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The human central nervous system needs time to organize task-specific covariation of finger forces

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Abstract

We studied how the central nervous system (CNS) organizes outputs of effectors in a redundant motor task. During four-finger ramp force production, finger forces show positive covariations across trials at low forces, which turn into negative covariations at a critical force value (F_{CR}). Subjects performed such tasks with different target amplitudes and durations of the ramp. F_{CR} showed significant linear relations to the rate of force change. The slopes of the relations varied across subjects corresponding to a critical time (T_{CR}) ranging from 0.13 to 0.84 s. Across subjects, T_{CR} showed no relation to maximal force production; T_{CR} increased with the ramp duration. We conclude that the CNS needs a certain time to organize stabilization of total force by a negative covariation among finger forces.

Keywords: Finger; Force production; Coordination; Human

At any level of description, the human motor system typically has more elements (effectors) than necessary to perform motor tasks. This poses a problem of choice for the central nervous system (CNS), frequently addressed as the problem of motor redundancy [1]. Multi-finger force production has been recently studied as an example of this problem [6,8]. It has been proposed, in particular, that the apparent redundancy may be used by the controller to assure high stability of important performance variables such as the total force produced by a set of fingers [5]. When the force of a finger in a particular trial is higher than its average contribution, it introduces an error into the total force that may be either partly compensated by a decreased contribution of other fingers or amplified by their increased force output [4,5,7]. In the former case, across-trials analysis is expected to show negative finger force covariations, while in the latter case, positive force covariations are expected.

A number of recent studies have shown that individual finger forces tend to show positive covariations at low total force values and negative covariations at high force values [4,7]. This tendency has been confirmed not only for young typical participants but also for persons with Down syndrome [4] and for the elderly [7]. In particular, in the latter study, it was shown that subjects of different age and gender, whose maximal voluntary contraction (MVC) force ranged broadly, switched from positive finger force covariations to negative covariations at the same total force of about 5 N. The finding was interpreted as being conditioned by manipulation of similar objects in everyday tasks.

However, all the mentioned studies did not vary the magnitude and the rate of the force ramp. Hence, the critical value of the total force of 5 N could be related to a magnitude of force that needs to be sensed by peripheral receptors to trigger negative finger force covariations or to a critical time that is necessary to organize such a covariation among finger force outputs. The purpose of the current study was to solve this problem by varying the magnitude and the time of the force ramp.

Six male and six female healthy, right-handed subjects participated in the study. The age of the subjects ranged from 21 to 30 years. We purposefully selected subjects whose MVC force during four-finger pressing task ranged broadly, from 29.7 to 108.7 N. All subjects gave informed consent according to the procedures approved by the Office for Research Protections of The Pennsylvania State University.

Subjects sat on a chair and faced a computer monitor with their upper arms at approximately 45° of abduction in the frontal plane and 45° of flexion in the sagittal plane, and their

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elbow joints about 135° flexed such that the forearm was horizontal, parallel to the sagittal plane. The forearm was held stationary on the table with Velcro straps. A wooden piece was placed underneath the palm of the right hand to help maintain a constant configuration of the hand and fingers. Metacarpophalangeal and interphalangeal joints were all approximately 20° of flexion, such that the hand formed a dome (Fig. 1). This hand configuration was used in earlier studies and proved to lead to reliable finger force data [4–7].

Four piezoelectric sensors (model 208C02, Piezotronics Inc.) measured the finger forces of the right hand. Analog output signals from the sensors were connected to separate signal conditioners (model 484B11, Piezotronics Inc.). Cotton covers were attached to the upper surface of the sensors to prevent the influence of skin temperature. The medio-lateral distance between adjacent sensors was 30 mm and the antero-posterior position of the sensors was adjusted to the individual finger anatomy (for more details see [6]).

The subjects performed two tasks: MVC force production and accurate ramp force production. During the MVC task, the subjects were instructed to produce maximal force with all four fingers by pressing on the sensors. The total force was displayed on the screen, and the subjects were required to reach the maximal force within 5 s after a trial had started. During the ramp trials, an oblique line was shown on the monitor screen, and the task was to follow the line with a cursor representing the current total finger force. Each trial started with a ‘get ready’ signal, and then a trace showing the total force started to move over the screen. The ramp started 2 s later, and corresponded to an increase in the total force from 0 to 10%, 20%, and 30% of the subject’s MVC over 3, 6, and 9 s. Twelve trials were performed for each of the nine conditions. The sampling frequency was 100 Hz.

For MVC trials, the peak total force was measured. For ramp trials, time profiles of the variances of individual finger forces [$\mathrm{Var}F_i(t)$, where $i = \mathrm{I}$ (index), M (middle), R (ring), and L (little)] and the variance of the total force [$\mathrm{Var}F_{\mathrm{TOT}}(t)$] were computed over 12 trials for each ramp condition. The time profile of the sum of the variances of individual finger forces [$\sum \mathrm{Var}F_i(t)$] was also computed. The difference between $\sum \mathrm{Var}F_i(t)$ and $\mathrm{Var}F_{\mathrm{TOT}}(t)$ [$\Delta\mathrm{Var}(t) = \sum \mathrm{Var}F_i(t) - \mathrm{Var}F_{\mathrm{TOT}}(t)$] was computed. Note that when $\Delta\mathrm{Var}(t) < 0$, positive covariations among $F_i(t)$ dominate, while when $\Delta\mathrm{Var}(t) > 0$, negative covariations prevail. The critical total finger force (F_{CR}) and the critical time (T_{CR}), when $\Delta\mathrm{Var}(t) = 0$ were defined. By definition, F_{CR} and T_{CR} correspond to the force and time at which the negative covariation of finger forces starts to stabilize the total force. Individual finger shares (S_i) were defined as percentages of the total force each finger produced during the ramp trials.

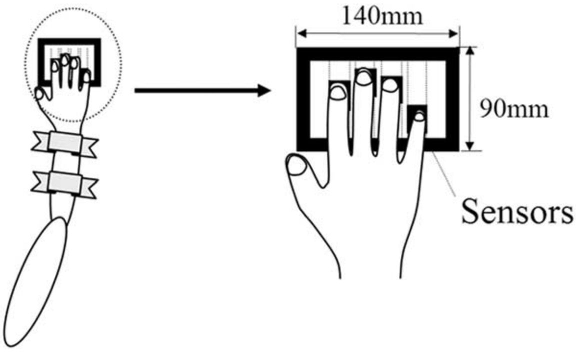

Fig. 1. A schematic illustration of the hand position.

Two-way repeated-measures analyses of variance (ANOVAs) with factors FORCE (10, 20, and 30% of MVC) and DURATION (3, 6, and 9 s) were used with appropriate contrasts. Changes in the sharing were analyzed using multivariate ANOVA (MANOVA) on S_{M}, S_{R}, and S_{L} with the same factors (cf. [6]).

All subjects in all ramp conditions showed predominantly positive covariations among the finger forces [$\Delta\mathrm{Var}(t) < 0$] at low forces, which turned into negative covariations [$\Delta\mathrm{Var}(t) > 0$] at higher forces. The critical force, F_{CR} [$\Delta\mathrm{Var}(t) = 0$] depended on both the duration of the ramp and the final target force (Fig. 2A) supported by significant main effects of both FORCE and DURATION in a two-way repeated-measures ANOVA ($P < 0.001$). When the relation between F_{CR} and the absolute rate of force production was analyzed for each subject individually, significant linear relations were found for each subject except one. Fig. 3 illustrates these relations. Note the different slopes of the regression lines corresponding to

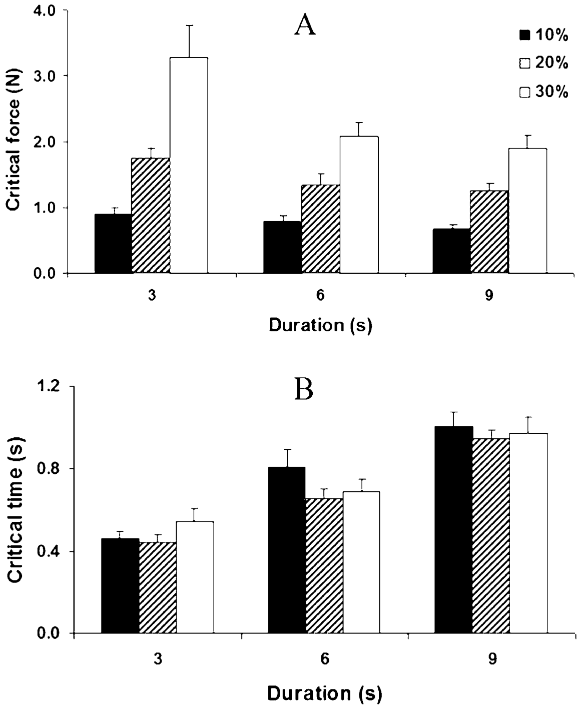

Fig. 2. Critical force (F_{CR}, A) and critical time (T_{CR}, B) values averaged across subjects (with standard error bars) for ramp force production trials over different durations and to different target force magnitudes (in % of MVC). Note the dependences of F_{CR} on both ramp duration and magnitude and the dependence of T_{CR} on ramp duration only.

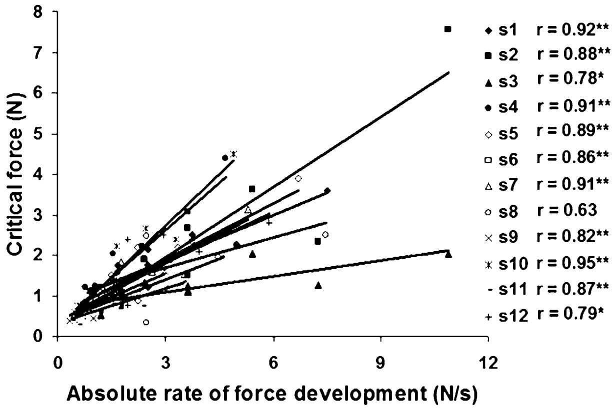

Fig. 3. The dependences of the critical force on the absolute rate of force production for individual subjects. Note the different slopes of the regression lines. $^*P < 0.05$; $^{**}P < 0.01$.

different critical times, T_{CR}, at which F_{CR} was reached. These times ranged from 0.13 to 0.84 s with the mean value of 0.39 ± 0.20 s (S.D.). When the values of T_{CR} were pooled across subjects, a logarithmic regression against the absolute rate of force production showed a better fit than a linear regression ($r^2 = 0.333$ and $r^2 = 0.256$ correspondingly). This reflected a dependence of T_{CR} on the duration of the ramp ($P < 0.001$) in the absence of such a dependence on the peak target force (Fig. 2B). In particular, when T_{CR} values were compared across conditions with the same rate of force production (10%/3 s, 20%/6 s, and 30%/9 s), one-way ANOVA showed a significant effect ($P < 0.05$). Pairwise contrasts showed significant differences between the 10%/3 s and 30%/9 s conditions, while the difference between 20%/6 s and 30%/9 s was close to the level of significance ($P = 0.06$). Across subjects, T_{CR} showed no relation to the MVC force.

Only minor changes in the sharing pattern were observed. In particular, MANOVA showed a significant decrease in the share of the little finger (S_L) by about 2.5% for trials at 30% of MVC as compared to trials at 10% of MVC. No significant changes in S_M and S_R occurred. Since the sum of all shares is 100%, this means that S_I increased by about 2.5%.

Our current results demonstrate that the previously reported constant critical value of force, at which finger forces begin to show negative covariations and stabilize the total force [4,7] may be an artifact resulting from the constant rates of force production used in those experiments. In our study, F_{CR} ranged more than threefold (Fig. 1A) and depended on both the duration of the ramp and the magnitude of the target force. Strong relations between F_{CR} and the rate of force production suggest that each subject took a certain time (T_{CR}) to switch from the initial pattern of positive covariations among finger forces to negative covariations. The instruction and the visual feedback required the subjects to stabilize a pattern of the total force. Our observations of stable T_{CR} within each subject suggest that the CNS needs time to organize covariation of finger forces to stabilize the total force. These observations refute the hypothesis that negative finger force covariation is turned on when the total force reaches a certain critical value. The values of T_{CR} (130–840 ms) are compatible with using sensory feedback in a good correspondence with studies that have shown the importance of the sensory feedback in finger force adjustments in grasping [2,3].

When T_{CR} values were compared across subjects, they showed a residual dependence on the duration of the ramp. In particular, Fig. 2B illustrates that there was a difference among conditions with the same rate of force production (10%/3 s, 20%/6 s, and 30%/9 s) with higher T_{CR} values for longer ramps. Since T_{CR} was under 1 s, this means that the subjects changed their strategy of finger covariation early in the trial depending on for how long they expected to produce the force ramp. As such, T_{CR} reflects not only physiological delays inherent to the process of finger coordination but also processes of motor planning. T_{CR} may reflect, in particular, the degree of mental concentration on the task and the reliance on visual feedback at early stages of the force production.

Acknowledgements

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