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Anticipatory covariation of finger forces during self-paced and reaction time force production

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Abstract

We tested a hypothesis that humans can change patterns of finger force covariation in a task-specific manner in preparation to a change in the total force. Subjects performed quick targeted force pulses by pressing with four fingers on force sensors from a certain background force level to a target level. In self-paced trials, finger force modes (hypothetical commands to fingers) showed changes in covariation, computed across trials, more than 100 ms before changes in the total force. Half of the subjects showed large early changes in force mode covariation, while in the other half these changes were much smaller and were followed by a larger positive covariation of finger modes potentially destabilizing the total force profile. Such early covariation changes were absent under the simple reaction time instruction. We conclude that anticipatory covariation reflects control processes that can be expressed differently in different persons and modified depending on the available time for action preparation.

Keywords

Hand; Force production; Coordination; Human

Force production by several fingers pressing in parallel has been used in several recent studies to investigate multi-finger synergies (reviewed in [4]). In those studies, covariation among finger forces or among finger modes was quantified over sets of trials at different tasks. Finger modes represent hypothetical independent signals to individual fingers [1,3]. Predominantly negative covariation has been interpreted as a synergy stabilizing the total force. A recent study [9] described a phenomenon of anticipatory covariation (ACV), a change in covariation among finger forces in preparation to producing a change in the total force. ACV has been interpreted as a means of destabilizing the total force without a change in its magnitude to facilitate a planned (anticipated) change in the force.

The purpose of this study has been to test a hypothesis that the central nervous system (CNS) is able to change patterns of finger mode covariation in a task-specific manner in preparation to an action. ACV has been described as occurring about 100 ms prior to a change in the total force [9]. Hence, if a person has to generate a response as quickly as possible after an auditory stimulus, the typically short simple reaction times may not allow ACV to occur, while it may be expected when a similar motor action is produced in a self-paced (SP) manner. Hence, we compared patterns of finger force covariation during the production of quick targeted pulses of force in a self-paced manner and under a typical simple reaction time instruction.

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Five male and five female university students volunteered to participate in the study. Their average age was 27 ± 4 years; average height 172 ± 12.1 cm, and average weight 66.1 ± 13.0 kg. All participants were healthy and right handed, according to their preferential hand use during writing and eating. All subjects gave written consent according to the procedures approved by the Office for Research Protection of The Pennsylvania State University in accordance with the Declaration of Helsinki.

Four piezoelectric sensors (Model 208A03, Piezotronics Inc.) amplified by ac/dc conditioners (M482M66) were used to measure the forces generated by the fingers. Cotton pads were attached to the surface of the sensors, in order to increase friction and prevent skin temperature effects on the sensors. The sensors were placed in a metal frame that sat in a groove on a wooden board. The sensors were medio-laterally spaced 30 mm apart and could be adjusted in the forward–backward direction within 60 mm to fit each subject's hand anatomy.

During the experiment, the subjects sat in a chair facing the testing table with the right shoulder at approximately 45° of abduction and flexion, and the elbow flexed about 135°. Metacarpophalangeal joints were flexed about 20° and all interphalangeal joints were slightly flexed such that the hand formed a dome. A wooden piece, shaped to fit comfortably under the subject's palm, helped maintain a constant configuration of the hand and fingers. The forearm was attached to the board with Velcro straps. A 17-in. computer monitor, located about 0.8 m away from the subject, displayed the task (see later) and the actual total force produced by all four fingers. In reaction time trials, imperative auditory signals were delivered through the headphones worn by the subjects. A LabVIEW-based program was used for data acquisition. The data were collected at 1000 Hz with a 12-bit resolution.

Prior to each trial the subject sat relaxed with the fingers of the right hand resting on the sensors. The computer generated two beeps (get ready) and a cursor showing the total force generated by all four fingers started to move across the screen. There were six control trials and two main series. First, maximal voluntary contraction (MVC) force was measured. In these trials, the subjects were required to press with all four fingers "as hard as possible" and given a time interval of 3 s to reach a peak force. Two attempts at MVC were recorded, and the attempt with the highest peak force was used to set up other tasks. Following the MVC task, subjects were asked to produce ramp patterns of force from 0 to 10% of MVC over 5 s by pressing with only one finger in each separate trial. An oblique red line was shown on the screen, and the participant's task was to trace this line in time with the cursor representing the force of the task finger. These data were used to generate linear estimates of the relations between changes in individual finger forces and change in the total force during a multi-finger task [3]. These relations are non-trivial because of the phenomenon of enslaving [6].

There were two main series, reaction time (RT) and self-paced. In these series, the screen displayed lines showing a background force (5% of MVC) and a target force (25% of MVC with 5% error margins). As soon as the program started, subjects were asked to produce force with all four fingers and match the background force line. In RT trials, subjects were instructed to react to a brief "chirp" sound (100 ms) delivered through the headphones by producing a quick force pulse to the target level and then relaxing. The "chirp" was delivered randomly within a 100 ms time interval starting 0.5 s after the force trace crossed a vertical line on the screen. In SP trials, the subjects were asked to produce a quick pulse to the target at any time within a 3 s time window. The onset of the window was shown on the screen by a vertical line. Each trial lasted 7 s. Subjects performed 15 trials for each condition with 8 s intervals between the trials and 3 min intervals between the conditions. The trials within each condition were blocked. Three practice trials were given prior to each condition.

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The data were processed off-line using MatLab-based software. The force data were low-pass filtered at 100 Hz using a 9-order, zero-lag Butterworth filter. Then, the first derivative of force was computed. Unfiltered data were used for the analysis of force variance components (see later). The following time indices were calculated for the SP and RT series. Time of initiation of change in the total force (t_F) during the force pulse was defined as the time when the first derivative of force reached 5% of its peak value. At t_F, the total force changes were under 0.3 N (illustrated later in Fig. 2). Reaction time (t_{RT}) was defined as the time from the beginning of the "chirp" to the initiation of change in the total force (t_F). Trials with t_{RT} shorter than 100 ms and longer than 300 ms, as well as trials that showed multiple force peaks were rejected. On average, 0.7 trials were rejected per subject for the RT series and 2.1 trials for the SP series. Time to peak force (t_{PF}) was defined as the time from t_F to the time when peak force occurred.

The trials within each series were aligned by t_F; force data were time-normalized by t_{PF} (taken as 100%). The following analyses were run at every 1% of the time across all trials collected for each subject within a condition (RT or SP).

Analysis of covariation of finger modes was performed similarly to previous studies [3,4]. Briefly, single-finger force ramp trials were used to compute the enslaving matrix ***E*** for each subject. The entries of the ***E*** matrix were computed as the ratios of the change in the force of each finger to the change in the total force over the ramp duration. As in earlier studies, we have not introduced explicitly the phenomenon of force deficit [6] into the analysis since it results only in proportional scaling of all finger forces [10]. The ***E*** matrix was used to compute changes in hypothetical independent commands to fingers (modes, **m**) based on force changes.

For further analysis, we used the framework of the uncontrolled manifold (UCM) hypothesis [4,8]. The hypothesis assumes that the controller organizes covariation among potentially independent elemental variables (modes) to stabilize a certain value of a performance variable (total force). At each time, a manifold was computed in the demeaned mode space. It represented mode values consistent with a stable value of the total force ($dF_{TOT} = 0$). The manifold was approximated linearly by the null-space of matrix ***E*** spanned by the orthonormal basis vectors, $\mathbf{e_i}$ computed numerically across trials at each time-normalized sample. The mode vectors, obtained at each sample of each trial, were projected onto the basis vectors of the null space. The variance (across trials) of the vector projections within the UCM (V_{UCM}) and orthogonal to the UCM (V_{ORT}) was estimated per degree-of-freedom in each space.

An index $\Delta V = (V_{UCM}\ \Delta V_{ORT})/V_{TOT}$, where V_{TOT} is total variance per degree-of-freedom, was used as the main index of force mode covariation. Note that positive values of ΔV correspond to negative force mode covariation, which may be interpreted as stabilization of the total force across trials.

In the text, the data are presented as means and standard deviations, while in the figures standard errors of the mean are shown. Non-parametric Friedman's test was used with factors *Condition* (RT and SP) and *Time* (six levels, 50% windows, see below). Wilcoxon's singed-rank tests were used for post hoc analysis. Significance level was set at $p < 0.01$ (corrected for multiple comparisons).

The insert in the upper panel of Fig. 1 illustrates a typical force pulse and its first time derivative (dF/dt) for the RT task produced by a typical subject. The subjects produced force pulses that, on average, reached the peak force of 24.5 ± 7.7 N in SP trials and 24.2 ± 7.2 N in RT trials. The time (t_{PF}) from the initiation of the force pulse (defined as the time when dF/dt reached 5% of its peak value) to the force peak was 122 ± 34 ms in SP trials and 105 ± 38 ms in RT trials. There were no statistically significant differences between the peak force values, while RT trials showed significantly lower t_{PF} values ($p < 0.001$). Average reaction time across subjects was 214 ± 34 ms.

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During the production of steady-state force (background force), the subjects showed predominantly negative covariation among finger modes—commands to individual fingers defined earlier. This was reflected in positive values of ΔV that were typically close to +1 (as illustrated in the upper panel of Fig. 1). During the force pulse, ΔV typically dropped and became negative corresponding to positive covariation of finger modes. In this and further Figures, for comparison across subjects, the time is shown in percent of t_{PF}. On average, 100% correspond to 113 ms.

During RT trials, subjects did not show consistent changes in ΔV prior to the initiation of the force pulse. In contrast, SP trials were accompanied by an early, gradual drift in ΔV before t_F that could be expressed differently in different subjects. During the force pulse, ΔV dropped to more negative values during RT tests as compared to the SP tests. The top panel of Fig. 1 illustrates an early drop in ΔV (anticipatory covariation) apparent about 50–60 ms prior to the change in the total force; these data are for a representative subject. The lower panel of Fig. 1 shows the average time profiles of changes in ΔV ($\Delta\Delta V$) after these time functions were corrected by a value observed in each subject at the beginning of the analysis interval (200% of t_{PF} prior to t_F). In RT tasks, changes in $\Delta\Delta V$ began at t_F, i.e. simultaneously with changes in the total force and dropped quickly to an average level of about −1.4. In SP tasks, $\Delta\Delta V$ showed a slow, gradual decline, which became significant about 100–150 ms prior to t_F, and $\Delta\Delta V$ dropped to about −1 during the force pulse production. Negative ΔV values during quick force changes have been reported in earlier studies [3,9]. They may reflect a trade-off between reaching a high rate of force change, which benefits from large positive covariation of finger modes reflected in negative ΔV indices, and ability to control the time profile of force accurately, which may be expected to suffer from positive covariation of finger forces.

For statistical analysis, we averaged $\Delta\Delta V$ values within 50% time windows starting 200% prior to t_F. The non-parametric Freidman's test with factors *Time* and *Task* showed significant effects of both factors ($p < 0.001$). Pairwise comparisons using Wilcoxon's signed-rank test showed significant ($p < 0.01$) differences in $\Delta\Delta V$ between the SP and RT trials for the time windows between −150 and −100%, −100 and −50%, −50 and 0%, and between +50 and +100%.

We noticed that some of the subjects showed large-amplitude early ΔV changes in SP trials while others showed relatively small early ΔV changes. To illustrate this phenomenon, we divided the subjects into two groups. The upper panel of Fig. 2 shows averaged data for five subjects who consistently showed large ACV, while the lower panel shows the data for five subjects who showed much smaller ACV in SP trials. Note the large difference in the $\Delta\Delta V$ time profiles between the SP and RT tasks prior to t_F in the first group but not in the second group. There were no significant differences in characteristics of the force pulse between the two groups. The same figure shows time profiles of changes in the total force (ΔForce) for the two groups (long-dashed lines). Note the lack of force changes until about 25% prior to time zero (on average, about 30 ms) and the lack of obvious differences between the two subject subgroups.

The experiments revealed early changes in the finger mode covariation prior to the rise of the total force when the subjects performed the task in a self-paced manner. No such changes were seen when the subjects performed the task under a simple reaction time instruction. These observations are somewhat similar to earlier reports on anticipatory postural adjustments (APAs, [7]) under the RT instruction [2,5]. They suggest that, like APAs, ACV reflects neural control processes that can be modified depending on the available time for action preparation.

We think that the term ACV adequately describes this phenomenon of an anticipatory (or preparatory) change in the interaction among the fingers. The controller anticipates the need to change the total force at some point in time and gets ready to do this by gradually modifying

covariation among the finger modes. The functional role of ACV seems to be turning off interactions among elements (fingers) that would otherwise counteract the planned change in the total force. As emphasized in several previous studies [3,4,8], covariation among elements and accuracy in the overall performance may be independent. Hence, the lack of differences in the accuracy in reaching the peak force between trials with and without ACV is not completely surprising.

In our experiments, visible changes in the total force in the self-paced trials were seen not earlier than 30 ms prior to time zero (t_F). This observation suggests that the much earlier changes in the index of covariation, 100–150 ms prior to t_F, were truly anticipatory, not reflecting a slow drift in the total force.

Despite the significant effects of *Task* over the pooled data in our study, it is important to mention that some subjects showed relatively small ACV (the bottom panel of Fig. 2). The relatively small total number of subjects does not allow us to speculate on possible consequences of using versus not using ACV in such tasks. We would like to mention, however, that the subjects who did show ACV seemed to avoid excessive destabilization of the total force during the force pulse production and showed smaller negative $\Delta\Delta V$ values (compare the upper and lower panels of Fig. 2).

We are unaware of publications that would show ACV or a similar neural control strategy purposefully destabilizing a variable without changing its current magnitude but in anticipation of the change. ACV is a novel finding reflecting a non-trivial property of motor synergies, which may have a diagnostic value.

Acknowledgments

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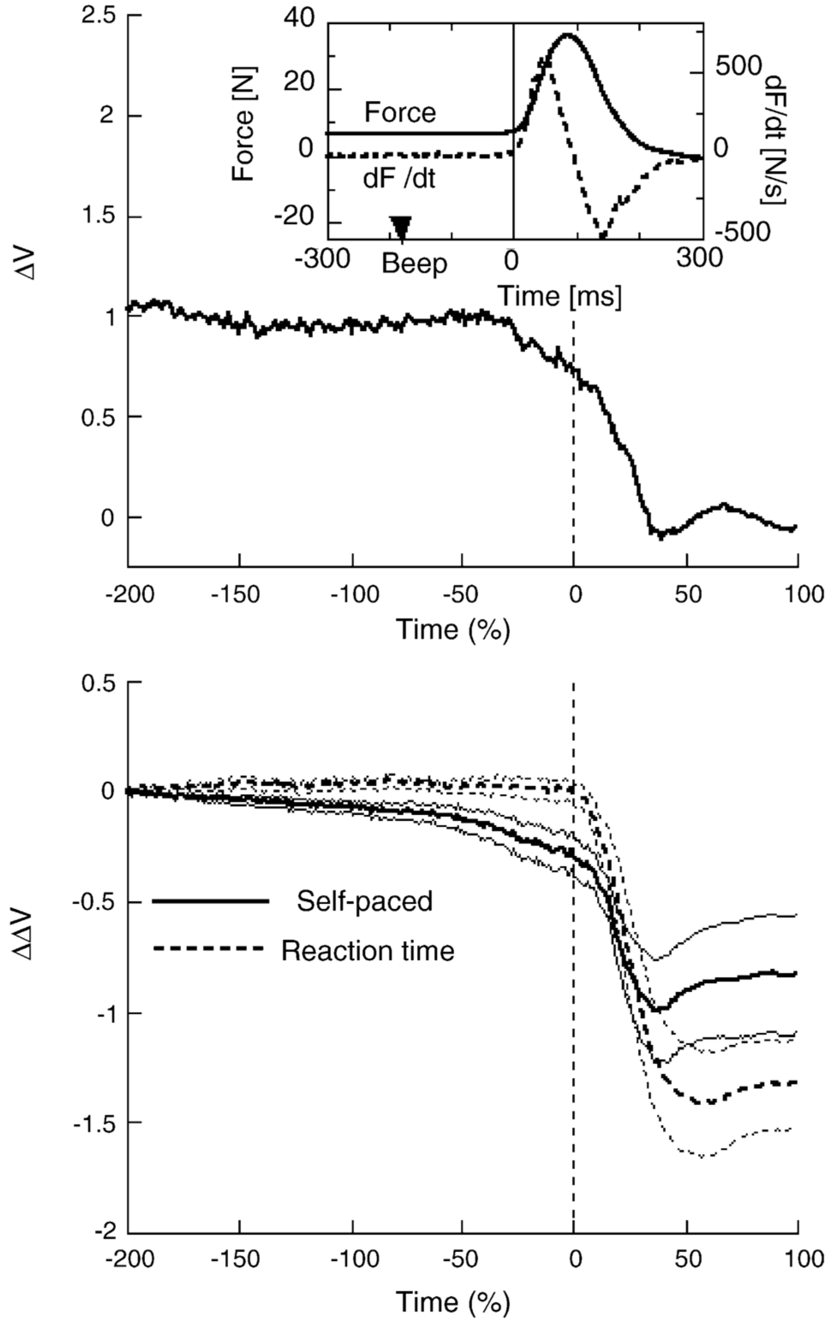

Fig. 1.

Upper panel: a typical time profiles of the Δ*V* index for a typical subject. The index was computed over a series of self-paced trials. Insert in the upper panel: a typical force pulse (solid line) and its first time derivative (dashed line) for the recation time task produced by the same subject. The triangle on the time axis shows the time of the imperative auditory stimulus. Lower panel: the average (across subjects) time profiles of changes in Δ*V* (ΔΔ*V*). Thick solid and dashed lines show averages for the SP and RT tasks, respectively, and thin lines show their standard errors. Time zero is the time of force pulse initiation (t_F), while the time scale is in percent of the time to peak force.

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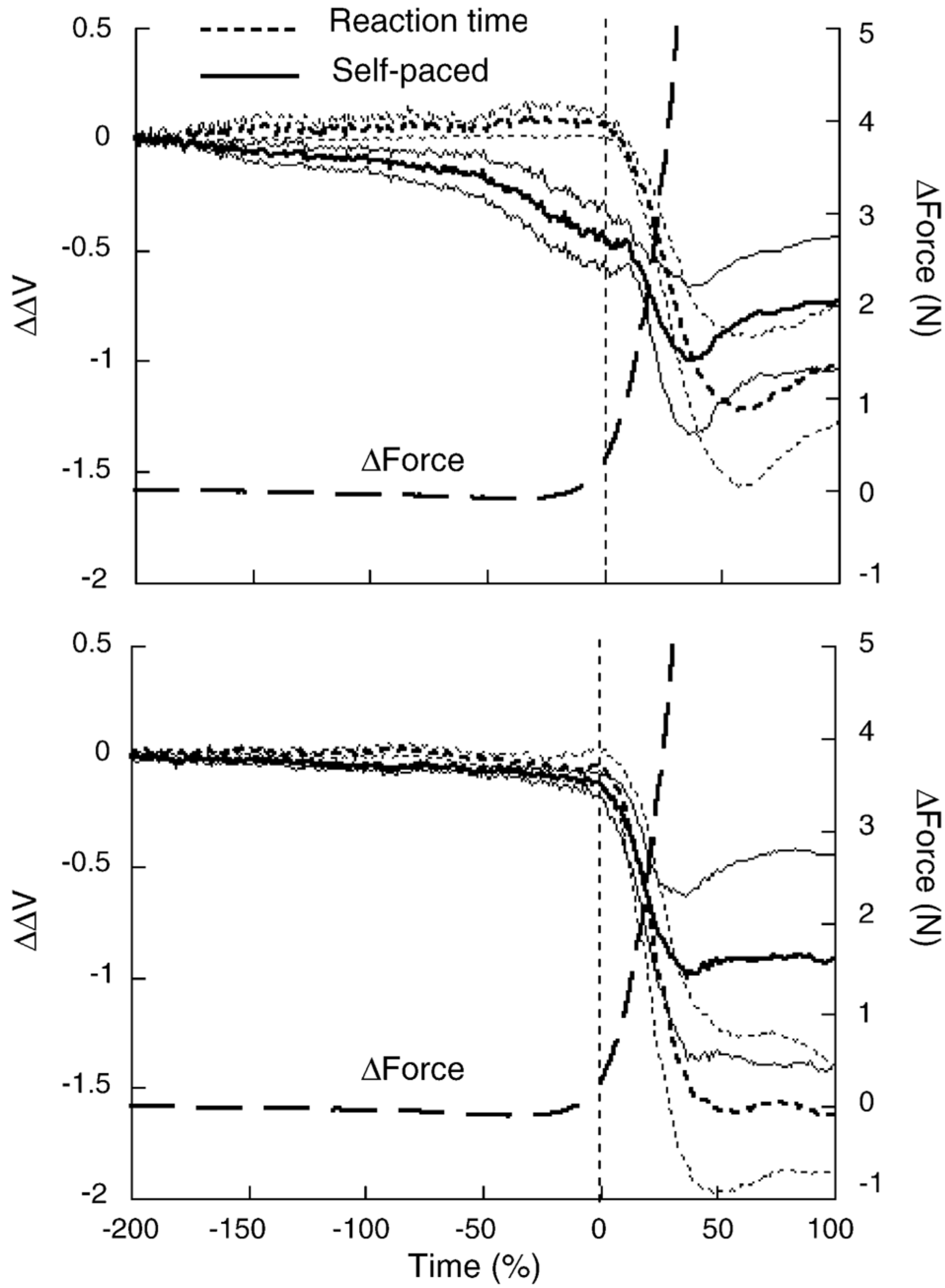

Fig. 2.

The average time profiles of changes in ΔV ($\Delta\Delta V$) for the five subjects who consistently showed large anticipatory covariation (upper panel) and for the other five subjects who did not (lower panel). Thick solid and dashed lines show averages for the SP and RT task, respectively and thin lines show the standard errors. Time zero is the time of force pulse initiation (t_F), while the time scale is in percent of the time to peak force. Long-dashed lines show force time profiles averaged over the subjects within the two subgroups. Note that an increase in the total force starts not earlier than 25% (under 30 ms) prior to time zero.