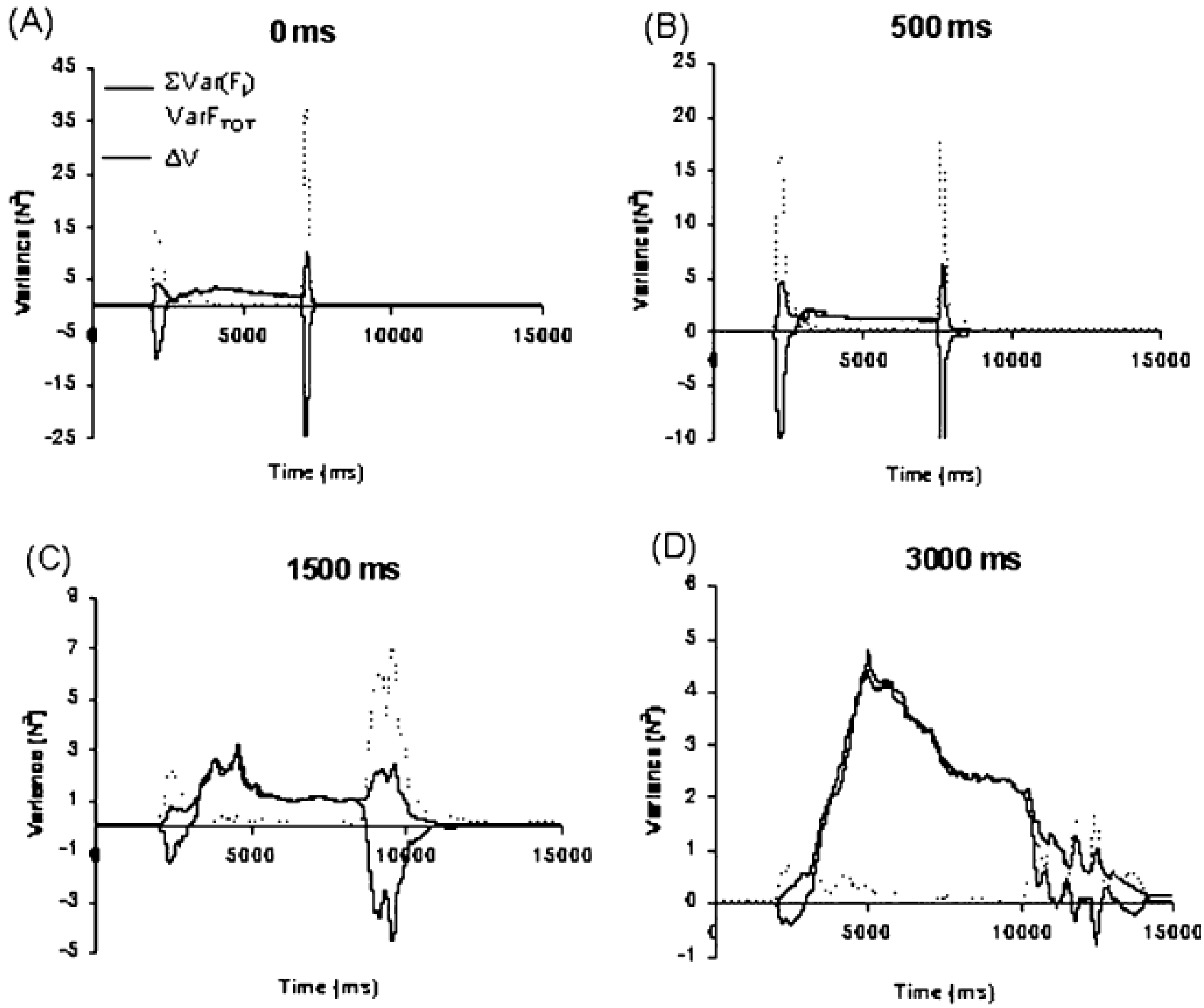

Fig. 5.

Typical time profiles of the sum of the variances of individual digit forces [ΣVar $F_j(t)$], the variance of the total force [Var $F_{TOT}(t)$], and the difference between the two, $\Delta V(t) = \Sigma\text{Var } F_j(t) - \text{Var } F_{TOT}(t)$. The data were computed over sets of 12 trials performed by a representative subject

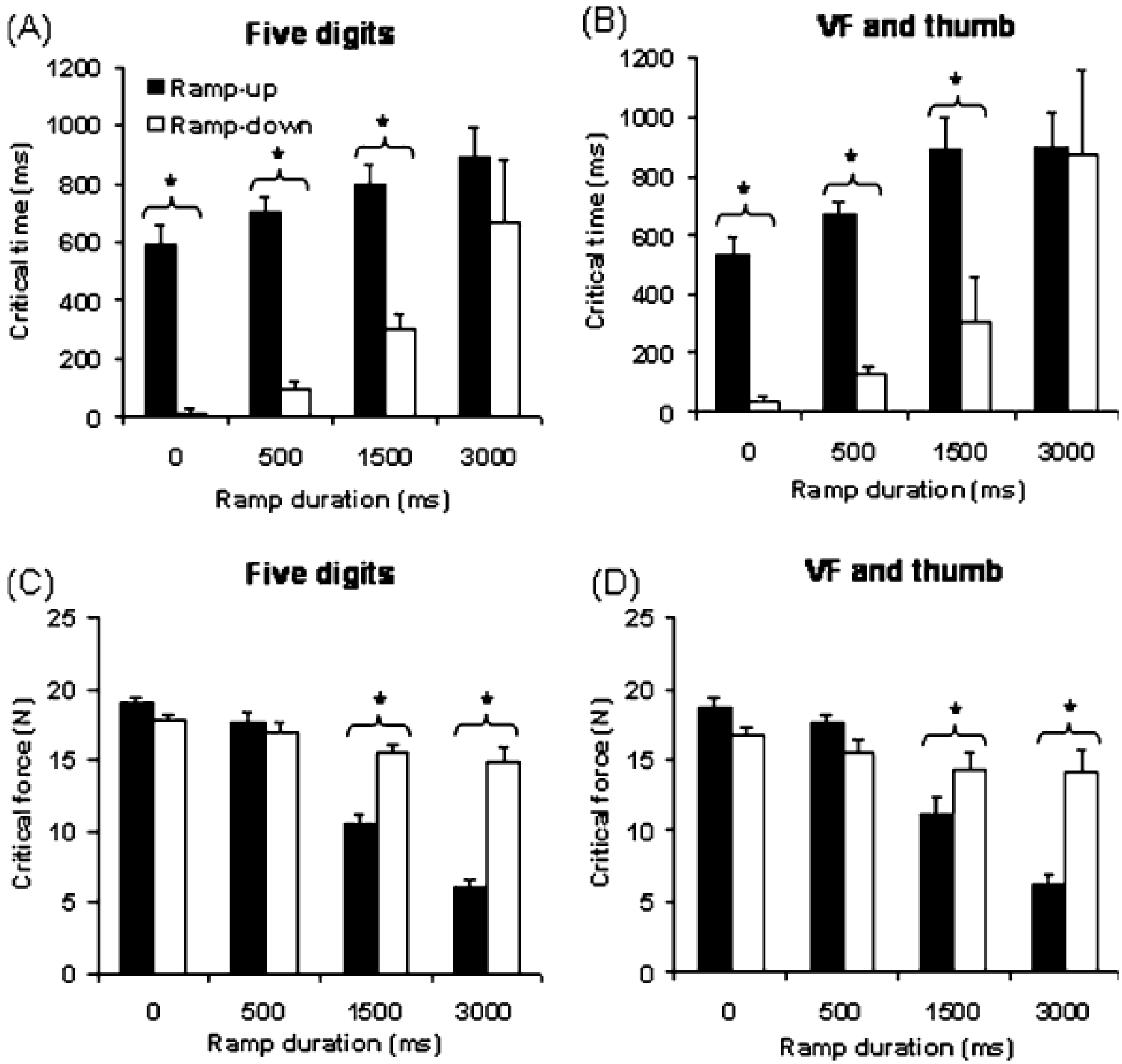

Fig. 6.
Critical times during ramp-up (t^{+}_{CR}) and ramp-down (t^{-}_{CR}) calculated using the forces of all the digits (**A**) and of the thumb and VF (**B**). **C** and **D** show corresponding magnitudes of the critical forces (F_{CR}). Averaged-across-subject data are presented with standard error bars. *Indicates a significant ($P < 0.05$) pair-wise difference between the ramp-up and ramp-down phases. Significant effects of ramp duration were found for **A**, **B**, **C**, and **D**

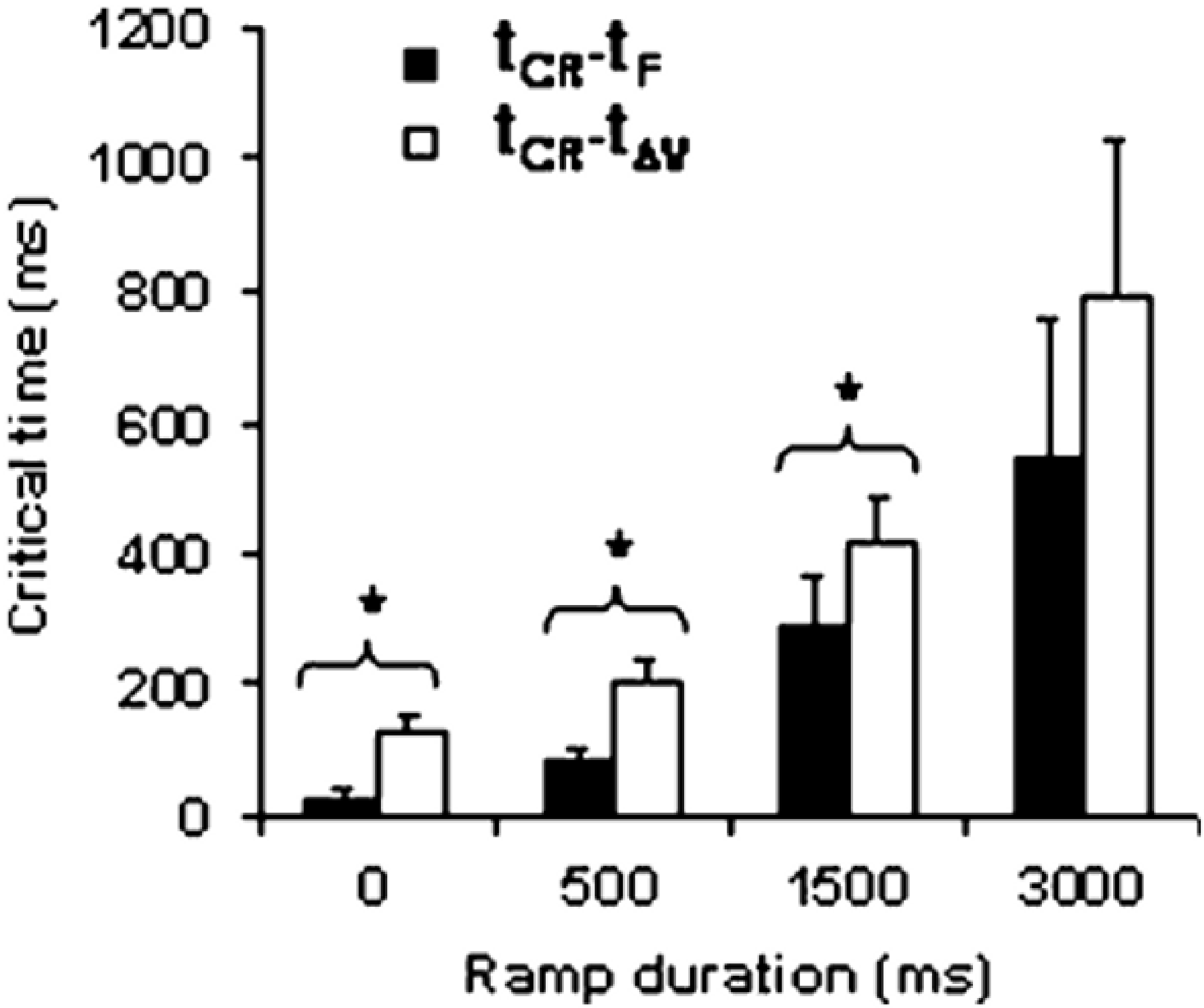

Fig. 7.

The difference ($t_{CR}-t_F$) between the critical time (t_{CR}) and the time of initiation of a decrease in the total force (t_F), and the difference between t_{CR} and the time of initiation of a decrease in ΔV ($t_{\Delta V}$) during the ramp-down phase. Note that ($t_{CR}-t_{\Delta V}$) is larger than ($t_{CR}-t_F$) for all conditions. Averaged-across-subjects data are presented with standard error bars. *Indicates a significant ($P < 0.05$) pair-wise difference between $t_{CR}-t_{\Delta V}$ and $t_{CR}-t_F$. A significant effect of ramp duration was found

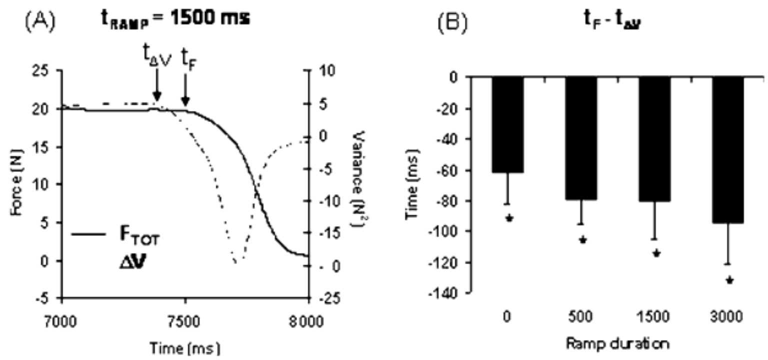

Fig. 8.

A Typical time profiles of the total force, $F_{TOT}(t)$, and $\Delta V(t)$ in a 1000-ms time window at the beginning of the ramp-down phase. Data for a representative subject are shown for t_{RAMP} = 1500 ms. **B** The difference ($t_F - t_{\Delta V}$) between the times of initiation of a change in the total force (t_F) and in ΔV ($t_{\Delta V}$). Averaged-across-subjects data are shown with standard error bars. Note that changes in ΔV always started before changes in the total force. *Indicates a significant ($P < 0.05$) pair-wise difference between $t_F - t_{\Delta V}$ and 0

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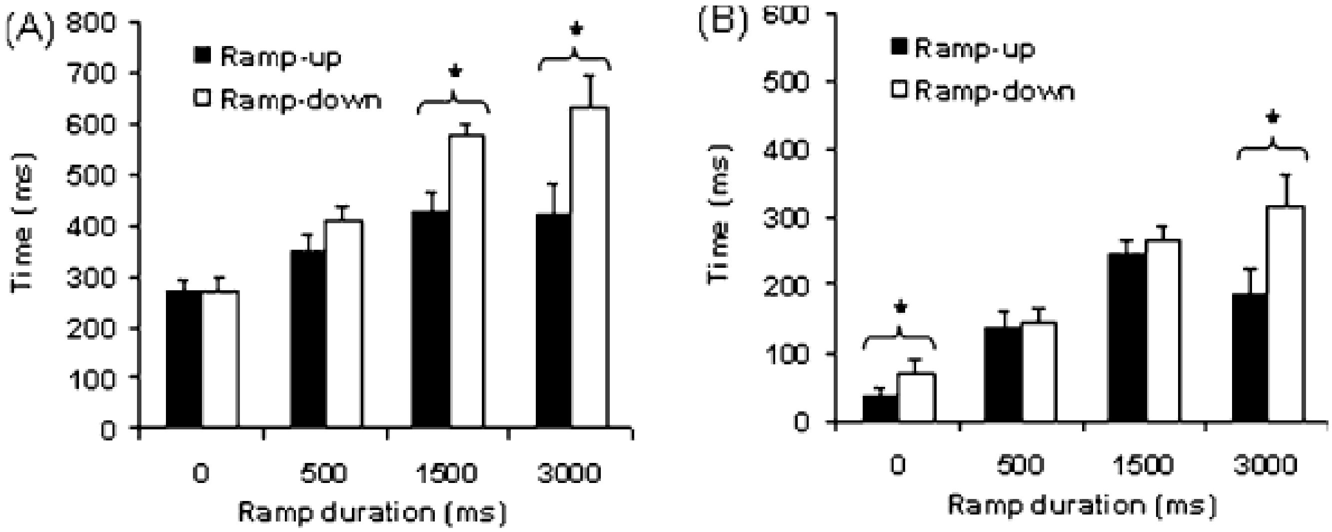

Fig. 9.
A The time from the required ramp initiation to the peak of the first derivative of Δ*V* and **B** the time from the required ramp initiation to the first zero crossing of d$\Delta V(t)$/d *t*. Averaged-across-subjects data are shown with standard error bars. *Indicates a significant ($P < 0.05$) pair-wise difference between the ramp-up and ramp-down phases. A significant effect of ramp duration was found for both (**A**) and (**B**)

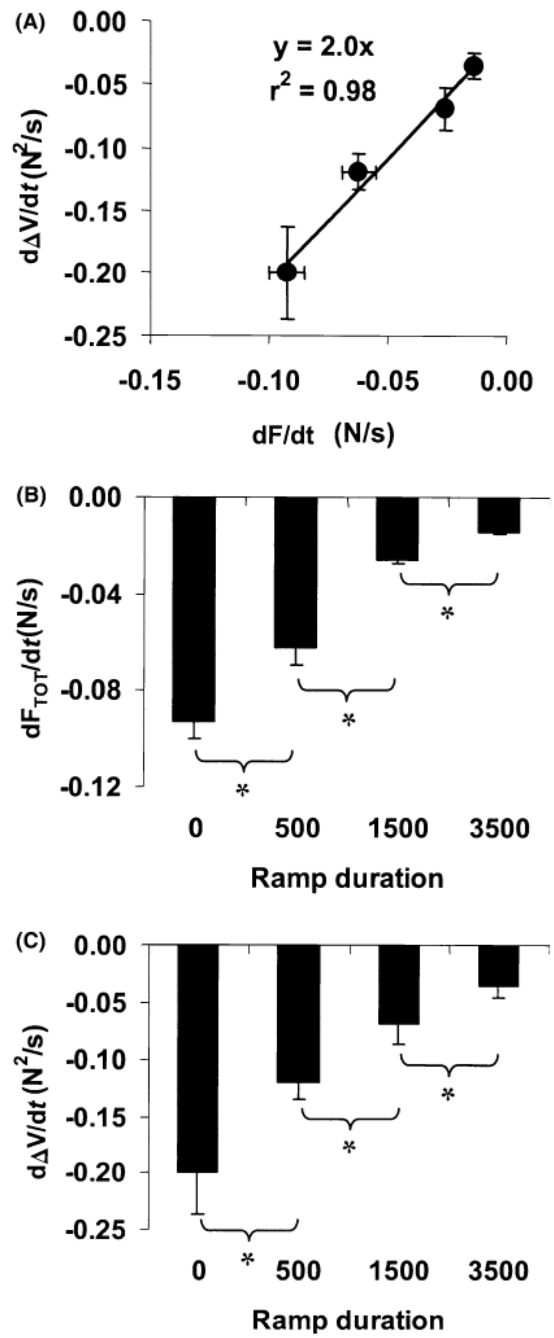

Fig. 10.

A The relationship between the peak of the first derivative of the total force (d $\Delta F_{TOT}(t)$/d t) and the peak of the first derivative of $\Delta V(t)$ [d $\Delta V(t)$/d t]. **B** and **C** show the dependances of d$\Delta F_{TOT}(t)$/d t and d $\Delta V(t)$/d t on the ramp duration. Averaged-across-trials and subjects data are shown with standard error bars. *Indicates a significant ($P < 0.05$) pair-wise difference

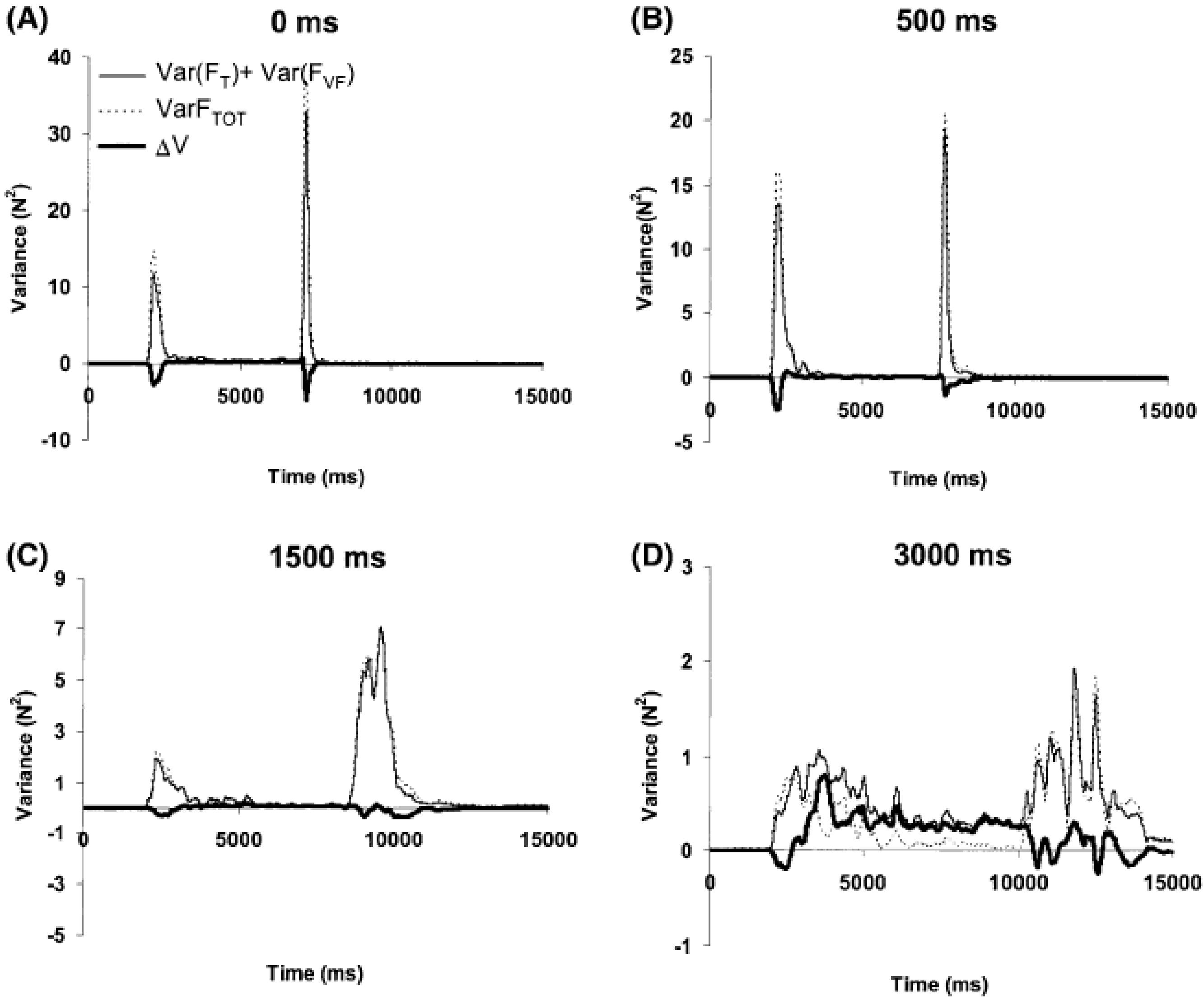

Fig. 11.

Typical time profiles of the sum of the variances of VF and thumb forces [Var $F_{TH}(t)$+Var $F_{VF}(t)$], the total force variance [Var $F_{TOT}(t)$], and the difference between the two, $\Delta V(t)$ = (Var $F_{TH}(t)$+Var $F_{VF}(t)$) − Var $F_{TOT}(t)$. All variances were computed over sets of 12 trials performed by a representative subject