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Anticipatory synergy adjustments reflect individual performance of feedforward force control

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Highlights

- We tested whether anticipatory synergy adjustments are related to feedforward control.
- We observed significant ASAs before a quick change of the total finger force.
- The ASA properties were correlated with the error of force pulse.
- Almost all subjects showed an increase of the variance that affects the total force.
- Multi-digit synergy is weakened to reduce future error based on prediction error.

Abstract

We grasp and dexterously manipulate an object through multi-digit synergy. In the framework of the uncontrolled manifold (UCM) hypothesis, multi-digit synergy is defined as the coordinated control mechanism of fingers to stabilize variable important for task success, e.g., total force. Previous studies reported anticipatory synergy adjustments (ASAs) that correspond to a drop of the synergy index before a quick change of the total force. The present study compared ASA's properties with individual performances of feedforward force control to investigate a relationship of those. Subjects performed a total finger force production task that consisted of a phase in which subjects tracked target line with visual information and a phase in which subjects produced total force pulse without visual information. We quantified their multi-digit synergy through UCM analysis and observed significant ASAs before producing total force pulse. The time of the ASA initiation and the magnitude of the drop of the synergy index were significantly correlated with the error of force pulse, but not with the tracking error. Almost all subjects showed a significant increase of the variance that affected the total force. Our study directly showed that ASA reflects the individual performance of feedforward force control independently of target-tracking performance and suggests that the multi-digit synergy was weakened to adjust the multi-digit movements based on a prediction error so as to reduce the future error.

Keywords:

synergy, finger, anticipatory synergy adjustments, feedback control, feedforward control, uncontrolled manifold analysis

1. Introduction

Humans grasp and manipulate objects by dexterously coordinating their multi-digit, especially the four fingers that oppose the thumb: the index, middle, ring, and little fingers. These four fingers produce a total finger force that is balanced by the thumb force to stably grasp objects. Multi-digit coordination is a mechanism that stabilizes the total force of fingers through the compensation of the variability of some fingers by other fingers. This point of view of coordination is based on the “principle of abundance” [1] in which the human central nervous system (CNS) finds not a unique optimal solution but a solution manifold to solve Bernstein’s redundancy problem [2]. Neurophysiological mechanisms generating multi-digit coordination are collectively called multi-digit synergy.

Uncontrolled manifold (UCM) analysis has been proposed [3-5] and used to evaluate and quantify this multi-digit synergy [6-11]. In the framework of UCM analysis, the variance of coordinated multi-elements across trials is projected onto two orthogonal subspaces: one consisting of a subset of multi-elements that does not affect a performance variable important for task success (UCM) and another that directly affects the performance variable (orthogonal to the UCM). The two projected variance elements are called UCM and ORT components, respectively. Using these two variance components, an index of synergy is defined to quantify a degree of coordination. UCM analysis, which has been used for multi-digit synergy and also the motor synergies of various movements, e.g., upper limb movements [12,13], whole body movements [14,15], and walking [16,17], has revealed a coordinated control mechanism of CNS.

When we voluntarily produce a finger force with one finger, the other fingers produce involuntary forces. The non-independence of individual fingers is called “enslaving”

[18], which is due to various factors, e.g., a biomechanical property of hand musculotendon and a neurological property of overlapping finger representations in the motor cortex. A motor command for individual fingers without the enslaving effect is called the "finger mode." A previous study using UCM analysis suggested that CNS controlled the finger modes by multi-digit coordination to stabilize the total force and the total moment of force [19]. In this study, we considered the coordination among the finger modes, i.e., finger mode synergy, to be multi-digit synergy.

The synergy index dropped when the performance variable quickly changed at self-paced timing [8, 20]. Moreover, the initiation time of the synergy drop was faster than the change's initiation time in the performance variable. This phenomenon is called an anticipatory synergy adjustment (ASA), which reflects the pre-adjustments of a synergy for quick changes of the performance variable. Moreover, ASA's time of initiation of patients with motor impairment was slower than the control group [21, 22], which implies that ASA is an index related to motor control ability. However, since the relationship between ASA properties and individual performance of motor control was not examined, ASA's functional role remains unclear. Previous studies concluded that ASA was observed before the voluntary quick change of the performance variable [8] and was affected by cerebellar disorders [21]. Based on these studies, we hypothesized that ASA is related to individual performance of feedforward force control.

To test this hypothesis, in this paper, we examine whether ASA properties (its initiation time and the magnitude of the drop of the synergy index) correlate with individual performance of feedforward force control. To observe an ASA phenomenon and to evaluate performance of feedforward force control, we used a quick force pulse production paradigm

[8, 21, 22]. The quick force pulse production task consisting of two phases: a target-tracking phase and a force pulse production phase. In the conventional quick force pulse production task, subjects produced force pulse at self-paced timing and with visual information. In this study, we changed the force pulse production phase into a phase in which subjects produced force pulse at a specific given time point and without visual information to more strongly require subjects to perform feedforward control. Since the force pulse production with above conditions is ballistic and quite fast movements, we considered that the force pulse production task is mainly performed by feedforward control, and evaluated the performance of feedforward force control by an error from target force. We assumed that the force pulse production contains a part of individual target-tracking ability, because the target of force pulse was given by visual information. Therefore, we also check the relationship between the ASA properties and individual target-tracking performance, i.e., tracking-error during steady state of the target-tracking phase. The ASA is occurred when the UCM component decreases and/or the ORT component increases. Therefore, we also investigate the changes in the UCM and ORT components from ASA's time of initiation to the time of the change's initiation in the total force. Finally, we discuss its functional role.

2. Methods

2.1. Subjects

Twenty healthy right-handed volunteers (19 males and 1 female) participated in our experiments. Their average age was 25.4 (22-42 years). The experiments were approved by the ethics committee at Advanced Telecommunication Research Institute International. All subjects received explanations about the experimental procedure and gave their written informed consent.

2.2. Apparatus

Four custom-made force sensors (FSR 402, Interlink Electronics Inc., CA, USA) were used to measure the finger forces in the vertical direction (Fig. 1a). The circular contact surface of each sensor was covered with a rubber pad. The positions of the force sensors were adjusted in the horizontal plane to match the individual finger positions in which the subjects easily produced finger force. A cushion material was placed under the subject's palm. The subject's forearm was fixed to the device by a strap. The force signals were recorded using an AD/DA device (DAQ NI USB-6353, National Instruments, TX, USA) at a 600-Hz sampling rate. The visual information related to each task was displayed on a computer screen (Figs. 1b and 1c).

2.3. Task procedures

Subjects sat on a chair with their right hands fixed to the finger force measurement device. The measurement experiments consisted of three tasks: (1) a maximal voluntary contraction (MVC) force production task, (2) a single-finger ramp-tracking task, and (3) a quick force pulse production task. Before the experiments began, the experimenter demonstrated the actual experimental procedure by briefly performing all of the tasks.

1. MVC force production task: We measured the MVC force of the four fingers. The subjects pressed on the force sensors with four fingers and produced a maximal total force after a 3-s countdown. The total force was visually fedback by the height of the vertical bar. This task was repeated twice. We determined the MVC force as the highest value of the finger force.

2. Single-finger ramp-tracking task: Subjects tracked the force target template by producing an individual single-finger force (from the index to the little finger). The force target template and the produced finger force are displayed in Fig. 1b. The small filled circle was horizontally moved for 20 s at a constant speed. The height of the circle corresponded to the force of the tested finger. During the first 4 s, subjects kept 0 %MVC force of the tested finger (rest). Over the next 12 s, they gradually increased the finger force of the tested finger from 0 to 40 %MVC. Finally, they kept 40 %MVC of the tested finger for 4 s and only produced finger force using the tested finger while keeping the rest of their fingers on the sensors.

3. Quick force pulse production task: The subjects tracked the force target template with visual information, and then, quickly produced a force pulse without visual information using all four fingers. The force target template and the produced total finger force are shown in Fig. 1c. The small filled circle was horizontally moved for 8 s at a constant speed. The height of the circle corresponded to the total force of the four fingers. The circle disappeared at the "Go" line (vertical solid line) and remained invisible until after the force pulse was produced. The target force template consisted of a target-tracking phase (first 4 s) and a force pulse production phase (last 4 s). During the target-tracking phase, the subjects produced 5 %MVC of total force to track the target line. At the initiation of the force pulse production phase (at the "Go" line), they quickly produced a force pulse within the 25 ± 5 %MVC target and immediately relaxed. During the force pulse production, no visual information of the produced total force was given. After relaxation, only the peak value of the force pulse was visually feedback. In previous studies using a similar paradigm [8, 21, 22], subjects produced

force pulses at a self-paced timing with visual information. In contrast, in the current study, the force pulse was produced at the specific time point ("GO" line) and without visual information to more strongly require subjects to perform feedforward control. We defined successful trials as those in which subjects produced a force pulse within the 25 ± 5% MVC target. They used all four fingers to perform the task and repeated it until 30 successful trials were achieved. They took a short break between trials to avoid fatigue.

2.4. Data analysis

All of the measured force data were filtered with a second-order Butterworth low-pass filter with a 10-Hz cutoff frequency. Using the force data in the single-finger ramp-tracking task, we calculated enslaving matrix ***E*** that reflects the unintentional finger force produced by the untested fingers when a tested finger produced force. The finger force data during the middle 12 s (dynamic phase) were used to calculate the ***E*** components by linear regression:

$$F_{i,j} = f_i^0 + k_{i,j} \times F_{TOT,j}, \tag{1}$$

$$\boldsymbol{E} = \begin{bmatrix} k_{I,I} & k_{I,M} & k_{I,R} & k_{I,L} \\ k_{M,I} & k_{M,M} & k_{M,R} & k_{M,L} \\ k_{R,I} & k_{R,M} & k_{R,R} & k_{R,L} \\ k_{L,I} & k_{L,M} & k_{L,R} & k_{L,L} \end{bmatrix}, \tag{2}$$

where subscripts i, j = {I (index), M (middle), R (ring), L (little), and j indicate the tested fingers. $F_{i,j}$, f_i^0, and $F_{TOT,j}$ respectively denote the individual i-finger force, the residual of the linear regression, and the total force. The enslaving index of j-finger EN_j was calculated as follows:

$$EN_j = \sum_j k_{i,j}/3 \qquad (i \neq j). \tag{3}$$

Using force data in the quick force pulse production task, we calculated the performances of force control and the time profile of the index of the multi-digit synergy. We removed the outlier data (e.g., tracking failures in the feedback phase), and used data of 28.3 ± 0.73 (mean ± SD) accepted trials for analysis. To remove an effect of trial-by-trial time directional variability of the change in the total force on the index of synergy, the time of the initiation of the change in the total force (t_0) was defined as the time when the force's time derivative reached 5% of its peak value. All of the analyzed force data were aligned with respect to t_0. We evaluated the target-tracking performance by the mean value of the normalized error across the steady state of the target-tracking phase (from −600 to −400 ms with respect to t_0) and the performance of feedforward force control by the normalized error when the peak of the total force appeared in the force pulse production phase. Since the finger force was affected by the signal dependent noise due to a neurophysiological property [23-25], we normalized the error as follows:

$$normalized\ error = \left(\frac{F_{TOT} - F_d}{F_{TOT}}\right)^2, \quad (4)$$

where F_d indicates the target total force. Using UCM analysis [3], we quantitatively evaluated the motor synergy of the finger modes (Fig. 1d). Finger mode vector $\boldsymbol{m}$ was calculated by finger force vector $\boldsymbol{F}$ and enslaving matrix $\boldsymbol{E}$ as $\boldsymbol{m} = \boldsymbol{E}^{-1}\boldsymbol{F}$. The relationship between total finger force F_{TOT} and finger mode vector $\boldsymbol{m}$ was $F_{TOT} = [1, 1, 1, 1]\ \boldsymbol{Em}$. Therefore, UCM was defined by the null space of the equation, $[1, 1, 1, 1]\ \boldsymbol{E}$. Basis vectors $\boldsymbol{\varepsilon}$ span the null space, according to $0 = [1, 1, 1, 1]\ \boldsymbol{E\varepsilon}$. Using basis vectors $\boldsymbol{\varepsilon}$, the variance of the finger modes in the $\boldsymbol{m}$ space across the trials was projected onto the direction along the UCM (UCM component: V_{UCM}) and orthogonal to it (ORT component: V_{ORT}), for each time step. We defined the index of synergy to quantify the multi-digit synergy:

$$\Delta V(t) = \frac{V_{UCM}(t)/3 - V_{ORT}(t)/1}{V_{TOT}(t)/4}, \quad (5)$$

where V_{TOT} denotes the total variance. All variance components were normalized by the dimensions of the finger modes and the total finger force. $\Delta V > 0$ indicates that the total finger force is controlled by the coordination of the four fingers. To statistically evaluate the index of synergy, we used a log-transformed index of synergy [26]:

$$\Delta V_z(t) = \log\left(\frac{\Delta V(t)+4}{4/3-\Delta V(t)}\right). \quad (6)$$

We defined the time of initiation of ASA (t_{ASA}) as the time when ΔV_z fell below its mean value during the steady state (from −600 to −400 ms with respect to t_0) by more than two standard deviations. We also calculated the magnitude of the drop of the index of synergy ($\Delta\Delta V_z = \Delta V_z(t_0)$ − (average value of ΔV_z during steady state)) as well as the changes in the UCM component ($V_{UCM}(t_0)$ −(average value of V_{UCM} during steady state)) and the ORT component ($V_{ORT}(t_0)$ −(average value of ΔV_{ORT} during steady state)) and the coefficients of the correlation between the properties of ASA (t_{ASA} and $\Delta\Delta V_z$) and the performances of force control: the normalized error at a time when the peak of total force appeared and average value of it during steady state.

3. Results

The average performance of the multi-digit force production across all subjects is presented in Table 1. The index of the enslaving *EN* indicated that the ring and little fingers showed a relatively high enslaving effect. The time of the initiation of ASA (t_{ASA}) was significantly earlier than the time of initiation of change in the total force (t_0), which was tested by a one-sample *t*-test ($P = 1.20 \times 10^{-4} < 0.01$, $t_{(19)} = -4.82$). Moreover, the index of synergy (ΔV_z) significantly dropped from t_{ASA} to t_0 (one-sample t-test, $P = 8.27 \times 10^{-7} < 0.01$, $t_{(19)} = -7.17$), indicating that the subjects showed significant ASAs before quick changes in their total finger force.

Figure 2 shows the time profiles of the index of synergy (ΔV_z) and the total finger force. During the steady state of the target-tracking phase (from −600 to −400 ms), the mean value of the index of synergy was significantly higher than the value of the uncoordinated index which is the value of index of synergy consisting of same value of UCM and ORT components (one-sample t-test, $P = 3.48 \times 10^{-11} < 0.01$, $t_{(19)} = 13.5$). This indicates that the total finger force was controlled by the coordination of the four fingers. During the force pulse production phase ($t > t_0$), the index of synergy quickly dropped below the uncoordinated index. As mentioned above, significant ASA was observed.

Figure 3 shows the relationships between the properties of ASA and the performances of force control. The upper figures (Figs. 3a and 3b) show that the time of initiation of ASA (t_{ASA}) and the magnitude of the drop of the index of synergy ($\Delta\Delta V_z$) significantly correlated with the performance of feedforward force control, i.e., the normalized error when a force peak appeared (coefficients of correlation for t_{ASA}: $r = 0.52$, $P = 0.019 < 0.05$; for $\Delta\Delta V_z$: $r = 0.55$, $P = 0.012 < 0.05$). In contrast, the lower figures (Figs. 3c and 3d) show that the ASA properties were not correlated with the target-tracking performance, i.e., the average normalized error across the steady state of target-tracking phase (coefficients of correlation for t_{ASA}: $r = -0.006$, $P = 0.98$; for $\Delta\Delta V_z$: $r = 0.044$, $P = 0.85$). Moreover, a relationship between the time of initiation of ASA and the magnitude of the drop of the index of synergy showed positive correlation ($r = 0.77$, $P = 0.0001 < 0.05$). These results indicate that the ASA properties reflect the performance of feedforward force control of individual subjects independently of the target-tracking performance.

When the index of synergy drops, one possibility is a decrease of the UCM component and/or an increase of the ORT component. We calculated the change in the UCM and ORT components from steady state to t_0 (Fig. 4). Almost all subjects (n = 19) increased the ORT component. In contrast, about half subjects (n = 9) decreased the UCM component, but the other subjects increased the UCM component. These results indicate that change in the ORT component was robust across subjects, but change in the UCM component differed between individuals, when the ASA was occurred.

4. Discussion

In this study, we hypothesized that ASA is related to the performance of feedforward force control and directly compared ASA's properties and the error of force pulse production and the tracking error. To more strongly require subjects to perform feedforward control, we modified the visual feedback condition in the conventional quick force pulse production task and observed a significantly earlier initiation time of ASA than the change in the total force and a significant drop of the index of synergy (Fig. 2). Moreover, the normalized error related to the individual performance of feedforward force control significantly correlated with the individual time of the initiation of ASA and the magnitude of the drop of the index of synergy (Figs. 3a and 3b). In contrast, the normalized error, related to the individual target-tracking performance, was not significantly correlated with the ASA properties (Figs. 3c and 3d). These results indicate that the ASA index reflects the individual performance of feedforward force control independently of the target-tacking performance. Moreover, the ASA properties were positively correlated each other, i.e., the earlier timing of ASA, the larger magnitude of the drop of index of synergy. This result implies that the speed of ASA was similar across subjects. Moreover, it was reasonable that the individual performance of feedforward force control correlated with both timing and magnitude of ASA. To the best of our knowledge, this is the first study to show the correlation between the individual properties of ASA and individual performances of feedforward force control across healthy participants.

According to the definition of the index of synergy, the ASA is occurred by decrease of the UCM component and/or increase of ORT component. In this study, the change in the ORT component was robust across subjects, but the change in the UCM component differed between individuals (Fig. 4). Since almost all subjects increased the ORT component, it is suggested that the CNS generally adopted a strategy in which the total force actively varied when the total force quickly changed without visual information, i.e., when feedforward control was performed. Weakening the stabilized synergy also seems to be required to quickly perform feedforward control. Such "weakened synergy" has been reported not only in multi-digit movements but also in walking [16], whole body movements [20], and dampening hand vibration while walking [27]. In this study, the stronger the weakened synergy is (earlier ASA initiation and the greater the magnitude of the drop of the index of synergy) the higher the performance of feedforward force control. When an individual performance of coordinated control is evaluated, both of the following are important: the synergy evaluation that stabilizes the performance variable and destabilizes the performance variable.

Finally, we discuss ASA’s functional role. The present study showed that the higher the ASA performance is, the greater the performance of feedforward force control, i.e., the smaller normalized error. Therefore, the ASA phenomenon would reflect the pre-adjustment of the multi-digit movements to accurately control the performance variable. Since a larger multi-digit pre-adjustment leads to better performance of feedforward force control, pre-adjustment of the multi-digit will reduce the output error. Next, we discuss the mechanism of the pre-adjustments. Since the finger force was adjusted before the force pulse production, the output error of the total force pulse was predicted. Recent computational neuroscience studies argued that CNS utilizes prediction error based on an internal model to body control [28, 29]. Since body control is affected by neurophysiological internal noise, the output movements are varied [23-25]. When the finger total force is controlled without visual information, CNS predicts the error of the total force based on an internal hand model and an internal state to reduce the future output error of the total force by an anticipatory adjustment of the multi-digit movements based on the prediction error. The ASA would reflect two kinds of purposes of the pre-adjustments. One is the purpose to destabilize the total force based on the prediction error so as to reduce future error, which would be reflected in the increase of the ORT components. The other is the purpose to control an initial state before force pulse production, i.e., to converge the specific balance of finger modes, which would be reflected in the decrease of UCM component. These two pre-adjustment of the multi-digit movements to reduce the future error is reflected in the both increase of the ORT component and decrease of the UCM component, dropping the index of synergy, i.e., ASA, suggesting that its functional role is the pre-adjustment of multi-digit movements based on prediction error to reduce future error. In this study, we only showed correlation between properties of ASA and individual performance of feedforward force control, and did not approach the causality. Therefore, important future work is to reveal the causal relationship between the ASA and feedforward control, and to approach the functional role of the ASA.

In conclusion, we investigated relationship between ASA phenomenon and individual performance of feedforward force control. In a quick force pulse production task, the time of ASA's initiation and the amplitude of the drop of the index of synergy significantly correlated with individual performance of feedforward force control, i.e., the normalized error from the target total force at the feedforward control phase. Moreover, almost all subjects showed significant increase of the variance of the finger modes that directly affects the total force. These results indicate that ASA is an index that reflects individual performance of feedforward force control independently of individual target-tracking performance and suggest that the ASA reflects pre-adjustment of multi-digit movements based on prediction error to reduce future error.

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Tables

Table 1

Performance of multi-digit force production of all subjects. Means and standard deviations (SD) of the maximal voluntary contraction (MVC) forces, enslaving index (EN), time of initiation of anticipatory synergy adjustments (ASAs) (t_{ASA}), and magnitude of drop of index of synergy ($\Delta\Delta V_z$) are presented. Subscripts denote the following: *I*, index; *M*, middle; *R*, ring; *L*, little fingers.

	MVC (N)	EN_I	EN_M	EN_R	EN_L	t_{ASA} (s)	$\Delta\Delta V_z$
Mean	72.6	0.0076	0.0157	0.0673	0.0850	−0.124	−0.580
SD	13.3	0.0191	0.0194	0.0571	0.0679	0.115	0.362

Figures

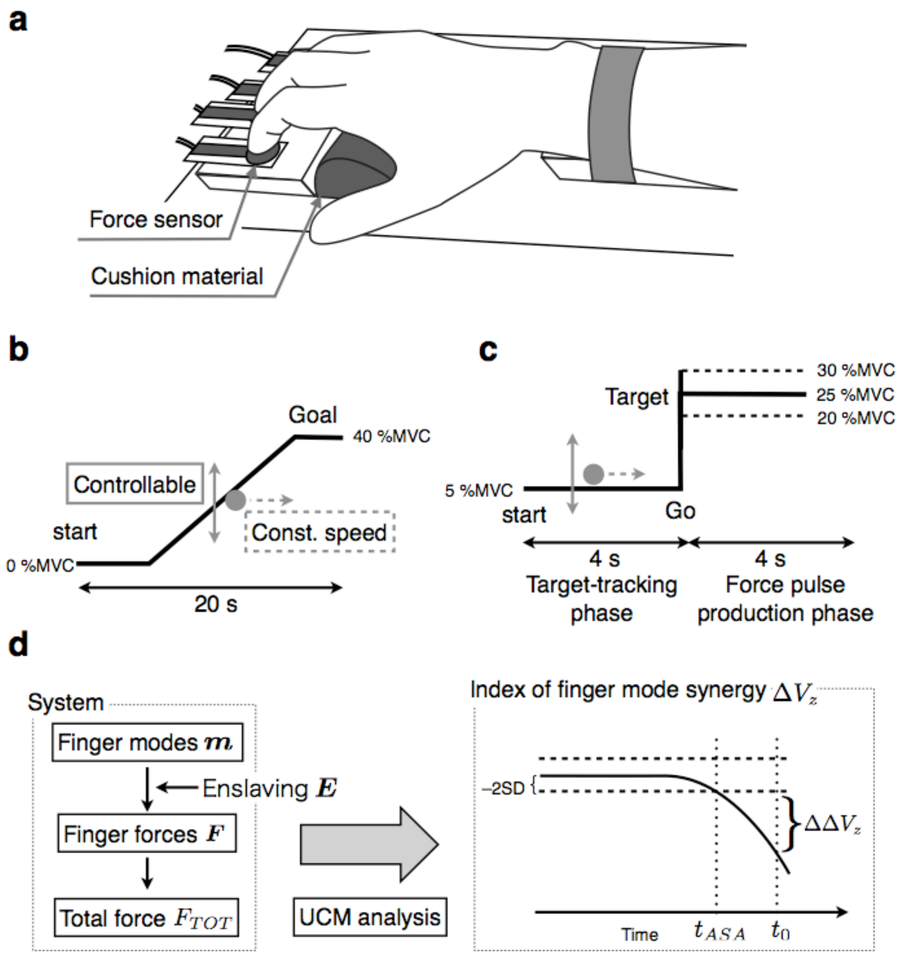

Fig. 1 Experimental setup and analysis method: (**a**) Subjects placed their fingers on four custom-made force sensors and their palm on a cushion material. (**b**) Computer screen display in single-finger ramp-tracking task. Gray circle was horizontally moved for 20 s with constant speed. Circle's height corresponded to finger force of tested finger. (**c**) Screen in quick force pulse production task. Circle was horizontally moved for 8 s with constant speed and disappeared during force pulse production phase. Circle height corresponded to total force.

(**d**) Total force is produced by finger modes and enslaving effect. Index of finger mode synergy is calculated through UCM analysis and used to define ASA properties.

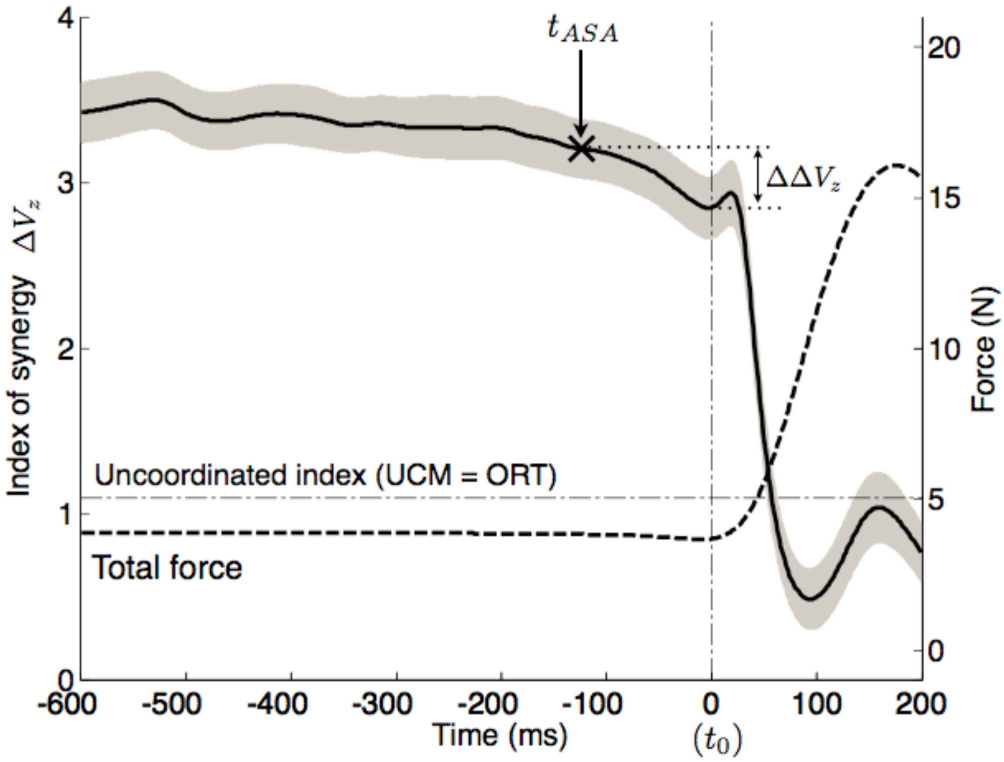

Fig. 2 Time profiles of total force (dash line) and index of synergy (solid line) in quick force pulse production task. Gray area indicates standard error of synergy index across all subjects. Vertical and horizontal dash-dotted lines denote time of initiation of change in total force and value of uncoordinated index (the value of index of synergy consisting of same value of UCM and ORT components), respectively. Cross mark indicates mean time of ASA initiation.

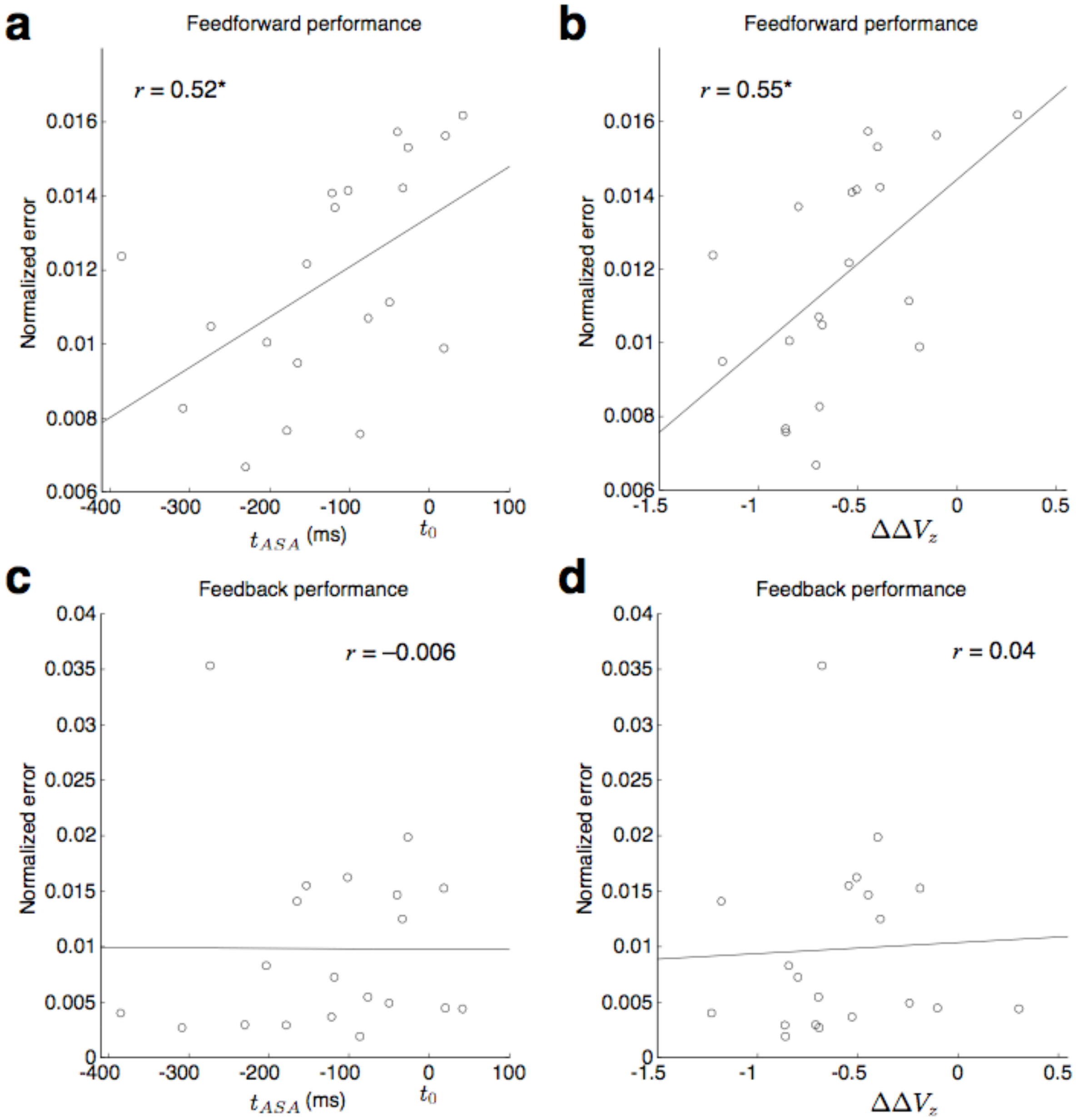

Fig. 3 Relationships between ASA properties and performances of force control. Upper (a and b) and lower (c and d) panels are associated with performance of feedforward force control and target-tracking performance, respectively. Left (a and c) and right (b and d) panels are related to time of initiation of ASAs (t_{ASA}) and magnitude of drop of index of synergy ($\Delta\Delta V_z$), respectively. Circles and lines denote values of individual subjects and linearly regressed lines, respectively. Coefficients of correlation (r) are presented (*$P < 0.05$).

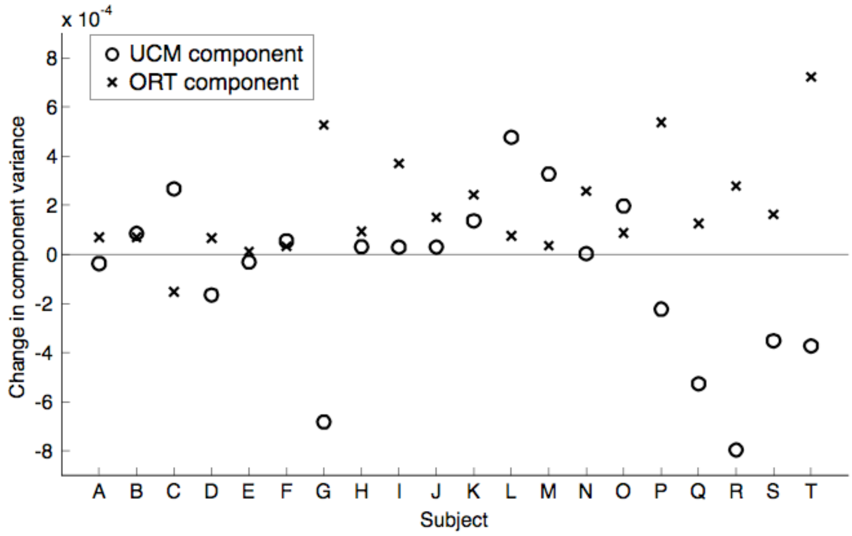

Fig. 4 Change in UCM and ORT components from steady state to that of change in total force (t_0). Circles and crosses indicate the change in the UCM component and ORT component, respectively. The horizontal axis denotes subjects' ID.