The Influence of Recent Actions and Anticipated Actions on the Stability of Finger Forces During a Tracking Task

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2 authors:

Mitchell Tillman
Stevens Institute of Technology

Satyajit Ambike
Purdue University

The influence of recent actions and anticipated actions on the stability of finger forces during a tracking task.

Mitchell Tillman[1] and Satyajit Ambike[1,2,*]

* Corresponding author.

[1]Department of Health and Kinesiology, Purdue University, West Lafayette, IN

[2]Center on Aging and the Life Course, Purdue University, West Lafayette, IN

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ADDRESSES

Satyajit Ambike: 800 W. Stadium Ave., West Lafayette, IN 47906, USA. sambike@purdue.edu

Mitchell Tillman: Edwin A. Stevens Hall, 24 5th St Hoboken, NJ 07030, USA. mtillman@stevens.edu

ABSTRACT

We examine how the stability of the current total isometric force (F_T) produced by four fingers is influenced by previous and expected voluntary changes in F_T. We employed the synergy index obtained from the across-trial uncontrolled manifold analysis to quantify the stability of F_T. The stability reduces while expecting changes in F_T when the history of F_T changes is consistent indicating the existence of a novel type of anticipatory synergy adjustment. Disparate histories of F_T changes yield inconsistent changes in stability, driven by individual differences in the covariation in the finger forces that leaves F_T invariant. Future research should focus on exploring these individual differences to understand better how previous and expected behavior changes influence the stability of the current motor behavior.

INTRODUCTION

Stability is the ability of the motor system to maintain the current static or dynamic movement pattern by rejecting disturbances. The ability to perform stable movements is a key feature of a healthy motor system. However, the motor system must also compromise between movement stability and maneuverability – the ability to switch between motor patterns – in a task-specific fashion so that functional movements can emerge (Hasan, 2005; Riccio, 1993; Riccio & Stoffregen, 1988; Riley & Turvey, 2002; van Emmerik & van Wegen, 2000). That is, the movement pattern associated with one behavior (e.g., locomotion in a straight line over flat ground) should be adequately stable, whereas, during movement transitions (e.g., gait termination), the stability of one movement pattern must be diminished so that another pattern can be established and stabilized (Hasan, 2005).

Indeed, stability-maneuverability tradeoffs have been observed in locomotor (Acasio, Wu, Fey, & Gordon, 2017) and upright postural tasks (Huang & Ahmed, 2011). Furthermore, the phenomenon of anticipatory synergy adjustment (ASA), describing the influence of upcoming voluntary movements on the stability of the current motor pattern, has been documented over the last decade. Synergies are systems that display task-specific covariation in redundant sets of inputs to ensure the stability of the output variables defining task performance (Latash, Scholz, & Schoner, 2002). Synergies can be quantified using the uncontrolled manifold (UCM) method (Scholz & Schoner, 1999). The analysis yields a synergy index (ΔVz), which also quantifies the stability of the task variables.. ASA is a reduction in the stability (i.e., ΔVz) prior to a volitional change in the motor pattern; it is a record of diminished stability, presumably to enhance maneuverability. ASAs have been observed in manual tasks (Kim, Shim, Zatsiorsky, & Latash, 2006; Olafsdottir, Yoshida, Zatsiorsky, & Latash, 2005, 2007; Olafsdottir, Kim, Zatsiorsky, & Latash, 2008; Park, Wu, Lewis, Huang, & Latash, 2012; Park & Xu, 2017; Shim, Park, Zatsiorsky, & Latash, 2006; Togo & Imamizu, 2016; Zhou et al., 2013) and in postural tasks that require a quick shift in the center of pressure (Klous, Mikulic, & Latash, 2011; Krishnan, Aruin, & Latash, 2011; Piscitelli, Falaki, Solnik, & Latash, 2017; Wang, Asaka, Zatsiorsky, & Latash, 2006).

Recently, we documented a reduction in ΔVz in response to an anticipated change in the total force produced by the four fingers of the dominant hand in isometric conditions (Tillman & Ambike, 2018a, 2018b). We labeled this novel finding 'stage 1 ASA' to distinguish it from the established version, which we rechristened 'stage 2 ASA'. The distinct names highlight key differences: in previous work, the stability reduction is observed just before the maneuver (Zhou et al., 2013), whereas, our result followed from data obtained during a period in which a maneuver was anticipated but not executed. Furthermore, stage 2 ASA usually occurs when the timing of the voluntary change is known to the actor (Olafsdottir et al., 2005; Zhou et al., 2013), whereas, stage 1 ASA occurs despite temporal uncertainty.

However, there is a potential confounding factor in our previous work that stems from the nature of the tasks that we employed. Participants tracked a prescribed total force target in two conditions. In the steady condition, participants tracked a stationary target, and were aware that the target would not move. In the dynamic condition, they tracked a moving target. Here, the target briefly stabilized at the same position as the first condition. The synergy index during this phase was compared to that in the steady tracking task. This ensured that the current total force was same, but the expectation of movement was different in the two conditions. ΔVz in the dynamic condition was lower than that in the steady condition, indicating the existence of stage 1 ASA. The confounding factor is that movement histories, i.e., the target trajectories and participants' behaviors before the estimation of stability, in the two conditions were also different, and this may have contributed to the observed difference in ΔVz.

Stability changes in motor behaviors cannot occur instantaneously but must evolve over a characteristic time that is determined by the inertial characteristics of the motor apparatus involved in the task. Therefore, the stability of a motor pattern at one instant in time will depend not only on how the individual intends to use the motor apparatus, but also on whether the motor apparatus was involved in another behavior in the recent past. For example, the stability of fingertip forces involved in maintaining grasp of an object of a specific weight and weight distribution is different if this weight or weight distribution is arrived at following smooth changes in those physical variables (Sun, Park, Zatsiorsky, & Latash, 2011; Sun, Zatsiorsky, & Latash, 2011). These changes in finger-force stability induced by movement history are attributed to mechanical sources (hysteresis in muscle forces (Kostyukov, 1998)) as well as neural control.

Effects of movement history are expected to decay over time. For example, levels of muscular co-activation, which influence the stability of the associated joints or end effectors, remain high following a quick action, and although they decay to pre-action levels over a few seconds, these dynamics are not well understood (Gottlieb, Corcos, & Agarwal, 1989; Latash, 2018; Suzuki & Yamazaki, 2005). In our previous work, we accounted for overt history effects in the dynamic tracking task by ensuring that the observed error in performance had reached relatively steady levels (in about 2 seconds) before assessing the stability of performance. However, the possibility remains that subtle effects of movement history influenced our findings. Therefore, the primary objective of the present work is to establish if anticipated voluntary changes in the total finger force leads to a reduction of the stability of the current total force in isometric conditions, while controlling for the history of changes in the total force. Our secondary objective is to explore the effect of disparate histories on the stability. Like our previous study, we will evaluate the stability of the total force produced by the four fingers pressing simultaneously on force sensors while the participant tracks a target force. All stability assessments will be made when the target force is stationary at the same value for the following tasks. In the Steady task, the participant will be aware that the target force will not change. In the Anticipation task, the target will initially be stationary, but the participant will expect it to move at any time. In the History task, the target will become stationary after having moved for some time, and the participant will be aware that no further movement of the target will occur. In the Combined task, the target will become stationary after some initial movement, but it will start moving again at any time. The Combined task is a concatenation of the History and the Anticipation tasks, and likely combines the effects of the two tasks.

We hypothesize that the stability in the Anticipation and Combined tasks will be lower compared to that in the Steady task, reflecting the stability-maneuverability tradeoff. We also hypothesize that the stability in the History task will be lower than that in the Steady task. If our hypotheses are validated, we will have found corroborating evidence for the existence of stage 1 ASA. It will also suggest that accounting for movement history is essential in the exploration of stage 1 ASA in other behaviors.

METHODS

Participants

Twenty-four young adults [21 female; age = 22.4 $\pm$ 3.1 years; weight = 77.9 $\pm$ 16.4 kg; height = 1.74 $\pm$ 8.7 m; (mean $\pm$ standard deviation)] participated in this study. All participants were right-hand dominant by self-report, and no participant had any history of neurological issues or musculoskeletal discomfort or injury in the dominant arm. All participants had normal or corrected-to-normal vison. All participants provided informed consent in accordance with the procedures approved by the Institutional Review Board of Purdue University.

Equipment and Procedures

Each participant sat in a chair, rested their right forearm on a table in front of them and placed four fingertips on four force sensors (Nano 17, ATI Industrial Automation, Garner, NC), as shown in Figure 1A. The signals from the transducers were collected by The MotionMonitor software (Innovative Sports Training Inc.) and sampled at 1000 Hz. The sensor locations in the anterior-posterior direction were adjusted to suit each participant's comfort. The medial-lateral distance between the sensor centers was

30 mm. The sensors were zeroed with the fingers resting on the sensors and with the muscles relaxed, so that the weight of the fingers was excluded from the sensor readings. For all trials, the sum of the vertical forces ($F_T = \Sigma F_i$; i = index, middle, ring, little) was presented as feedback to the participant as a cross on a computer screen in front of the participant (Figure 1B). The cross moved vertically upward if the participant increased F_T and it moved vertically downward when the participant decreased F_T.

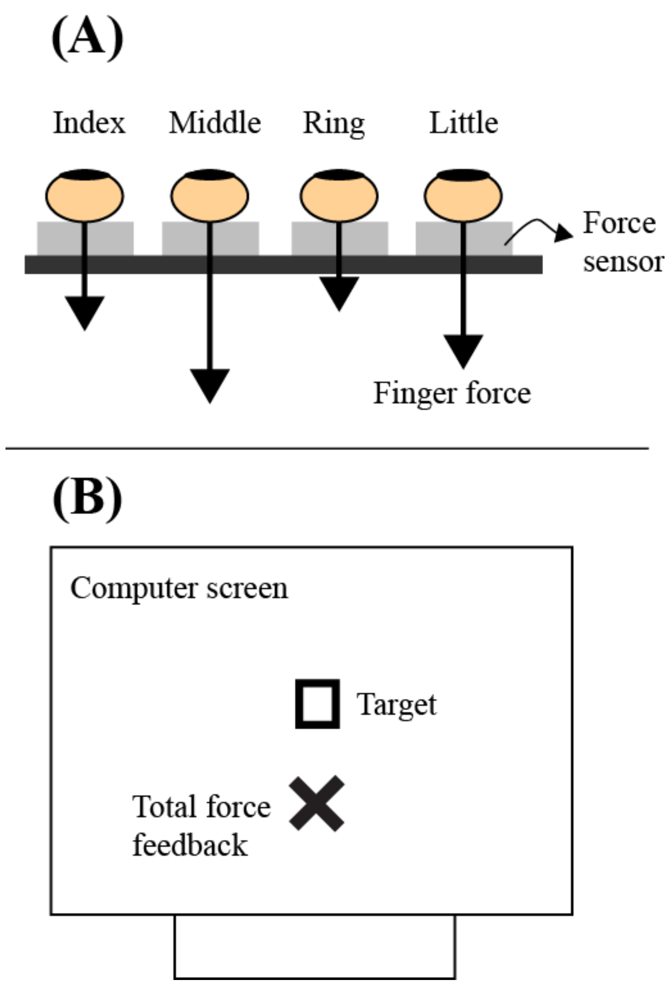

Figure 1. Four fingertips placed on four finger force sensors (A) and the visual feedback provided to the participant (B).

The participants first performed maximal voluntary contraction (MVC) trials in which their goal was to generate the maximal downward force with all four fingers. They performed three MVC trials, each lasting 7 seconds with 1-minute rest intervals between trials. The maximum F_T from the three trials was the MVC force, and it was used to scale the experimental tasks described below.

The experimental protocol consisted of four tasks – Steady, Anticipation, History and Combined – administered in block-randomized fashion. Each task block consisted of 20 trials. For each trial, the participant was required to track a target force trajectory. Before beginning the trials, the participants received the following instructions: (1) the task is always to modulate the total fingertip force and track a square target that could move in the vertical direction on the screen, (2) the target is color-coded, and (3) a purple target will not move from its current position, a yellow target could move vertically at any time, and the target may switch color once and only once during a trial for certain experimental tasks. We informed the participants before starting each task block if the target would change color mid-trial. Figure 2 depicts the target trajectories and participant responses for one trial from each of the four tasks.

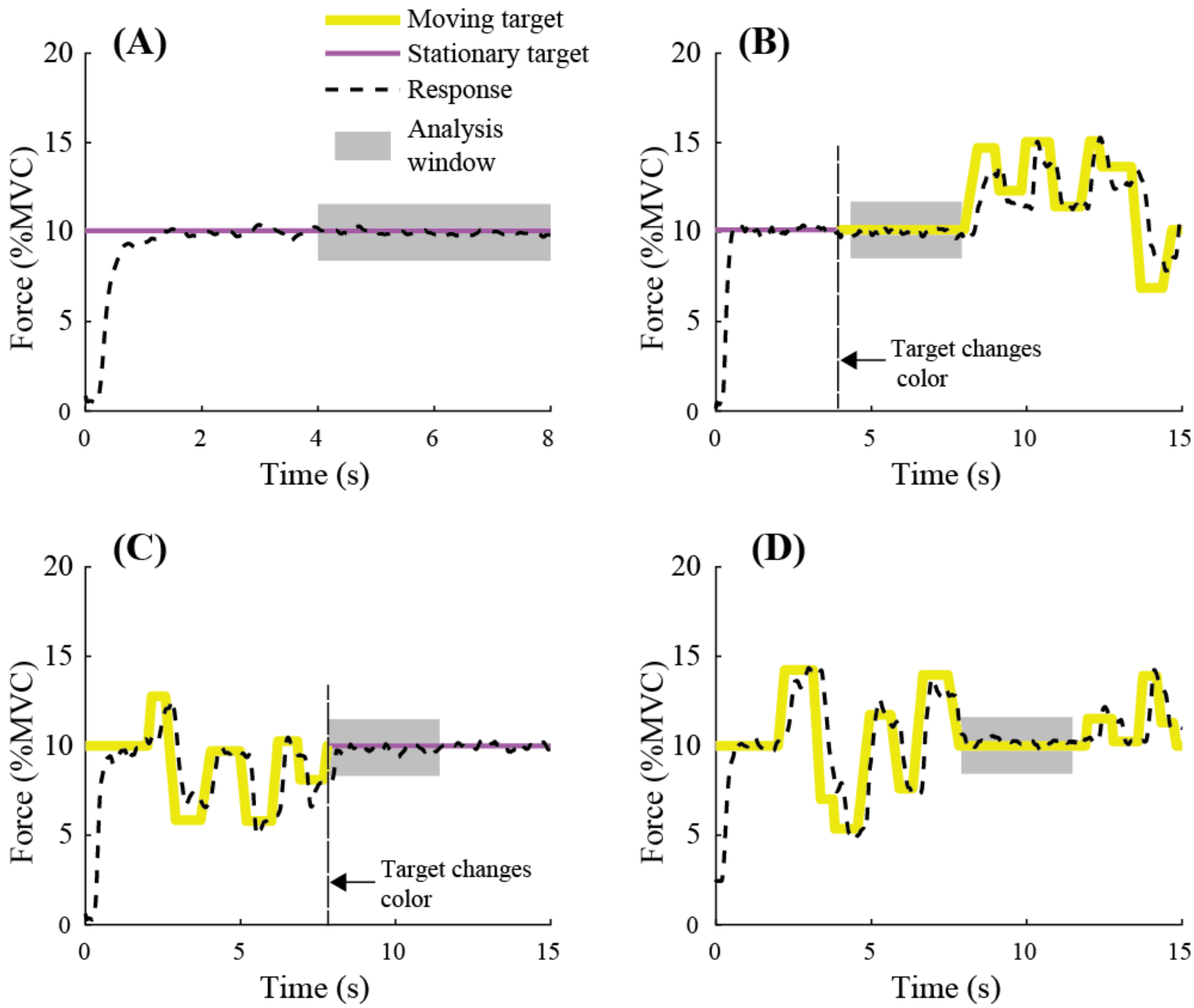

Figure 2. Representative data of the four experimental conditions – Steady (A), Anticipation (B), History (C) and Combined (D). The thick/thin solid curve is the target trajectory and the dashed curve is the participant's response. The target represented by the thin line never moves, and the target represented by the thick line can move at any time. Four-second analysis windows are indicated as the gray rectangles.

Trials for each task type (Steady, Anticipation, History, and Combined) have specific types of target trajectory. For the Steady task (Figure 2A), the target appeared at the 10% MVC location in the center of the screen. It was always purple (i.e., stationary) and remained purple throughout the 8-second trial.

The target trajectory for the Anticipation task began with a purple (i.e., stationary) target at the 10% MVC level (Figure 2B). The target changed color to yellow (i.e., moving) and stayed yellow for the remainder of the 15-second trial. We designed four different target trajectories in which the target was purple for the first four seconds, then turned yellow but stayed at the 10% MVC level for an additional four to five seconds (different duration for each trajectory), and then began moving vertically.

Target trajectories for the History task began with a yellow (i.e., moving) target (Figure 2C). The target turned purple and stabilized at the 10% MVC level eight to nine seconds into the trial (different time for each trajectory) and stayed purple for the remainder of the 15-second trial. Four different trajectories were constructed.

For the Combined task, the target was yellow throughout the 15-second trial (Figure 2D). There was a four- to five-second-long duration in each trajectory (different duration for each trajectory), during which the yellow target stabilized at the 10% MVC level and then resumed its vertical movement. This portion began 8 to 9 seconds into the trajectory (different time for each trajectory). Four distinct target trajectories were constructed.

Note that every trial of every task contained an epoch at least four seconds long when the target (either yellow or purple) was stationary at the 10% MVC level. We used a four-second portion of the participants' finger forces during this epoch for stability analyses (described below). These analysis windows are depicted as gray rectangles in Figure 2. For the Steady task, the last four seconds constitute the analysis window. For the Anticipation task, the four seconds immediately before the target starts moving constitute the analysis window. For the History and Combined tasks, the four seconds immediately following the stabilization of the target to the 10% MVC level constitute the respective analysis windows.

Within the analysis windows for the Steady and Anticipation tasks, the expectation of future movement is different (i.e., target color is different), whereas the target trajectory preceding the analysis window is consistent (i.e., the target is stationary and purple for both tasks). Similarly, within the analysis windows for the History and Combined tasks, the expectation of future movement is different (i.e., target color is different). However, in contrast to the Steady and Anticipation tasks, the target is moving prior to the analysis window. Finally, although the movement histories and expectations are modulated across tasks, the participant is attempting to match the same total force (10% MVC) within each analysis window.

The target-force trajectory for the Steady task was tracked 20 times. We used the finger forces from the last 15 trials for stability analyses. For each of the remaining three tasks, the first three trajectories were tracked four times each, and the fourth trajectory was tracked three times to yield a set of 15 trials. We used the finger forces from these trials for stability analyses. In addition to these 15 trials, participants tracked one more trajectory five times to yield a set of 20 trials per task. We designed additional target trajectories for these tasks to minimize the possibility of the participants anticipating the duration of the epoch with the stationary target. These trajectories adhered to the color codes of the respective tasks but did not contain that epoch. For the Anticipation task, the target changed color to yellow after the first four seconds, but started moving vertically after a much shorter interval (2 seconds). For the History task, the target remained yellow and moving for a longer duration that the other four trajectories and became purple and stationary after 13 seconds. For the combined task, there was no epoch where the target was stationary at 10% MVC for over 2 seconds. The data from these trials was not used for the stability analyses.

The movements of the yellow target for any trajectory consisted of a set of steady forces linked with linear ramp segments. The magnitudes and durations of the steady target forces and the slopes and durations of the ramp segments varied within and across the trajectories. The target force magnitudes for all tasks were between 5 and 15% MVC, and the ramp slopes were well within the participants' maximal force-modulation abilities (Tillman & Ambike, 2018a).

The participants first performed eight practice trials to familiarize themselves with the tasks. Each practice trial was 15 seconds long. Each participant performed six trials that resembled the Combined task, and two trials that resembled the History task. The first five trials of the Steady task were also considered practice. Following the practice trials, the participants performed the experimental tasks. The four tasks were block randomized, and the five trajectories for the Anticipation, History and Combined tasks were randomized within each task block.

To limit fatigue, 15-s rest intervals were enforced between all trials. One-minute breaks were given between MVC trials, 15 second rests between trials within each task block, and two-minute breaks were enforced between blocks. Participants were instructed to ask for additional rest if they felt any fatigue. None of the participants asked for additional rest or reported fatigue during the study.

Data analysis

Custom MATLAB programs were written for data analysis (R2017a, The MathWorks Inc). All finger-force data were low-pass filtered at a cutoff frequency of 10 Hz using a fourth-order, zero-lag Butterworth filter.

To quantify task performance, we computed the root mean squared error (RMSE) in total force with respect to the target for all trials that are included in the analysis (See Methods) starting from time t = 2s (to exclude the time it takes to reach the target from the resting state) to the end of the trial.

The finger force data within the analysis windows for the four tasks (Figure 2) were utilized for the uncontrolled manifold (UCM) analyses. The UCM analysis (Scholz & Schoner, 1999) is a tool to quantify the structure of variability that exists in the repeated performance of a task using a redundant set of inputs and then make inferences about the stability of the salient task variable(s). For the current study, the task is described by the equation $F_T = \Sigma(F_i)$; i = [index, middle, ring, little]. Four fingers (inputs) produce a single output (task) variable (F_T). Therefore, the task is redundant. For each time instant, t = t*, the four finger forces for all repetitions were isolated and used to obtain three UCM variables: (1) $V_{UCM}(t^*)$ – the variance along the UCM, (2) $V_{ORT}(t^*)$ – the variance along the manifold orthogonal to the UCM, and (3) DV(t*) – the synergy index defined as $\Delta V(t^*) = (V_{UCM}(t^*)/3 - V_{ORT}(t^*))/(V_{TOT}(t^*)/4)$. V_{UCM} is the component of the force variance that does not change F_T, and V_{ORT} is the component that changes F_T. A positive ΔV indicates that the input variables coordinate to stabilize the output variable, while a negative ΔV indicates that the input variables coordinate to change the task variable. $\Delta V = 0$ implies that there is no task-specific coordination. Higher ΔV indicates greater stabilization of F_T. The synergy index for this system is bounded: $-4 \leq \Delta V \leq 4/3$. Therefore, for statistical analysis the ΔV values were z transformed (Zhou et al., 2013):

$$\Delta V_z(t^*) = 0.5 * \log\left[\frac{4 + \Delta V(t^*)}{4/3 - \Delta V(t^*)}\right]$$

Note that $\Delta V = 0$ corresponds to $\Delta V_Z = 0.5493$. Therefore, a ΔV_Z value greater than 0.5493 indicates a synergy that stabilizes F_T. Additional details of this analysis are provided elsewhere (Tillman & Ambike, 2018a). These computations are repeated for each time instant within the four-second window, yielding the time series $V_{UCM}(t)$, $V_{ORT}(t)$, and $\Delta V_Z(t)$ for each task type. An exponential function of the form $y(t) = ae^{(-t/\tau)} + b$ was fit in the least-squared sense to these curves for the History and Combined tasks, where τ is the time constant in seconds, b is the steady-state value that the variable y reaches after infinite time, and *a* is the change in the value of *y* over that duration. We are interested in the time constant, which indicates the rate of convergence to the steady-state value.

Statistics

Data are presented in "Results" as means and standard errors (SE), unless mentioned otherwise. V_{UCM} and V_{ORT} are normalized by the dimension of the corresponding manifold [dimension(UCM) = 3; dimension(ORT) = 1], and then log transformed to meet normality requirements for conducting ANOVAs. However, non-log-transformed values for V_{UCM} and V_{ORT} are presented in the "Results" section. The transformed variance components and ΔV_Z values for the last one second of the four-second analysis window were averaged for each participant. Note that for the Combined and the History tasks, it will take some time for the total force to converge to the target force value of 10% MVC. These total force changes will appear as large-amplitude changes in the UCM variables early in the four-second analysis window. In our previous work, we observed that the UCM variables for the Combined task stabilize in about two seconds (Tillman & Ambike, 2018a). We expect similar behavior here for the History and Combined tasks. Our hypotheses pertain to the portion of the data after the total force, on average, has converged to the target. Therefore, the transformed variance components and ΔVz values for the last one second of the analysis window were averaged for each participant and analyzed using a one-way, repeated measures ANOVA with *Task* (4 levels) as the repeated (within-subject) factor. The task sequence was randomized to avoid confounding their effects with time. Therefore, *Task Sequence* was added as a blocking factor to the ANOVA to account for learning effects or fatigue over the series of tasks. We determined the appropriate covariance structure (e.g., compound symmetry, AR(1)) using the AIC model selection criterion. Post-hoc comparisons with the Steady Task were conducted using

Dunnett's multiple-comparison method. All statistics were performed using an α-level of 0.05 using the SAS statistical software (Version 9.4; SAS Institute, Cary, NC).

RESULTS

Task performance

Participants were able to perform all experimental tasks. Figure 2 shows representative data from one trial for each task type. The response follows the target profile with some lag. This is expected, since the target trajectory was unknown to the participant. We quantified the performance of the target tracking task by computing the RMSE in total force starting from t = 2 s to the end of the trial. The RMSE values, averaged across the repetitions for each task and across participants were 0.17 ± 0.01 %MVC for the Steady task; 1.44 ± 0.02 %MVC for the Anticipation task; 1.56 ± 0.03 %MVC for the History task; 1.69 ± 0.02 %MVC for the Combined task. Overall, the error in performance is under 2 %MVC, which is less than one fifth of the average value of the target (~10 %MVC). Since the participants were tracking a randomly moving target for much of the experiment, we conclude that the participants were able to perform the tasks.

Changes in the synergy index and the variance components

Figure 3 shows the trajectories of the UCM variables for the four tasks. The trajectories for the Steady and the Anticipation tasks do not show any dynamics other than local fluctuations. This is expected, since the force target did not change during the analysis window and the participants' response was relatively invariant for these tasks. In contrast, the UCM variables for the History and the Combined tasks show large amplitude changes that evolve over 0.5 to 2 seconds. Figure 3A shows the presence of a synergy that works to change the total force ($\Delta V_z < 0.5493$) during an initial period up to about $t = 0.5$

s (also referred to as an 'anti-synergy' (Robert, Bennett, Russell, Zirker, & Abel, 2009; Wang et al., 2006)). This reflects convergence to the stationary target force (10% MVC) from various earlier target values. As this convergence proceeds, the synergy index increases and then settles to a steady value 2 to 2.5 s after the target first stops moving (i.e., from the start of the analysis window). The trajectories for these two tasks were well approximated as exponential processes. The medians (inter-quartile ranges) of the R^2 values of the exponential fits were 0.9 (0.05) and 0.87 (0.07) for the History and the Combined tasks, respectively. The time constants were $\tau_{History} = 0.68 \pm 0.04$ s and $\tau_{Combined} = 0.92 \pm 0.17$ s. These values resemble the time constants for ΔVz obtained in our earlier work.

The trajectories for V_{UCM} for the History and Combined tasks are less consistent across participants. Seven of the 48 trajectories (24 participants × 2 tasks) exhibited non-monotonic changes early in the analysis window, and then settled to a steady value. The remaining V_{UCM} trajectories were well approximated by exponential functions, and this is apparent in the across-participant mean trajectories in Figure 3B. The median (inter-quartile range) of the R^2 values are 0.72 (0.4) and 0.84 (0.29) for the History and the Combined tasks, respectively. The time constants for these two tasks were $\tau_{History} = 0.55 \pm 0.48$ s, and $\tau_{Combined} = 0.42 \pm 0.39$ s. These values are also close to the time constants obtained in our earlier study.

Figure 3C shows the trajectories of V_{ORT} for the four tasks. V_{ORT} is initially large for the History and Combined task, consistent with the low ΔVz values during this period, and then decays exponentially. The medians (inter-quartile ranges) of the R^2 values for the exponential fits to these trajectories are 0.95 (0.04) and 0.93 (0.06) for the History and the Combined tasks, respectively. The time constants were $\tau_{History} = 0.2 \pm 0.01$ s, and $\tau_{Combined} = 0.29 \pm 0.03$ s, which are close to those obtained in our previous study. Figure 3D shows a close up view of the V_{ORT} time series, and it visually illustrates that the error in the task performance decays and reaches a steady level at about 2 – 2.5 seconds.

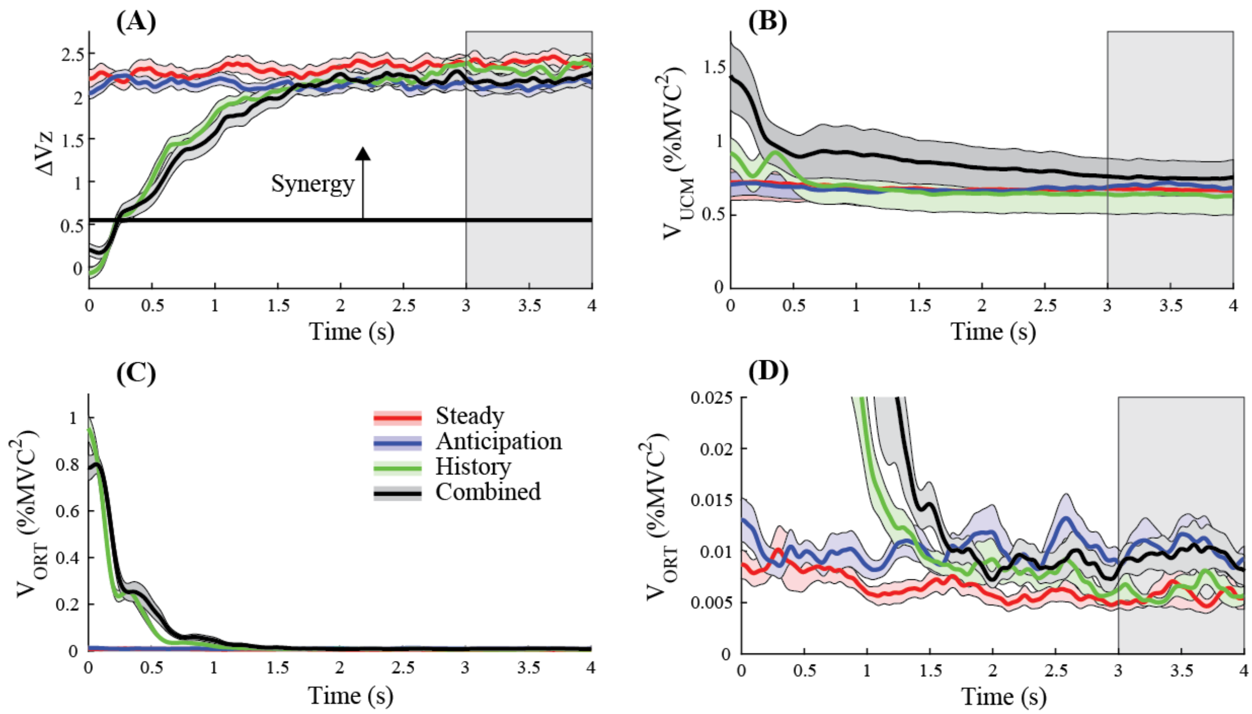

Figure 3. Across-participant mean ± SE of the UCM variables ΔVz (A), V_{UCM} (B) and V_{ORT} (C) for all four task types. The variance components V_{UCM} and V_{ORT} are normalized by the dimension of the corresponding manifold (see text). A close up view of V_{ORT} trajectories is shown in (D). The data over the last one second (gray rectangle in (A), (B), and (D)) is averaged and used for statistical analysis.

Figure 4A shows the synergy index averaged over the final one-second window of the ΔVz(t) time series. The ANOVA reveals an effect of *Task* [$F(3,66) = 3.88$; $p = .01$]. Post-hoc comparisons revealed that compared to the Steady task (ΔVz = 2.4 ± 0.08), the synergy index for the History task (ΔVz = 2.32 ± 0.08) is not statistically different ($p = .78$), it is lower for the Anticipation task (ΔVz = 2.1 ± 0.08; $p = .01$), and it tends to be lower for the Combined task (ΔVz = 2.18 ± 0.08; $p = .056$). Figure 4B shows V_{UCM} averaged over the final one-second window of the $V_{UCM}(t)$ time series. The ANOVA did not reveal a *Task* effect [$F(3,66) = .26$; $p = .85$]. Figure 4C shows V_{ORT} averaged over the final one-second window of the $V_{ORT}(t)$ time series. The ANOVA reveals an effect of *Task* [$F(3,66) = 16.32$; $p < .0001$]. Post-hoc comparisons revealed that compared to the Steady task (V_{ORT} = 0.006 ± 0.001 %MVC^2), V_{ORT} for the History task is not statistically different (V_{ORT} = 0.006 ± 0.0007 %MVC^2; p = .1), it is higher for the anticipation task (V_{ORT} = 0.01 ± 0.001 %MVC^2; $p < .001$) and for the combined task (V_{ORT} = 0.01 ± 0.001 %MVC^2; $p < .001$).

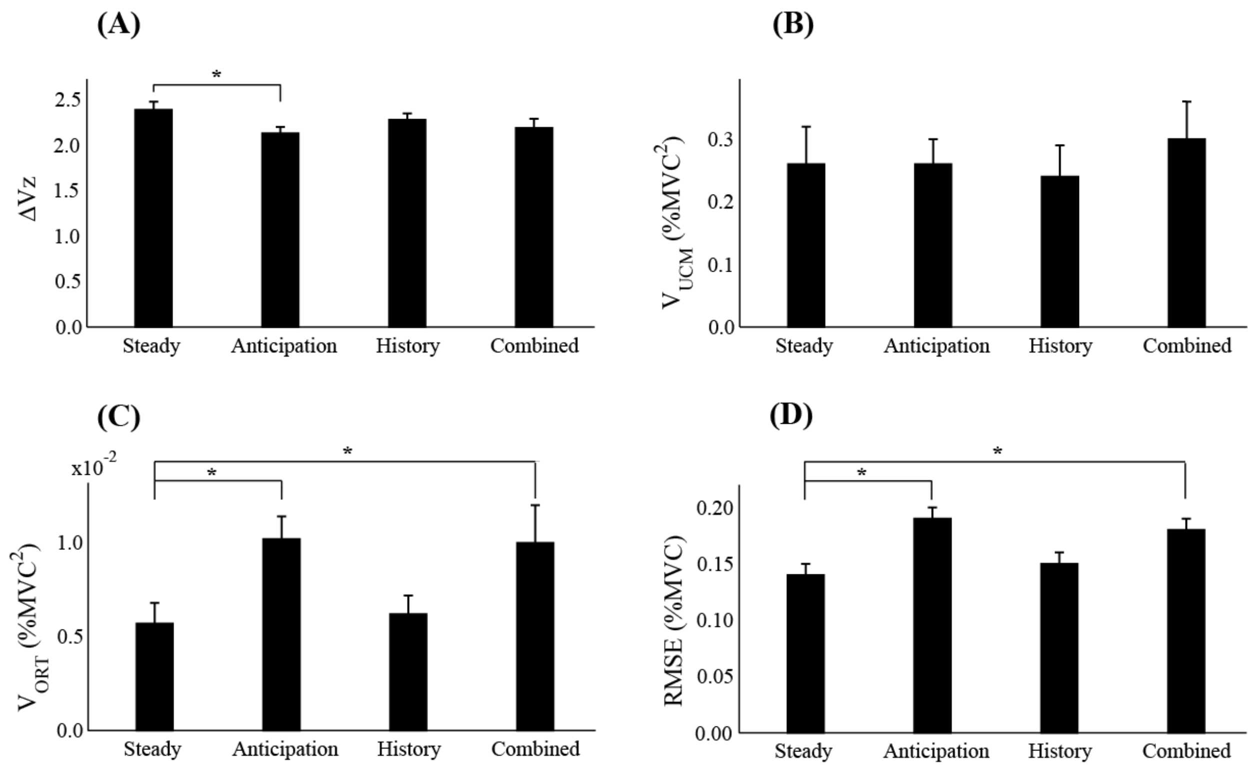

Figure 4. Mean ± SE of the UCM variables ΔVz (A), V_{UCM} (B), V_{ORT} and (C) averaged over the last one second of the analysis window. Asterisks indicate statistically significant differences.

Finally, the effect of *Task Sequence* was not significant for any of the dependent measures, indicating that the results presented above are not influenced by learning or fatigue effects. The *F* and *p* values obtained from the ANOVAs for these variables for *Task Sequence* are as follows. ΔVz: $F(3,66) = 1.18$; p = .32; V_{UCM}: $F(3,66) = 1.39$; p = .25; V_{ORT}: $F(3,66) = .31$; p = .82.

DISCUSSION

The primary objective of the present work was to establish if expected voluntary changes in the total finger force lead to a reduction in the stability of the current total force in an isometric force-production task, while controlling for the history of changes in the total force. Our secondary objective was to explore the effects of disparate histories of total force changes on the stability of the current total force.

We addressed our primary objective by postulating our first hypothesis that the stability of the total force, quantified using the synergy index ΔVz, in the Anticipation task would be lower than that in the Steady task. The data supported this hypothesis; we observed the stability for the Anticipation task reduced by about 12.5%. To address our second objective, we hypothesized that the stability of the total force will be lower in the History task compared to that in the Steady task. Furthermore, we assumed that in the Combined task, the effects of movement history and of anticipated movement would be additive. Therefore, if prior and expected changes in the total force both lead to reduced stability of the current total force, then the stability of the current total force in the Combined task will be lower compared to that in the Steady task. We did not observe a difference in the ΔVz values for the Steady and the History tasks, and therefore, our second hypothesis was not supported. The third hypothesis was also not supported by our data, although the stability in the Combined task tended to be lower (p = .056).

The synergy index is a function of the variance within the UCM (V_{UCM}) and orthogonal to the UCM (V_{ORT}). We explored changes in these variance components and found that V_{UCM} in the History, Anticipation and Combined tasks did not differ from that in the Steady task. In contrast, V_{ORT} for the Anticipation and the Combined tasks was higher (by ~67%) than that for the Steady task, and V_{ORT} for the History and Steady tasks were not statistically different.

Below, we discuss the implications of these findings and other relevant issues.

Two stages of anticipatory synergy adjustment

Anticipatory synergy adjustments (ASAs) are of two types – stage 1 and stage 2. Stage 1 ASA is a novel phenomenon that we proposed recently (Tillman & Ambike, 2018a, 2018b), and we provide evidence to support its existence in the present work. It is the difference in the synergy index between two experimental conditions in which the current values of the task variables are identical (i.e., the participant is producing the same total force), but the expectation to change those variables is different. Stage 1 ASA is agnostic to whether the change expected in one of the compared conditions is executed by the individual. In contrast, stage 2 ASA was reported previously by Latash and colleagues in finger force production and upright postural tasks (Falaki, Huang, Lewis, & Latash, 2017; Olafsdottir et al., 2005; Olafsdottir et al., 2008; Piscitelli et al., 2017; Shim, Olafsdottir, Zatsiorsky, & Latash, 2005; Zhou et al., 2013). Stage 2 ASA is observed prior to a volitional change in the task variables and is reflected in a positive value for the quantity $\Delta Vz(T_1) - \Delta Vz(T_2)$. The task variables first change at time T_2, and the synergy index at T_2 is lower than that measured at an earlier time T_1 when the task variables are invariant. These synergy indices are obtained from the same set of trials in which the individual always expects to change the task variables. Furthermore, stage 2 ASA is observed only when the timing of the change is known sufficiently in advance (Olafsdottir et al., 2005; Zhou et al., 2013). In other words, stage 1 ASA is the reduction in stability in response to a cue to change the task variables, and stage 2 ASA is (further) reduction in stability immediately prior to executing that change. The names of the two phenomena reflect the fact that the cue must occur prior to execution. Finally, the durations of the two ASAs are different. Stage 2 ASA begins 150 -300 ms before the action [cf. (Latash & Huang, 2015)]. Stage 1 ASA lasts longer (Figure 3A). ΔVz is lower in the Anticipation task compared to the Steady task for at least one second, which is 2.5 times longer than stage 2 ASA. The duration of stage 1 ASA is a conservative estimate based on the observations from our studies. It is not known how long the difference in ΔVz between the Steady and Anticipation tasks will persist.

In our previous work, we observed reduction in the stability of the total finger force in the Combined task compared to the Steady task, it was not possible to rule out any influence of disparate histories of total force changes on the observed reduction in stability. Our data here overcome that deficiency. In the two conditions where the current total force is achieved through similar motor histories (in Stable and Anticipation tasks) the current stability of the total force is diminished when the participant expects to change the force soon. This result provides compelling evidence for the existence of stage 1 ASA.

Effect of history on the stability of the total force

The stability of a motor behavior is a dynamic property. It evolves over time, and the stability at any instant can be influenced by the past and the intended use of the motor apparatus (Scholz & Kelso, 1990). In the context of manual behaviors, digit force synergies in static prehension tasks depend on the history of the changes in the external loads on a hand-held object (Sun, Park, et al., 2011; Sun, Zatsiorsky, et al., 2011). Therefore, the secondary goal of this study was to explore the effect of movement history on the stability of the current behavior.

We observed that when the total force is achieved via dissimilar force changes, the current stability of the total force is indistinguishable if the participant expects no further changes in total force (in Stable and History tasks). Of course, in the History task, the stability becomes indistinguishable after some finite time that the system needs to relax into the current behavior (Figure 3A).

The synergy index results for the Combined task, however, create ambiguity in understanding the effect of history on the current stability. For the Combined task, we expected that the current stability of the total force would be lower than that for the Steady task. This was based on the expectations of lower stability in the History and the Anticipation tasks, and the assumption that those effects would add for the Combined task. Note that under this assumption, the expectation of lower stability for the Combined task would hold despite the result that stability is not different in the History and Stable tasks. Although we observe that the stability for the Combined task compared to the Stable task tended to be lower, this decline did not reach statistical significance, indicating that the effects of history and anticipation may not be additive. Furthermore, we have a counter-intuitive result that the current stability of the total force increases with time in the History task, but it increases more rapidly if the participant anticipates changing the force in the future.

Changes in variance components

The changes in V_{ORT} observed here are consistent with our previous work. There, we observed that stage 1 ASA in older adults resulted from increased V_{ORT} (Tillman & Ambike, 2018b), and in young adults it resulted primarily from reduced V_{UCM}, with V_{ORT} showing a tendency to increase (Tillman & Ambike, 2018a). In the present study, the number of participants that increased V_{ORT} for the Anticipation, History, and Combined tasks were 22 (92%), 16 (67%), and 19 (80%), respectively (Figure 5A). Combined with the findings of the present study, we find that increase in V_{ORT} is the more consistently employed strategy for stability reduction in isometric finger force production tasks. This is an intuitive finding: lower stability of performance is reflected in greater variability in performance. It is also consistent with the dynamical-systems view stating that increased variability in order parameters (a few variables that capture the essential dynamics of a high-dimensional dynamical system) facilitates movement transitions (Kelso, Scholz, & Schöner, 1986; Kiefer & Myer, 2015; Riley & Turvey, 2002; Scholz & Kelso, 1990).

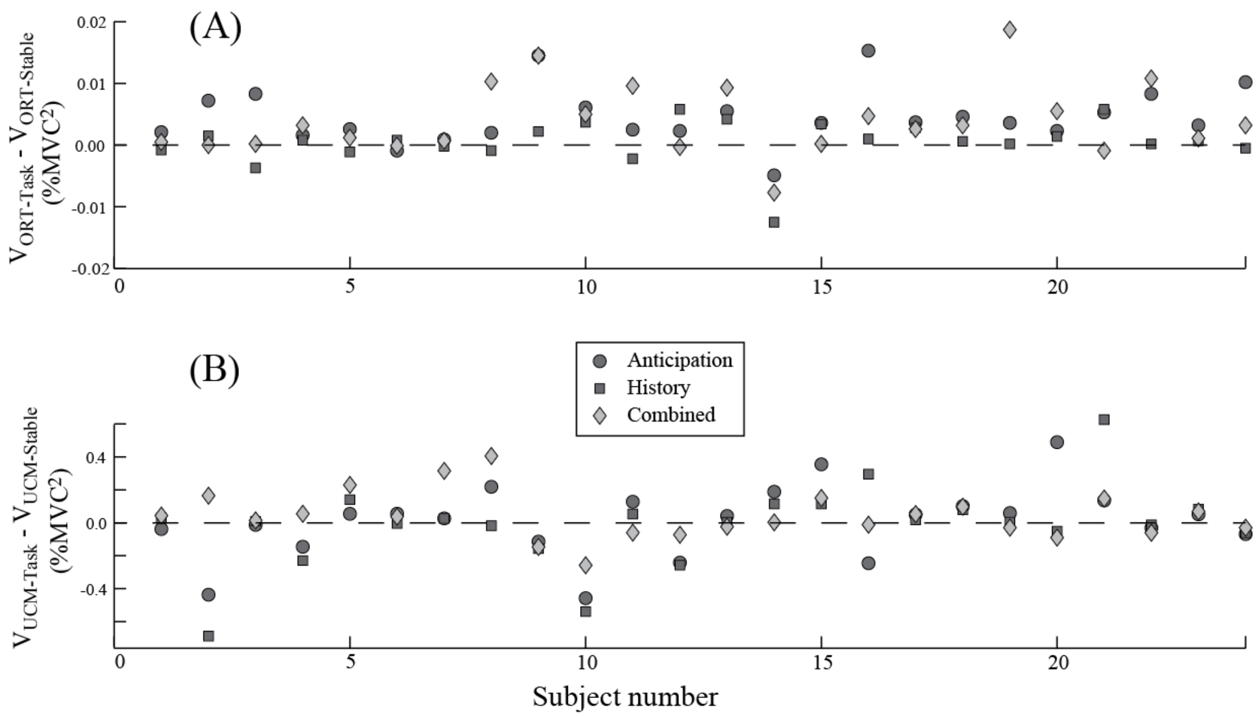

Figure 5. Change in the variance components V_{ORT} (A) and V_{UCM} (B) for the Anticipation, History and Combined tasks compared to the Steady task for all participants. Positive values indicate an increase in the variance component for a task compared to the Steady task.

In contrast to V_{ORT}, 14 out of the 24 participants (58%) increased V_{UCM} for each of the three tasks (Figure 5B). The participants are split more evenly into groups that increase and decrease V_{UCM} in all the test conditions, suggesting that neither movement history nor planning for anticipated motor changes leads to consistent changes in V_{UCM}. Togo & Imamizu (2016) also report inconsistent V_{UCM} changes in a cohort of young healthy individuals in a similar isometric finger-force-production experiment.

Inconsistent changes in V_{UCM} are common in studies using the UCM framework. In motor learning studies, skill acquisition is reflected in decline in V_{ORT} with practice. However, concomitant changes in V_{UCM} are variable; V_{UCM} is known to increase, decrease and remain invariant in various studies (reviewed in (Latash, 2010)). Similarly, different movement disorders lead to a decline in ΔVz compared to healthy controls, but inconsistent changes in V_{UCM} (reviewed in (Vaz, Pinto, Junior, Mattos, & Mitra, 2019)). In one sense, this is not surprising. Since the task does not explicitly constrain the movement in the UCM, individuals make different choices regarding the magnitude of this movement. Furthermore, individuals may exploit the UCM movement for various reasons. It has been suggested the existence of the UCM is exploited by the nervous system to accomplish additional goals like (1) explore the UCM to promote motor learning (Singh, Jana, Ghosal, & Murthy, 2016), (2) tuning the performance within the UCM to resist disturbances (Latash, Yarrow, & Rothwell, 2003), (3) minimize noise in the task-relevant directions (Gorniak, Duarte, & Latash, 2008), (4) maximize the efficiency of transitions (de Freitas, Scholz, & Stehman, 2007; Tillman & Ambike, 2018a, 2018b), or (5) accomplish additional tasks without compromising the performance of the current task (Latash, 2010). Individual differences in V_{UCM} are an important topic for further investigation.

Each of the possible ways to reduce ΔVz (increase V_{ORT}, decrease V_{UCM}, or both) can constitute a strategy to reduce the stability of the current total force. Overall, compared to the Steady task, V_{ORT} is similarly high in the Combined and Anticipation task, and this leads to similar reductions in ΔVz. On the other hand, V_{UCM} tends to be higher for the Combined task only (Figure 4B), and although this difference was not statistically significant, it diminished the decline in ΔVz for that task, which led to the ambiguous results. This result for the Combined task may be driven by increased muscular co-contraction within the analysis windows. It is known that co-activation remains high following a quick action, and although it decays to pre-action levels over time, these dynamics are not well known (Gottlieb et al., 1989; Latash, 2018; Suzuki & Yamazaki, 2005). We selected the analysis window based on our previous study, but the interval between the convergence to the 10%MVC target and the start of the analysis window (~1.5 seconds; Figure 3D) for the Combined task may have been too short, at least for some participants. The co-contraction seems to be primarily contained within the UCM for the total force (since $V_{ORT} << V_{UCM}$), and this may have led to the increase in V_{UCM} for this task, which cancels out the significant effect of V_{ORT} when ΔVz is analyzed.

ASA and the stability-maneuverability tradeoff

ASAs can be considered as the stability-reduction portion of the so-called stability-maneuverability tradeoff. This tradeoff has been explored more in the animal locomotion literature (Dickinson et al., 2000), and has been observed during some locomotor (Acasio et al., 2017) and balance manipulation (Huang & Ahmed, 2011) studies in humans. In upper-extremity research, ASAs have been recorded in reaching (de Freitas et al., 2007; Freitas & Scholz, 2009) and finger force production (Latash & Huang, 2015) behaviors, but none of the studies establish a relation between the stability reduction and the performance of the subsequent volitional action. The present study is of a similar kind: it elucidates the nature of ASAs in manual behavior, but it does not attempt to link stage 1 ASA with the performance of the transition. One exception is the study by (Togo & Imamizu, 2016) which demonstrated that in an isometric finger force production task, greater stage 2 ASAs are associated with improved accuracy of subsequent force pulses, thereby illustrating the stability-maneuverability tradeoff. Therefore, establishing the relation between ASA and subsequent task performance in upper-extremity movements in humans remains an important topic for future research.

Limitations

The main limitation of this study is the lack of electromyographic measurements from the hand muscles. Muscular co-contraction leads to stiffer effectors, and this facilitates faster movements (Latash, 2018). Recording agonist-antagonist co-contraction and its decay following previous changes in isometric finger forces will elucidate the underlying mechanisms of stage 1 ASAs. Another limitation of this work is that we do not map the reduced stability onto improved maneuverability in this work. Maneuverability in our task could be quantified using reaction times, or the sensitivity of the total force to changes in EMG amplitudes. The focus of this paper was on establishing the validity of stage 1 ASA. Finally, stage 1 and stage 2 ASAs occur one after the other in a typical choice reaction time task. However, we do not attempt to demonstrate both ASAs in the same set of trials in this work. This remains a challenge for future work.

Conclusion

We have demonstrated that anticipation of upcoming changes in the total force produced by the fingers in isometric conditions results in lower stability of the current force, thereby corroborating the existence of stage 1 ASA. Furthermore, the expectation of voluntary changes in total force led to greater variability in the current total force, independent of the previous changes in the total force that led to its current value. However, we observed individual differences in the task-specific covariation in the finger forces due to different histories of total force changes. Understanding these individual differences is key to comprehending how past movements and anticipated movements interact to determine the stability of the current motor behavior.

REFERENCES

Acasio, J., Wu, M., Fey, N. P., & Gordon, K. E. (2017). Stability-maneuverability trade-offs during lateral steps. *Gait & Posture, 52*, 171-177. doi:10.1016/j.gaitpost.2016.11.034

de Freitas, S. M., Scholz, J. P., & Stehman, A. J. (2007). Effect of motor planning on use of motor abundance. *Neurosci Lett, 417*(1), 66-71. doi:10.1016/j.neulet.2007.02.037

Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A., Kram, R., & Lehman, S. (2000). How animals move: an integrative view. *Science, 288*(5463), 100-106. doi:10.1126/science.288.5463.100

Falaki, A., Huang, X., Lewis, M. M., & Latash, M. L. (2017). Dopaminergic modulation of multi-muscle synergies in postural tasks performed by patients with Parkinson's disease. *J Electromyogr Kinesiol, 33*, 20-26. doi:10.1016/j.jelekin.2017.01.002

Freitas, S. M. S. F., & Scholz, J. P. (2009). Does hand dominance affect the use of motor abundance when reaching to uncertain targets? *Human Movement Science, 28*(2), 169-190. doi:10.1016/j.humov.2009.01.003

Gorniak, S. L., Duarte, M., & Latash, M. L. (2008). Do synergies improve accuracy? A study of speed-accuracy trade-offs during finger force production. *Motor Control, 12*(2), 151-172.

Gottlieb, G. L., Corcos, D. M., & Agarwal, G. C. (1989). Organizing principles for single-joint movements. I. A speed-insensitive strategy. *J Neurophysiol, 62*(2), 342-357. doi:10.1152/jn.1989.62.2.342

Hasan, Z. (2005). The human motor control system's response to mechanical perturbation: should it, can it, and does it ensure stability? *J Mot Behav, 37*(6), 484-493. doi:10.3200/JMBR.37.6.484-493

Huang, H. J., & Ahmed, A. A. (2011). Tradeoff between Stability and Maneuverability during Whole-Body Movements. *PLoS One, 6*(7). doi:10.1371/journal.pone.0021815

Kelso, J., Scholz, J. P., & Schöner, G. (1986). Nonequilibrium phase transitions in coordinated biological motion: critical fluctuations. *Physics Letters A, 118*(6), 279-284.

Kiefer, A. W., & Myer, G. D. (2015). Training the Antifragile Athlete: A Preliminary Analysis of Neuromuscular Training Effects on Muscle Activation Dynamics. *Nonlinear Dynamics Psychol Life Sci, 19*(4), 489-510.

Kim, S. W., Shim, J. K., Zatsiorsky, V. M., & Latash, M. L. (2006). Anticipatory adjustments of multi-finger synergies in preparation for self-triggered perturbations. *Exp Brain Res, 174*(4), 604-612. doi:10.1007/s00221-006-0505-8

Klous, M., Mikulic, P., & Latash, M. L. (2011). Two aspects of feedforward postural control: anticipatory postural adjustments and anticipatory synergy adjustments. *J Neurophysiol, 105*(5), 2275-2288. doi:10.1152/jn.00665.2010

Kostyukov, A. I. (1998). Muscle hysteresis and movement control: a theoretical study. *Neuroscience, 83*(1), 303-320. doi:10.1016/s0306-4522(97)00379-5

Krishnan, V., Aruin, A. S., & Latash, M. L. (2011). Two stages and three components of the postural preparation to action. *Exp Brain Res, 212*(1), 47-63. doi:10.1007/s00221-011-2694-z

Latash, M. L. (2010). Stages in learning motor synergies: a view based on the equilibrium-point hypothesis. *Hum Mov Sci, 29*(5), 642-654. doi:10.1016/j.humov.2009.11.002

Latash, M. L. (2018). Muscle coactivation: definitions, mechanisms, and functions. *J Neurophysiol, 120*(1), 88-104. doi:10.1152/jn.00084.2018

Latash, M. L., & Huang, X. (2015). Neural control of movement stability: Lessons from studies of neurological patients. *Neuroscience, 301*, 39-48. doi:10.1016/j.neuroscience.2015.05.075

Latash, M. L., Scholz, J. P., & Schoner, G. (2002). Motor control strategies revealed in the structure of motor variability. *Exerc Sport Sci Rev, 30*(1), 26-31.

Latash, M. L., Yarrow, K., & Rothwell, J. C. (2003). Changes in finger coordination and responses to single pulse TMS of motor cortex during practice of a multifinger force production task. *Exp Brain Res, 151*(1), 60-71. doi:10.1007/s00221-003-1480-y

Olafsdottir, H., Yoshida, N., Zatsiorsky, V. M., & Latash, M. L. (2005). Anticipatory covariation of finger forces during self-paced and reaction time force production. *Neurosci Lett, 381*(1-2), 92-96. doi:10.1016/j.neulet.2005.02.003

Olafsdottir, H., Yoshida, N., Zatsiorsky, V. M., & Latash, M. L. (2007). Elderly show decreased adjustments of motor synergies in preparation to action. *Clin Biomech, 22*(1), 44-51. doi:10.1016/j.clinbiomech.2006.08.005

Olafsdottir, H. B., Kim, S. W., Zatsiorsky, V. M., & Latash, M. L. (2008). Anticipatory synergy adjustments in preparation to self-triggered perturbations in elderly individuals. *J Appl Biomech, 24*(2), 175-179.

Park, J., Wu, Y. H., Lewis, M. M., Huang, X., & Latash, M. L. (2012). Changes in multifinger interaction and coordination in Parkinson's disease. *J Neurophysiol, 108*(3), 915-924. doi:10.1152/jn.00043.2012

Park, J., & Xu, D. (2017). Multi-Finger Interaction and Synergies in Finger Flexion and Extension Force Production. *Front Hum Neurosci, 11*, 318. doi:10.3389/fnhum.2017.00318

Piscitelli, D., Falaki, A., Solnik, S., & Latash, M. L. (2017). Anticipatory postural adjustments and anticipatory synergy adjustments: preparing to a postural perturbation with predictable and unpredictable direction. *Exp Brain Res, 235*(3), 713-730. doi:10.1007/s00221-016-4835-x

Riccio, G. E. (1993). Information in movement variability about quantitative dynamics of posture and orientation. In K. M. C. Newell, D. (Ed.), *Variability and Motor Control* (pp. 317-357). Champaign, IL: Human Kinetics.

Riccio, G. E., & Stoffregen, T. A. (1988). Affordances as constraints on the control of stance. *Human Movement Science, 7*, 265-300.

Riley, M. A., & Turvey, M. T. (2002). Variability of determinism in motor behavior. *J Mot Behav, 34*(2), 99-125. doi:10.1080/00222890209601934

Robert, T., Bennett, B. C., Russell, S. D., Zirker, C. A., & Abel, M. F. (2009). Angular momentum synergies during walking. *Exp Brain Res, 197*(2), 185-197. doi:10.1007/s00221-009-1904-4

Scholz, J. P., & Kelso, J. A. (1990). Intentional switching between patterns of bimanual coordination depends on the intrinsic dynamics of the patterns. *J Mot Behav, 22*(1), 98-124. doi:10.1080/00222895.1990.10735504

Scholz, J. P., & Schoner, G. (1999). The uncontrolled manifold concept: identifying control variables for a functional task. *Exp Brain Res, 126*(3), 289-306.

Shim, J. K., Olafsdottir, H., Zatsiorsky, V. M., & Latash, M. L. (2005). The emergence and disappearance of multi-digit synergies during force-production tasks. *Exp Brain Res, 164*(2), 260-270. doi:10.1007/s00221-005-2248-3

Shim, J. K., Park, J., Zatsiorsky, V. M., & Latash, M. L. (2006). Adjustments of prehension synergies in response to self-triggered and experimenter-triggered load and torque perturbations. *Exp Brain Res, 175*(4), 641-653. doi:10.1007/s00221-006-0583-7

Singh, P., Jana, S., Ghosal, A., & Murthy, A. (2016). Exploration of joint redundancy but not task space variability facilitates supervised motor learning. *Proc Natl Acad Sci U S A, 113*(50), 14414-14419. doi:10.1073/pnas.1613383113

Sun, Y., Park, J., Zatsiorsky, V. M., & Latash, M. L. (2011). Prehension synergies during smooth changes of the external torque. *Exp Brain Res, 213*(4), 493-506. doi:10.1007/s00221-011-2799-4

Sun, Y., Zatsiorsky, V. M., & Latash, M. L. (2011). Prehension of half-full and half-empty glasses: time and history effects on multi-digit coordination. *Exp Brain Res, 209*(4), 571-585. doi:10.1007/s00221-011-2590-6

Suzuki, M., & Yamazaki, Y. (2005). Velocity-based planning of rapid elbow movements expands the control scheme of the equilibrium point hypothesis. *J Comput Neurosci, 18*(2), 131-149. doi:10.1007/s10827-005-6555-2

Tillman, M., & Ambike, S. (2018a). Cue-induced changes in the stability of finger force-production tasks revealed by the uncontrolled manifold analysis. *J Neurophysiol, 119*(1), 21-32. doi:10.1152/jn.00519.2017

Tillman, M., & Ambike, S. (2018b). Expectation of movement generates contrasting changes in multifinger synergies in young and older adults. *Experimental Brain Research, 236*(10), 2765-2780. doi:10.1007/s00221-018-5333-0

Togo, S., & Imamizu, H. (2016). Anticipatory synergy adjustments reflect individual performance of feedforward force control. *Neurosci Lett, 632*, 192-198. doi:10.1016/j.neulet.2016.08.032

van Emmerik, R. E., & van Wegen, E. E. (2000). On Variability and Stability in Human Movement. *Journal of Applied Biomechanics, 16*, 394-406.

Vaz, D. V., Pinto, V. A., Junior, R. R. S., Mattos, D. J. S., & Mitra, S. (2019). Coordination in adults with neurological impairment - A systematic review of uncontrolled manifold studies. *Gait & Posture, 69*, 66-78. doi:10.1016/j.gaitpost.2019.01.003

Wang, Y., Asaka, T., Zatsiorsky, V. M., & Latash, M. L. (2006). Muscle synergies during voluntary body sway: combining across-trials and within-a-trial analyses. *Exp Brain Res, 174*(4), 679-693. doi:10.1007/s00221-006-0513-8

Zhou, T., Wu, Y. H., Bartsch, A., Cuadra, C., Zatsiorsky, V. M., & Latash, M. L. (2013). Anticipatory synergy adjustments: preparing a quick action in an unknown direction. *Exp Brain Res, 226*(4), 565-573. doi:10.1007/s00221-013-3469-5