RESEARCH ARTICLE

Expectation of movement generates contrasting changes in multifinger synergies in young and older adults

Mitchell Tillman[1] · Satyajit Ambike[1]

Abstract

Anticipatory synergy adjustment (ASA) is a feed-forward control mechanism that describes a continuous decrease in the stability of the current motor state beginning about 150 ms prior to a state transition. Recently, we described an associated phenomenon in which the system stability was reduced solely in response to a cue that generates an expectation of a state change, independent of whether the state change actually occurs. Both phenomena are of the same kind (stability reduction), but evoked by distinct antecedent conditions. Since, logically, cuing for movement must occur before the initiation of that movement, we named this new phenomenon 'Stage-1 ASA' and rechristened the well-established version 'Stage-2 ASA'. Here, we used a four-finger, isometric force production task to explore (1) the effect of healthy aging on Stage-1 ASA, and (2) if Stage-1 ASA resulted in a more rapid state change. Young and older adult participants produced 10% of their maximal force when they did not expect to produce any change in the force, and when they expected to change their force in an unknown direction and at an unknown time. In the latter condition, the 10% constant-force phase was followed by a choice reaction time task, in which the participants rapidly changed their force to follow a moving target presented on a computer monitor. Both young and older adults displayed equivalent amount of Stage-1 ASA. This was driven by a 42% reduction in finger-force variability in young adults. In contrast, it was driven by a 38% increase in finger-force variability in older adults. We speculate that the reduction in finger force variability assists the young adults in rapid state changes via two mechanisms: (1) the finger forces occupy a restricted set of states that are optimal for quick state transitions, and (2) lower variability during steady state translates into lower self-motion during state transition. Self-motion is the covariation between finger forces that fails to change the total force. The older adults are unable to adopt this strategy, and the increase in finger-force variability arises from (1) the adoption of an alternative strategy of destabilizing the attractor associated with the current state to facilitate state transitions and (2) the inability to coordinate multiple finger forces. Finally, older adults displayed longer reaction times than young adults, but a clear relation between Stage-1 ASA and consequent behavioral benefit in terms of reduced reaction time remained elusive.

Keywords Finger force · Isometric · Anticipatory synergy adjustment · Choice reaction time · Manual dexterity

Introduction

Manual function declines with healthy aging starting at age 60 years (Desrosiers et al. 1999; Cole et al. 2010), with some deficits appearing even in middle age (Lindberg et al. 2009; Dayanidhi and Valero-Cuevas 2014). Aging-induced changes are observed at the level of hand muscles (Enoka et al. 2003), individual fingers (Christou et al. 2003; Cole 2006), digit forces during the pinch grasp of an object (Cole 1991, 2006; Cole et al. 1999, 2010; Smith et al. 1999; Cole and Rotella 2001; Lindberg et al. 2009; Dayanidhi and Valero-Cuevas 2014), and multidigit grasping behaviors (Shinohara et al. 2003a, b, 2004; Shim et al. 2004). Loss in strength (Kallman et al. 1990), tactile acuity (Stevens and Patterson 1995), and the ability to coordinate multiple elements (muscles, joints, or digits) (Shinohara et al. 2003b, 2004; Park et al. 2011) contribute in complex ways to the decline in manual function. Furthermore, widespread neuronal death and reorganization (Seidler et al. 2010) leads to cognitive slowing (Birren 1974; Salthouse 1996; Hedden and Gabrieli 2004) which adds to the decline.

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One aspect of function loss is the slowing down of motor actions with aging. In particular, older adults (OA) take longer to switch between motor tasks (Morgan et al. 1994; Salthouse 1996; Hoff et al. 2015). Clinical measures of manual dexterity—the time taken to complete some version of a pick-and-place task—consistently report that OA take longer compared to young and middle-aged adults (Yancosek and Howell 2009; Marmon et al. 2011; Hamilton et al. 2017). There is evidence to suggest that coordination deficit plays an independent and critical role in the decline in task-switching speed (Morgan et al. 1994; Park et al. 2011).

The present paper focuses on the coordination issues that underlie the task-switching deficits in manual function in OA. In particular, we focus on the phenomenon of anticipatory synergy adjustment (ASA) in manual tasks and its well-known decline with aging (Olafsdottir et al. 2007a, b, 2008). Synergy is defined as a neural organization that ensures covariation in a redundant set of input variables such that values of a fewer number of important output (task) variables are stabilized (Latash 2008). Synergies are quantified using the uncontrolled manifold (UCM) method (Scholz and Schoner 1999), and it yields a synergy index (ΔV) that reflects the stability of performance, conceived as the reproducibility of task variables across multiple trials. Larger ΔV implies a stronger synergy and greater stability of the task variable (See "Methods"). ASA has been observed in manual tasks in which participants began a trial by producing a constant specified level of total force by pressing with their four fingertips (steady-state force production), and at a self-selected time, produced a rapid increase in the total force by pressing harder. In such trials, ΔV reduces in magnitude starting about 150 ms prior to the change in the total force (Olafsdottir et al. 2005; Shim et al. 2005; Kim et al. 2006). This drop in ΔV is called ASA, and it is a feed-forward control mechanism that progressively destabilizes the current state as the system transitions into a new state (Goodman and Latash 2006). It is a record of a continuous change in the coordination of the individual finger forces. The finger forces must covary negatively during steady-state force production to maintain the total force. In contrast, positive covariation between the individual finger forces will lead to effective changes in the total force. ASA, then, captures the transition from negative to positive covariation.

Aging affects this controlled destabilization during manual state transitions. The ~ 150 ms duration of the ASA is typical for young adults (YA) (Olafsdottir et al. 2005; Shim et al. 2005; Kim et al. 2006; Togo and Imamizu 2016). In contrast, OA show ASA in manual tasks that are reduced in duration (~ 50 ms) and magnitude (Olafsdottir et al. 2007a, 2008; Park et al. 2012). The reduced ASA in OA is a specific motor coordination deficit that may contribute to their slower task-switching performance (Morgan et al. 1994).

Recently, we hypothesized that just as the stability of the current state reduces prior to a self-paced action, stability would be reduced in uncertain situations when the actor expects state changes in the near future (Tillman and Ambike 2018). This is consistent with notions (1) that the CNS utilizes probabilistic models of the task to optimize performance (Kording and Wolpert 2004; Wolpert and Landy 2012), (2) of 'generalized motor preparation', or planning that occurs during the foreperiod of a choice reaction time task and leads to improved performance (smaller reaction time; lower error rate) (Niemi and Naatanen 1981; Jahanshahi et al. 1992; Brunia 1993), and (3) that reduction in the stability of a physical system will lead to an efficient (e.g., faster, or less energy consuming) transition from that stable state. Therefore, a biological system will likely exhibit a volitional reduction in the stability of its current motor state when it desires to move away from that state (Riccio and Stoffregen 1988; Riccio 1993; Bernstein 1996; Riley and Turvey 2002; Hasan 2005). The key departure from prior work was that the hypothesized stability change occurred in response to the expectation to move, independent of whether that movement actually occurred.

We found evidence in support of this hypothesis in a finger-force production study conducted with YA, and consequently, we described two stages of ASA (Tillman and Ambike 2018). We compared ΔV for trials in which no force change was expected to ΔV for trials in which the participant expected to produce a force change (cued trials), and observed a significant decrease. This was in stark contrast to ASA observed earlier which report the reduction in ΔV measured just prior to initiation of a state change relative to the ΔV measured earlier (about 500 ms) in the same set of trials. Therefore, it was not surprising that this earlier version of ASA appeared only when the participant self-selected the time and nature of the upcoming state change, and disappeared in reaction time tasks or in tasks where external perturbations are administered unexpectedly by an experimenter (Olafsdottir et al. 2005, 2008; Shim et al. 2006; Zhou et al. 2013). Since cuing must occur before task execution, we called the new feed-forward synergy adjustment Stage-1 ASA, and renamed the older version Stage-2 ASA.

The goals of this paper are (1) to investigate the effect of aging on Stage-1 ASA, and (2) to explore if Stage-1 ASA results in faster reaction times. Participants in this study performed four-finger, isometric force production tasks with visual feedback on the total force (F_T) produced by the fingers of the dominant hand. Participants produced the same constant F_T in three conditions: (a) when they expected the target force (F_{target}) to be stationary, (b) when they expected F_{target} (and, therefore, F_T) to change in the near future, and (c) when they expected faster changes in F_{target} and F_T in the near future. ΔV was computed in the stable condition (a) and in the two dexterous conditions (b and c). The uncertainty

in the timing of the upcoming force change in the dexterous conditions ensures that any change in ΔV observed between the stable and dexterous tasks can be unambiguously classified as Stage-1 ASA. Furthermore, the reaction time (RT) immediately following the constant-F_T periods for the dexterous tasks, when F_{target} began to move, was also computed.

Similar to the findings regarding Stage-2 ASA, we hypothesize that Stage-1 ASA will have a smaller magnitude in OA compared to YA (H1). Furthermore, the slow and fast dexterous tasks were designed to establish that Stage-1 ASA is a graded process, i.e., the stability of the current state is lowered in response to the estimated difficulty of the impending movement. This is consistent with the view that the CNS utilizes probabilistic models of the task to optimize performance (Kording and Wolpert 2004; Wolpert and Landy 2012). Therefore, if such a model generates an expectation of a faster required response, we hypothesize that ΔV will be reduced more (i.e., greater Stage-1 ASA) for the fast dexterous task for both age groups (H2). Consistent with previous literature, we hypothesize that RT will be longer for OA (H3). Finally, we have argued that a less stable system is more agile (Bernstein 1996; Hasan 2005). Therefore, the greater Stage-1 ASA for the fast dexterous task will lead to a reduction in the RT of the ensuing motor action. Therefore, the RT for the fast dexterous task will be shorter than that for the slow dexterous task (H4).

Methods

Participants

25 young [19 female; age $= 20.4 \pm 2.6$ years; weight $= 65.4 \pm 13.3$ kg; height $= 1.68 \pm 0.08$ m; (mean $\pm$ standard deviation)] and 18 older [12 female; age $= 70.4 \pm 6.7$ years; weight $= 76.6 \pm 21.0$ kg; height $= 1.67 \pm 0.09$ m] individuals participated in the study. 39 participants were right-hand dominant and 4 participants were left-hand dominant by self-report, and no participant had any history of neurological issues or musculoskeletal discomfort or injury in the upper arm. All participants had normal or corrected to normal vision. All participants provided informed consent in accordance with the procedures approved by the Institutional Review Board of Purdue University.

Equipment and procedures

Participants were seated in a chair and placed the fingers of the dominant hand facing downward on four separate force sensors on a table in front of them (Nano 17, ATI Industrial Automation, Garner, NC), as shown in Fig. 1a. The signals from the transducers were collected by The MotionMonitor

Fig. 1 Experimental setup (**a**). Participant's four fingers of the dominant hand are on four force sensors. Feedback (**b**). A computer screen displayed the total finger force as a cross. The cross moved upward when the total finger force increased, and vice versa. Various total force target(s) were displayed as square icon(s). Feedback for the rapid force-oscillation tasks (**c**). The computer screen displayed two square targets at 5 and 15% MVC, along with the participant's current total force. A typical total force target trajectory for the dexterous tasks (**d**). Each trajectory contained one portion of 10% MVC that lasted at least 4 s. This portion was embedded in a longer trajectory composed of linear ramps connecting varying durations and magnitudes of constant force
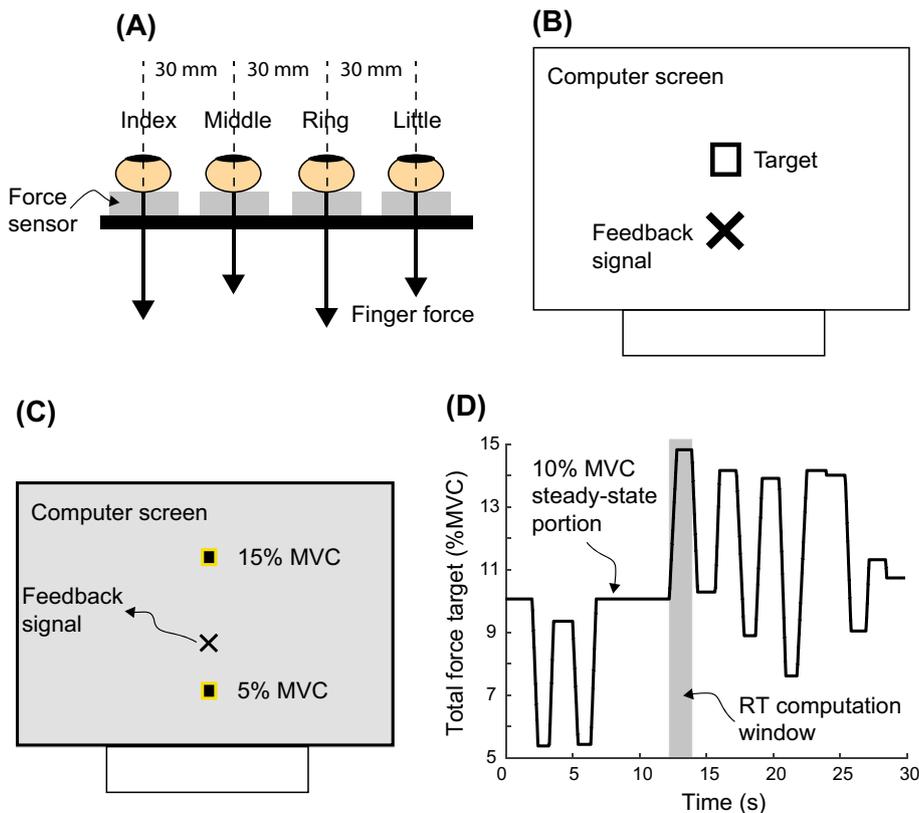
software (Innovative Sports Training Inc.) and sampled at 1000 Hz. Participants adjusted the anterior–posterior position of each sensor individually to suit their comfort. The medial–lateral distances between the sensor centers were fixed at 30 mm. The sensors were zeroed with the fingers resting on the sensors and with the muscles relaxed, so that the weight of the fingers was excluded from the sensor readings. For all experimental 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 (Fig. 1b). The cross moved only vertically, upward if the participant increased F_T, and vice versa.

The participants first performed maximum voluntary contraction (MVC) trials in which their goal was to press downward as hard as possible with all four fingers and produce the maximal possible total force while maintaining an upright, stationary body posture. They performed three MVC trials, each lasting 7 s, with 1 min rest intervals between trials. The average of the three F_T maxima was used to scale the experimental tasks described below.

During the next task, two square targets the same size as the feedback cursor were displayed on the central vertical axis of the computer screen at locations corresponding to 5 and 15% of the participant's MVC, respectively (Fig. 1c). The participant generated force fluctuations between the targets with the highest possible frequency, and the maximum absolute force rate was recorded. These values were used to ensure that the tracking tasks described below required force production rates that were significantly lower than the participants' maximal abilities. This force oscillation task lasted 7 s, and the participants repeated the task three times with 30-s rests between trials.

Next, participants completed three experimental tasks. The stable task consisted of a yellow target box that appeared at the 10% MVC location and remained stationary for 7 s. The participants were instructed to generate force with all four fingers and maintain their total force cursor inside the target box. They were informed that the target would remain fixed during each trial. Next, for the slow and fast dexterous tasks, the participant varied F_T and tracked the square target as it moved in the vertical direction. Participants were told that the target will move, but they did not know the time course of the target. A typical dexterous task trajectory, depicted in Fig. 1d, lasted 30 s. The trajectories were generated randomly within the freedom allowed by the following constraints. Each trajectory is 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. Target force magnitude was between 5 and 15% MVC, and the ramp slopes were well within the participants' maximal abilities (estimated from pilot data and the oscillation task). Each trajectory contained one extended portion of 10% MVC target force. Across trials, the time of initiation of this portion was randomly distributed between 5 s after the trial commenced, and up to about 24 s into the trial. The duration of this portion varied between 4.04 and 5.5 s. The trajectories produced similar impulse.

Eight different target force trajectories were composed for the slow and fast dexterous tasks, each. The slow and fast dexterous task trajectories contained 15–18 jumps and 30–38 jumps in the target, respectively. YA and OA tracked the same set of dexterous task trajectories. Therefore, across trials, the average time of occurrence of the 10% MVC portion was identical for all participants. Each of the eight trajectories was presented twice to obtain a set of 16 trials for the slow and the fast dexterous tasks, and the stable task was also repeated 16 times. The number of trials for each task was chosen based on the typical number of trials used in most UCM analyses of finger-force production studies (Olafsdottir et al. 2005; Zhou et al. 2013). The task types were block randomized across participants, and the trial sequences were randomized within each block for the slow and the fast dexterous tasks. To gain familiarity with the dexterous tasks, participants performed ten 15 s trials similar to the dexterous tasks. The trajectories used for these practice trials were different from those used for the experimental trials.

On average, the target profiles for the slow and fast dexterous tasks produced the same impulse (slow dexterous profiles = 293.5 ± 18.9% MVC-s; fast dexterous profiles = 293.5 ± 7.2% MVCs; $t_{(7)} = 0.001$; $p = 0.999$). However, the target moved faster for the fast dexterous task. Across the eight profiles for this task type, the maximum absolute force rate was 102.58 ± 92.1% MVC/s, and the power concentrated within the 0–2 Hz band was 65.32 ± 5.14%. In contrast, across the target profiles for the slow dexterous task, the maximum absolute force rate was 20.56 ± 10.7% MVC/s, and the power concentrated within the 0–2 Hz frequency band was 81.75 ± 6.08%. Compared to the trajectories for slow dexterous task, the trajectories for the fast dexterous task were designed to elicit faster responses during the entire trial and expectation of faster responses during the 10% MVC steady-force production portion of these trials.

To limit fatigue, rest was enforced between all repetitions. 2 min breaks were enforced after each kind of task was performed: MVC trials, the rapid force-oscillation trials, the practice trials, and the three kinds of experimental trials. 30 s breaks were taken after each trial in the practice set, 15 s breaks after each trial of the stable task, and 30 s breaks after each trial of the slow and fast dexterous tasks. The entire experiment took approximately 90 min, and none of the participants reported any fatigue during this study.

Note that during the extended steady-force period, the task demands of the dexterous tasks are identical to those of

the stable task. Since each dexterous trial contained multiple instances of steady force, the participants were unaware that each trial contained the one instance of steady force that lasted longer that was the focus of the study. Also note that during this steady-force period, the participants expected to change F_T without knowing the timing or direction of that change, similar to a typical choice reaction time test.

Data analysis

MATLAB programs were written for data analysis (R2017b, 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. The last 4 s of data from the stable task (Fig. 2a) were isolated. For the slow and fast dexterous tasks, the finger-force data from the first 4 s of constant target force portion of each trial were isolated (Fig. 2b). Note that the local task demands for all three task types are identical ($F_T = 10\%$ MVC) for the constant-force production portion, but the participant's expectations of future movement have been modulated across task type. These 4 s finger-force data were utilized for UCM analysis.

## The uncontrolled manifold (UCM) analysis

The UCM analysis (Scholz and Schoner 1999; Latash et al. 2002) is a tool used to quantify the variability structure exhibited in the repeated execution of a task using redundant sets of inputs, and then to draw inferences about the stability of the task variables. For the present study, the task is described by the equation $F_T = \Sigma(F_i)$; $i = $ [index, middle, ring, little]. Four fingers contribute to the production of a single output (task) variable (F_T), and therefore, the task is redundant. For each time instant, $t = t^*$, the individual finger forces across the 16 repetitions were isolated. The mean-subtracted individual finger forces (i.e., the input variables) were projected onto two orthogonal manifolds. The first manifold—called the uncontrolled manifold (UCM)—is the

null space of the Jacobian relating small changes in the input variables (F_i) to small changes in the task variable (F_T). The Jacobian is a list of the partial derivatives of the task function with respect to the input variables. Here, $J = [1\ 1\ 1\ 1]$. The null space of this Jacobian, i.e., the UCM, is a three-dimensional linear space in the four-dimensional space of the input variables. Variance within the UCM has no influence on F_T. In contrast, the second manifold (ORT) is orthogonal to the UCM, and variance within this manifold influences the F_T value. The dimension of ORT equals the number of constraints on the input variables (one in the present case), and $\dim(\text{UCM}) + \dim(\text{ORT}) = $ number of input variables. The individual finger forces from the 16 trials are projected onto these manifolds, and the variances of the projections—called $V_{\text{UCM}}(t^*)$ and $V_{\text{ORT}}(t^*)$—are computed. Next, the synergy index for that time point $\Delta V(t^*)$ is computed as the relative amount of V_{UCM} in the total variance, V_{TOT}, normalized by the dimensions of the spaces in which the variances are computed: $\Delta V(t^*) = (V_{\text{UCM}}(t^*)/3 - V_{\text{ORT}}(t^*))/(V_{\text{TOT}}(t^*)/4)$. A positive ΔV shows the presence of appropriate covariation between the inputs that stabilizes the output variable, a negative ΔV shows that the input variables are coordinated to change (i.e., destabilize) the task variable, and $\Delta V = 0$ implies that there is no task-specific coordination. This also implies that higher positive ΔV values imply greater stabilization of the task variable (F_T). The synergy index is bounded: $-4 \leq \Delta V \leq 4/3$. Therefore, for statistical analyses, the ΔV values were transformed using the Fisher z-transform adapted for the asymmetrical bounds (Zhou et al. 2013):

$$\Delta V_z(t^*) = 0.5 \log\left(\frac{4 + \Delta V(t^*)}{1.33 - \Delta V(t^*)}\right).$$

Note that $\Delta V = 0$ implies $\Delta V_z = 0.5493$. Therefore, a ΔV_z value greater than 0.5493 indicates the presence of a synergy that stabilizes F_T. These computations were repeated for each time instant within the 4-s window, thus yielding the curves $V_{\text{UCM}}(t)$, $V_{\text{ORT}}(t)$, $\Delta V(t)$, and $\Delta V_z(t)$, for each task type.

Fig. 2 Representative response for the stable (**a**) and the slow dexterous (**b**) tasks. Each plot shows 16 separate trials. The last 4 s of the stable task (gray rectangle in **a**) were isolated and used for the UCM analysis. The trials for the slow dexterous trials were time aligned so that the extended 10% MVC constant target force portions began at the same instant. The first 4 s of the participant's responses (gray rectangle in **b**) were used for the UCM analysis
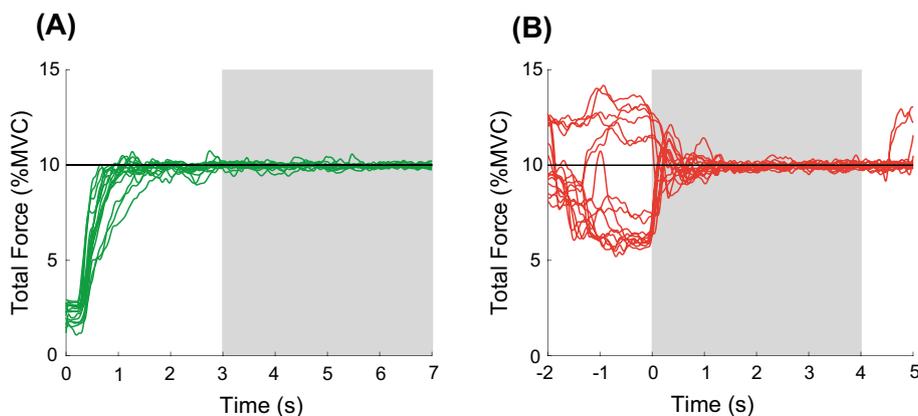
Statistics

Data are presented in "Results" as means and standard errors (SE), unless mentioned otherwise. To characterize performance of the slow and fast dexterous tasks, the mean absolute force rate ($MAFR = mean(|d(F_T)/dt|)$) was used to quantify the speed of total force production during each trial of each dexterous task. Next, the root-mean-squared error (RMSE) was utilized to quantify the performance accuracy of each trial of each dexterous task. These metrics were computed using the entire 30 s responses. The MAFR and RMSE for a participant was the mean of those metrics computed for all 16 trials for each dexterous condition. Both metrics were subjected to separate two-way, repeated measures mixed ANOVAs with within-subject factor Task Type (two levels) and between-subjects factor Age (two levels).

V_{UCM}, V_{ORT}, normalized by the dimension of the corresponding manifold [dim(UCM) = 3; dim(ORT) = 1], and ΔV_z values for the last 1 s of the 4 s analysis window were averaged for each participant. We chose the last second to estimate these variables because (1) previous work indicated that the dynamics in the time profiles of these variables die out in about 2 s (Tillman and Ambike 2018), making comparisons across all three task types valid, and (2) this state of the system is most likely to influence the reaction times (RT) computed when the target resumed its vertical movement (Fig. 1d). The RT was computed for each dexterous task as the time between the first instant that the target resumed its movement following the prolonged static phase and the instant that F_T changed by more than 1.5 times its standard deviation computed in a 1 s moving window (Fig. 1d). The RT for a participant is the mean of the RT values obtained for the 16 trials for each dexterous condition. The UCM variables and RT were subjected to separate two-way, repeated measures mixed ANOVA with within-subjects factor Task Type (three levels for UCM variables, and two levels for RT), and between-subject factor Age (two levels). The V_{UCM} and V_{ORT} data were log transformed to meet the normality requirement before conducting the ANOVA. However, non-transformed values are presented in the "Results" section. ANOVAs on the variance components were conducted to explore the mechanisms employed to achieve Stage-1 ASA. Changes in ΔV_z are driven by changes in the two variance components. For example, a drop in ΔV_z can occur due to a decrease in V_{UCM}, an increase in V_{ORT}, or both.

Mauchly's sphericity tests were performed to verify the validity of using repeated measures ANOVA. The Greenhouse–Geisser adjustment to the degrees of freedom was applied whenever departure from sphericity was observed. Significant effects of ANOVA were further explored using pairwise comparisons with Bonferroni corrections. All possible pair-wise contrasts were conducted.

Finally, we regressed the RT against the frequency with maximum power obtained from the Fourier transform of the total force trace in the rapid force oscillation task. Data were pooled across *Age*. A lack of correlation or weak correlation will indicate that RT was influenced by factors other than the participants' maximal force production abilities.

All statistics were performed using an α-level of 0.05 and with SPSS statistical software (IBM SPSS Statistics, Version 24).

Results

Maximum voluntary contractions (MVC tasks)

The four-finger MVC values were $MVC_{YA} = 69.2 \pm 5.9$ N and $MVC_{OA} = 69.9 \pm 6.2$ N, with no statistically detectable difference between the two age groups (independent-sample *t* test; $F_{(41)} = 0.27$; $p = 0.94$). This result is consistent with earlier reports (Olafsdottir et al. 2007a, b), although (Shinohara et al. 2003a, 2004) report lower four-finger MVC values for OA compared to YA.

Performance of the rapid force oscillation tasks

Recall that the participants produced rapid oscillations of the total force between 5 and 15% MVC targets—the extreme force values used to compose the slow and fast dexterous tasks. The purpose of this task was to quantify the ability to rapidly change finger force. Fourier analysis of the total force time series indicated that YA produced force oscillations at 4.3 ± 0.1 Hz (frequency with maximum power) and OA produced oscillations at 3.5 ± 0.2 Hz. In contrast to the participants' abilities, over 60% of the power in the target profiles was concentrated in the 0–2 Hz band. Similarly, the maximum absolute force rates were 379.59 ± 19.6 and $346.43 \pm 52.9\%$ MVC/s for the YA and OA, respectively. These are significantly greater than the maximum force rates of the target force profiles ($102.58 \pm 32.6\%$ MVC/s for the fast dexterous task). This indicates that the designed target force profiles for the slow and fast dexterous tasks were well within the force production abilities of the participants. Therefore, it is unlikely that any differences discovered in this study can be attributed entirely to the participants' finger-force production limits.

Performance of the stable and slow and fast dexterous tasks

Figure 2a depicts the performance of the stable task from a representative participant. The participants require between 1 and 2 s to achieve the target (10% MVC), and then F_T remains stable although with some fluctuations

about the target. Figure 2b depicts the performance of the slow dexterous tasks from a representative participant. These data are aligned with respect to the start of the 10% MVC portions that last at least 4 s.

Recall that the mean of the absolute force rate (MAFR) was used to characterize the speed of total force production during the dexterous tasks. The fast dexterous task elicited higher force rates compared to the slow dexterous task, and YA and OA produced similar force rates (Fig. 3a). The two-way, *Age* x *Task Type* ANOVA revealed a main effect of *Task Type* [$F_{(1,41)} = 115.14$; $p < 0.001$; partial $\eta^2 = 0.74$; $\mathrm{MAFR_{SlowDexterous}}$ (3.0 ± 0.2 N/s) $<$ MAFR$_{\mathrm{FastDexterous}}$ (4.0 ± 0.2 N/s)]. Furthermore, the increase in the MAFR from the slow to fast dexterous tasks was more drastic for the YA, as reflected by a significant *Task Type* x *Age* interaction [$F_{(1,41)} = 7.05$; $p = 0.011$; partial $\eta^2 = 0.14$]. The effect of *Age* was not significant ($p = 0.126$).

The root-mean-squared error (RMSE) was utilized to quantify the performance of the slow and fast dexterous tasks. RMSE was greater for the fast dexterous task [*Task Type* main effect, $F_{(1,41)} = 230.11$; $p < 0.001$; partial $\eta^2 = 0.85$; $\mathrm{RMSE_{FastDexterous}}$ (1.6 ± 0.09 N) $>$ $\mathrm{RMSE_{SlowDexterous}}$ (1.1 ± 0.06 N)]. The effect of *Age* was not significant ($p = 0.202$), and neither was the interaction ($p = 0.91$). (Fig. 3b).

The MAFR and RMSE were computed using the entire total-force trajectories for the two dexterous tasks. In contrast, the performance over just the stable portions of all three tasks was accurate for both age groups. We computed the mean total force and absolute mean error in the same 1 s window over which the UCM variables were averaged and subjected to statistical analysis. The mean total force was within 0.2% MVC units of the 10% MVC target, and the absolute mean error was less than 1.3% MVC (or 0.9 N).

## Changes in synergy index and the variance components

Figure 4 shows the z-transformed synergy index for the OA (Fig. 4a) and the YA (Fig. 4b). The figure 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 for the dexterous tasks. This reflects convergence to the stationary target force (10% MVC) from various earlier target values (cf. Fig. 2b). As this convergence proceeds, the synergy index increases and then settles to a steady value at the end of about 3 s. However, the ΔV_z values for the dexterous tasks never reach the values for the stable task.

These trajectories show that OA display Stage-1 ASA, similar to YA. That is, there is a drop in ΔV_z for the dexterous tasks compared to the steady task in both age groups. Recall that the ΔV_z values in the last 1 s window (depicted in Fig. 4) were averaged and subjected to a two-way, mixed *Age* $\times$ *Task Type* ANOVA. Figure 5a shows the averaged ΔV_z values. This analysis yielded a significant *Task Type* effect ($F_{(2,82)} = 29.597$; $p < 0.01$; partial $\eta^2 = 0.419$). Post hoc comparisons indicated that $\Delta V_{z\text{-Stable}}$ (2.66 ± 0.06) $>$ $\Delta V_{z\text{-SlowDexterous}}$ (2.28 ± 0.08), and $\Delta V_{z\text{-Stable}} > \Delta V_{z\text{-FastDexterous}}$ (2.26 ± 0.08). However, there was no *Age* effect ($p = 0.878$). Furthermore, the degree of synergy adjustment across *Task Type* was not consistent across *Age*: ΔV_z for the stable and fast dexterous tasks is larger for the OA compared to the YA, but this relation is reversed for the slow dexterous task. This was reflected in a significant *Task Type* x *Age* interaction ($F_{(2,82)} = 5.07$; $p = 0.0084$; partial $\eta^2 = 0.11$).

Fig. 3 The mean absolute force rate (**a**) and the root-mean-square error (**b**) of the F_T trace during the fast and slow dexterous tasks for both age groups. The data show mean and standard errors across repetitions and subjects
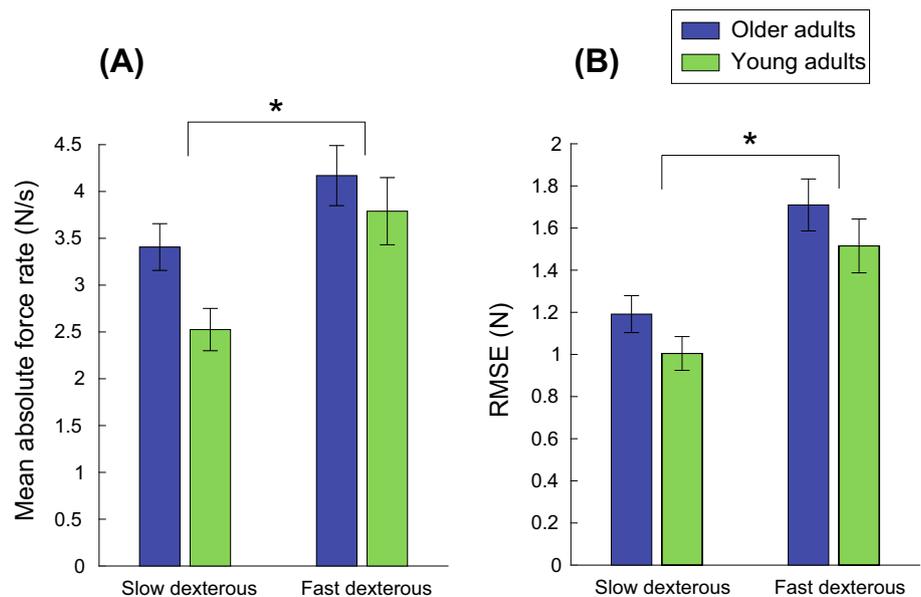
Fig. 4 Across-participant mean ± SE of the z-transformed synergy index for the older (**a**) and young adults (**b**) are plotted against time. ΔV_z > 0.5493 indicates presence of synergy stabilizing total force F_T
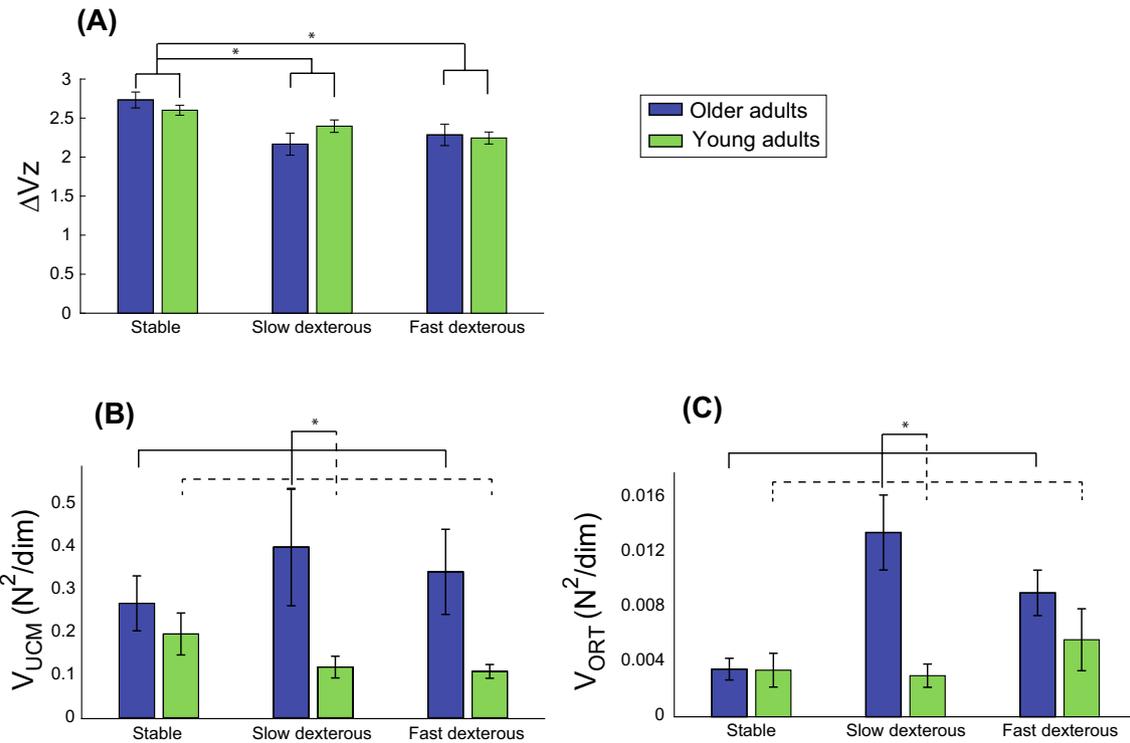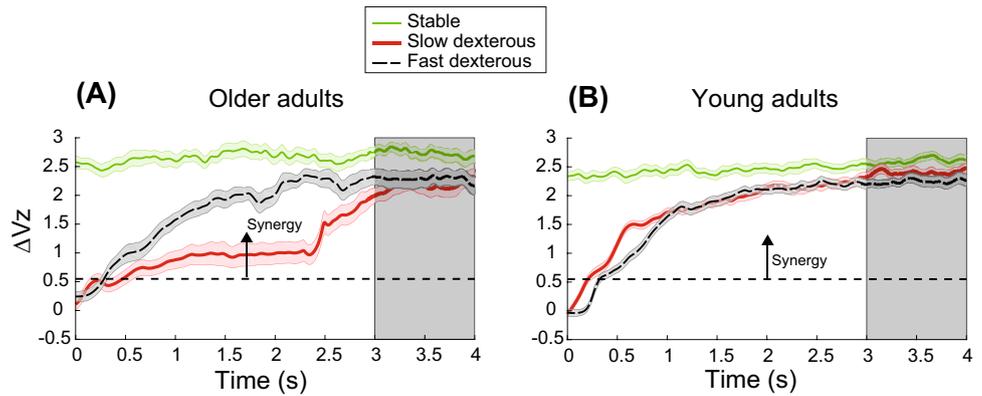
Fig. 5 Mean ± SE of the z-transformed synergy index (**a**), V_{UCM} (**b**), and V_{ORT} (**c**) averaged over the last 1 s of data within the 4 s analysis window for all three task types and both age groups. V_{UCM} and V_{ORT} are normalized by the dimensions of the corresponding manifolds (i.e., 3 and 1, respectively)

Changes in the two variance components V_{UCM} and V_{ORT} yield changes in ΔV_z. A drop in ΔV_z can occur due to a decrease in V_{UCM}, an increase in V_{ORT}, or both. Figure 6 shows the time courses of the variance components (normalized by the dimension of the corresponding manifold) for both age groups. Note the rapid decline in V_{ORT} traces (Fig. 6c, d). V_{UCM} traces also indicate some decline in the initial stages (Fig. 6a, b). These changes are consistent with the convergence of the total force F_T to the stationary target (cf. Fig. 2b), and the corresponding increase in

ΔV_z (Fig. 4). All these dynamics dissipate after about 3 s for both age groups.

Similar to the synergy index trajectories, the V_{UCM} and V_{ORT} values in the last 1 s window were averaged and subjected to a two-way, mixed *Age* x *Task Type* ANOVA. The averaged values are provided in Fig. 5b, c. OA display larger V_{UCM} compared to YA across all Task Types. There is a significant *Age* effect ($F_{(1,41)} = 6.79$; $p = 0.013$; partial $\eta^2 = 0.14$); V_{UCM-OA} (0.33 ± 0.07 N^2/dim) > V_{UCM-YA} (0.14 ± 0.06 N^2/dim). Furthermore, YA show a decline in

Fig. 6 Across-participant mean $\pm$ SE of the V_{UCM} (**a, b**) and V_{ORT} (**c, d**) traces for the older and younger adults. V_{UCM} and V_{ORT} are normalized by the dimensions of the corresponding manifolds (i.e., 3 and 1, respectively)
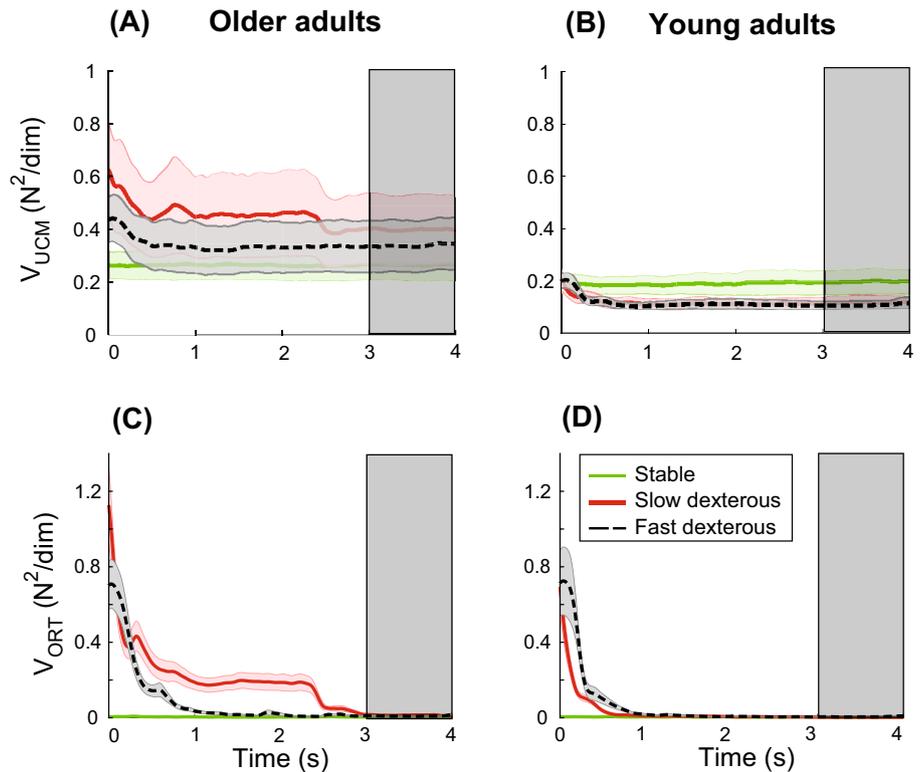

V_{UCM} for the dexterous tasks compared to the stable task. In contrast, OA show an increase in V_{UCM} for the dexterous tasks compared to the stable task (see Figs. 5b, 6a, b). This is reflected in a significant *Task Type* x *Age* interaction ($F_{(2,82)} = 3.69$; $p = 0.03$; partial $\eta^2 = 0.082$).

OA display larger V_{ORT} compared to YA. Most of the increase in V_{ORT} for the OA comes from the dexterous tasks. There is a significant *Age* effect ($F_{(1,41)} = 10.13$; $p = 0.003$; partial $\eta^2 = 0.2$); V_{ORT-OA} (0.009 ± 0.002 N^2/dim) $> V_{ORT-YA}$ (0.004 ± 0.001 N^2/dim), and a significant *Task Type* effect ($F_{(2,82)} = 3.82$; $p = 0.026$; partial $\eta^2 = 0.09$). V_{ORT} increases for the dexterous tasks: $V_{ORT-SlowDexterous}$ (0.008 ± 0.001 N^2/dim) $> V_{ORT-Stable}$ (0.003 ± 0.001 N^2/dim); and $V_{ORT-FastDexterous}$ (0.007 ± 0.001 N^2/dim) $> V_{ORT-Stable}$. Furthermore, YA manage to maintain V_{ORT} levels for the dexterous tasks similar to those for the stable task, with a modest increase in V_{ORT} for the fast dexterous task. In contrast, OA show a significant increase in V_{ORT} for the slow dexterous task, and then a partial recovery in V_{ORT} for the fast dexterous task. This is reflected in a significant *Task Type* x *Age* interaction ($F_{(2,82)} = 27.08$; $p < 0.001$; partial $\eta^2 = 0.4$) (See Figs. 5c, 6c, d).

Reaction time (RT)

OA are slower to resume dynamic tracking compared to YA, and the RT was greater for the fast dexterous task (Fig. 7). The two-way, mixed ANOVA revealed a significant effect
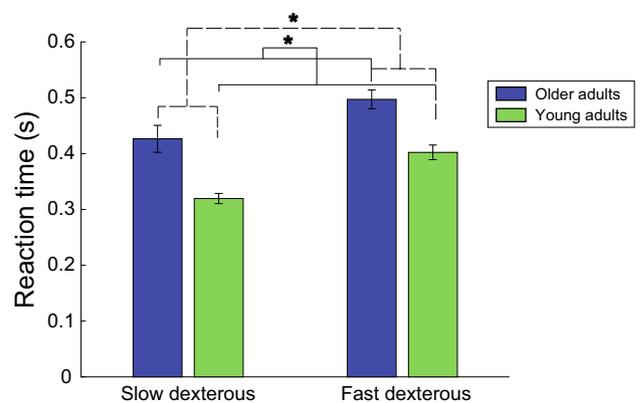
Fig. 7 Mean $\pm$ SE of the reaction time computed immediately following the portion of steady-force production for the slow and fast dexterous tasks and for both age groups

of *Age* ($F_{(1,41)} = 52.59$; $p < 0.001$; partial $\eta^2 = 0.53$); RT$_{OA}$ (0.49 ± 0.01 s) $>$ RT$_{YA}$ (0.37 ± 0.01 s), and a significant effect of *Task Type*: ($F_{(1,41)} = 25.11$; $p < 0.001$; partial $\eta^2 = 0.38$); RT$_{SlowDexterous}$ (0.40 ± 0.01 s) $<$ RT$_{FastDexterous}$ (0.45 ± 0.01 s).

We separately regressed the RT for the slow and the fast dexterous tasks against maximum oscillation frequency obtained from the rapid force oscillation task. Data were pooled across *Age*. Linear regressions yielded significant slopes (slow dexterous task: -0.05 s/Hz; fast dexterous task: -0.03 s/Hz), with low R^2 values (slow dexterous task: 0.22;

fast dexterous task: 0.13). Thus, the reduction in the ability to produce rapid force changes explains only a portion of the variance in RT, meaning that other factors also influence RT.

Discussion

Both hypotheses regarding the stability (H1 and H2) were not supported by the data. Consistent with earlier findings pertaining to Stage-2 ASA (Olafsdottir et al. 2007a), we hypothesized that older adults (OA) will exhibit lower Stage-1 ASA than the young adults (YA) (H1), and that the stability would be reduced more for the fast dexterous task compared to the slow dexterous task (H2). We observed that ΔV_z (our measure for task stability) was lower for the dexterous task compared to the stable task in both YA and OA. However, we found that YA and OA exhibit similar reduction in ΔV_z (Figs. 4a, b, 5a). Across the dexterous task types, YA and OA show the opposite trends in ΔV_z (Fig. 5a). Overall, there is no significant difference in ΔV_z between the slow and fast dexterous tasks, which implies that the change in ΔV_z relative to the stable task is similar for both dexterous tasks.

Our first hypothesis on the reaction time (RT) was supported by the data. The RT was indeed longer for OA by about 120 ms compared to the YA (H3) (Fig. 7). Finally, RT for the fast dexterous task was larger than that for the slow dexterous task (~ 50 ms), which contradicts our last hypothesis (H4).

We also explored the changes in variance components (V_{UCM} and V_{ORT}) across *Age* and *Task Type* to understand how Stage-1 ASA was produced. Stage-1 ASA (i.e., reduction in ΔV_z) can occur due to a drop in V_{UCM}, an increase in V_{ORT}, or both those changes. We found that OA and YA use contrasting mechanisms to achieve similar amounts of reduction in ΔV_z for the dexterous tasks. YA reduce ΔV_z by decreasing V_{UCM} (~ 42%) and maintaining V_{ORT}. OA reduce ΔV_z by increase in V_{UCM} (~ 38%) and in V_{ORT} (~ 267%) (Fig. 5b, c). That is, when cued to execute a RT task, YA reduce the total variability in the finger forces. They maintain the accuracy of performance of the current task, and simultaneously, the sharing of the total force between the individual fingers becomes more consistent. In contrast, OA become more variable. The performance of the current task suffers, and their sharing of the total force between the individual fingers becomes more variable.

We discuss these findings and other relevant issues below.

Age differences in the tracking performance of the dexterous tasks

Analysis of the total force (F_T) generated by the participants indicated that (1) the mean absolute force rate (MAFR) and the RMSE were greater for the fast dexterous task compared to the slow dexterous task (Fig. 3), and (2) OA had longer RT compared to YA for the dexterous tasks (Fig. 7). The larger MAFR for the fast dexterous task indicates that the target trajectories elicited faster responses from both age groups. The larger RMSE for the fast dexterous task is a consequence of the target trajectories and the participants' responses.

The longer RT for OA is consistent with earlier findings (de Bruin et al. 2016), and it has previously been related to changes in the central and the peripheral neuromuscular systems. For example, age-related atrophy in the motor cortical regions and the corpus callosum, degeneration of the dopaminergic system may relate to decline in movement speed and manual dexterity (Seidler et al. 2010). In the periphery, size of motor units increases with age (due to death of α−motoneurons), and this suggests that OA are less able to produce small changes in force (Enoka 2015). Furthermore, aging leads to reduction in the twitch contraction speed of muscle that results from increased proportions of Type-I muscle fibers (Lexell 1997), and mal-adaptations in the excitation–contraction coupling (Clark and Manini 2008). Aging also leads to increased time for processing information (Birren 1974; Salthouse 1996), which manifests as cognitive slowing and contributes to longer RT.

We also observed a weak but significant relation between RT and the ability to produce rapid force oscillations. Changes in force-oscillation ability likely stem from the aging-related neuromuscular changes. However, the variance in RT that remains unexplained by this regressor could be attributed to aging-induced changes in control mechanisms. However, we were unable to demonstrate a clear relation between RT and the specific feed-forward control mechanism—Stage-1 ASA. We discuss this point in the "Limitations" section.

Age effects on the two stages of anticipatory synergy adjustment (ASA)

Over the past decade, Latash and colleagues have identified ASA [reviewed in (Latash and Huang 2015)] as a feed-forward adjustment of the stability of motor behavior prior to a planned state change. ASA has been observed in manual tasks (Olafsdottir et al. 2005; Kim et al. 2006; Shim et al. 2006; Park et al. 2012; Togo and Imamizu 2016; Park and Xu 2017) and postural tasks involving quick shifts of the center of pressure (Wang et al. 2006; Klous et al. 2011; Krishnan et al. 2011; Piscitelli et al. 2017). A common feature of these studies is that the participants were able to plan the change in their motor state. If the task variable first changed at time T, and the ΔV_z time trace deviated from its steady value dT seconds prior to T, then the magnitude of ASA was defined as the change$[\Delta V_z(T-dT) - \Delta V_z(T)]$.

Our recent work was the first to examine changes in ΔV_z due to a cue that generated an expectation to move, but did not allow the construction of an unambiguous movement plan (Tillman and Ambike 2018). That work led us to propose the two stages of ASA: Stage-1 ASA is the change in ΔV_z that is observed solely in response to such a cue. Stage-2 ASA occurs later, if the expected movement is performed at a self-selected time. These stages are depicted in Fig. 8. When the participant expects no change in the steady-state behavior, the stability of the current state is high, irrespective of age group. This is depicted as the shaded ellipses in Fig. 8a, b, and it is reflected in the relations $V_{UCM} > V_{ORT}$, and $\Delta V > 0$. For YA, Stage-1 ASA is the reduction of V_{UCM} and invariance of V_{ORT} in response to a movement cue (Fig. 8b). For OA, it is the increase in both V_{UCM} and V_{ORT} (Fig. 8a). For both age groups, ΔV is lower than before, but still greater than zero, indicating that the current state has lower stability, but it is not unstable. If this state is followed by self-paced movement, Stage-2 ASA will be observed, during which V_{ORT} increases, and V_{UCM} may decrease or increase (Klous et al. 2011; Arpinar-Avsar et al. 2013; Jo et al. 2017). ΔV decreases further (ellipse with the dashed edges in Fig. 8), eventually becomes negative, the system transitions from being stable to unstable, and the output variable begins to change.
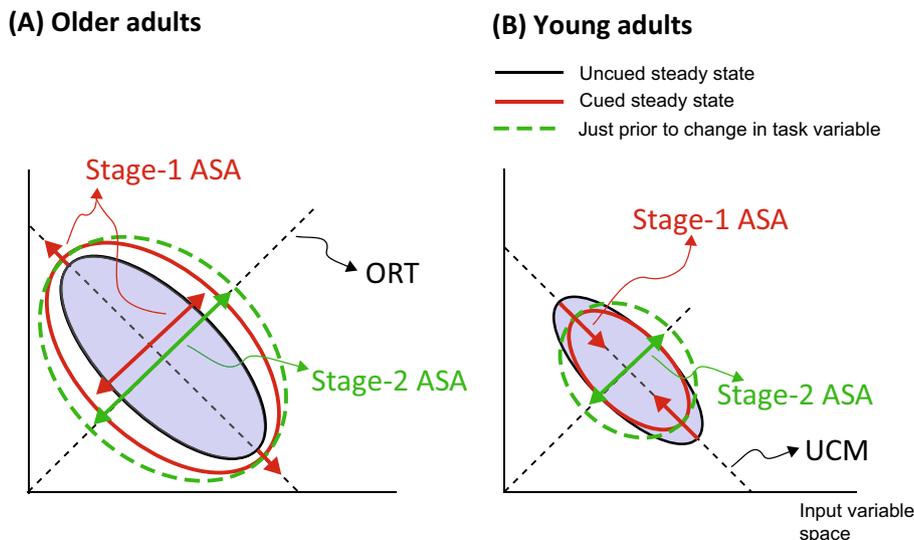
The distinct mechanisms identified for the two stages of ASA in this work (Fig. 8) may be specific to the task that we investigated. However, other key differences between Stage-1 and Stage-2 ASA may be less dependent on the behavior type. First, the two adjustments occur in a specific order: logically, cuing for movement occurs before the movement, so Stage-1 ASA must occur before Stage-2 ASA. Second, the two stages are triggered by different environmental events: Stage-1 ASA is a response to an external cue, and Stage-2 ASA occurs when the individual initiates

the process of changing behavior. Third, the necessary conditions for observing the two stages are different. Stage-1 ASA occurs if a participant is cued for movement, but it does not depend on whether the movement actually occurs, or, if it does occur, whether it is a reaction time or a self-paced movement. Indeed, the dexterous tasks in this study resemble the typical choice reaction time task. In contrast, Stage-2 ASA is observed prior to a self-paced movement and disappear in reaction time tasks (Olafsdottir et al. 2005; Shim et al. 2006; Zhou et al. 2013). Fourth, the duration of the two stages is different. Stage-2 ASA begin between 300 and 150 ms, and up to 400 ms in rare cases (Togo and Imamizu 2016), before the action [cf. (Latash and Huang 2015)]. Stage-1 ASA seems to last much longer (Fig. 4). ΔV_z is lower in dexterous tasks compared to the stable task for at least 1 s (at least 2.5 times longer than Stage-2 ASA). This is a conservative estimate obtained after discounting for the dynamics in the ΔV_z time traces for both age groups. The difference in ΔV_z will likely persist if the target trajectory remains invariant.

Age-specific mechanisms of destabilization

The contrasting changes in YA and OA point to different ways of destabilizing the current state. The YAs' behavior suggests the first method: lowering stability (lower ΔV_z) by reducing the component of variance that does not influence the current task (V_{UCM}). This relation between variability and stability contradicts a traditional view that stability and variability are inversely related. However, there is sufficient evidence to suggest that the relation between stability and variability should not be assumed without considering underlying movement dynamics and overall task objectives (van Emmerik and van Wegen 2000). For example, people who are at a higher risk of falling walk slower to improve

Fig. 8 Two stages of anticipatory synergy adjustments for older (**a**) and young (**b**) participants. The reference frame represents n-dimensional space of the input variables, the inclined line represents the UCM, and the ellipses depict variability distributions during various phases leading up to a change in the output task variable

(A) Older adults

(B) Young adults

— Uncued steady state
— Cued steady state
- - - Just prior to change in task variable

Stage-1 ASA

Stage-2 ASA

ORT

Stage-1 ASA

Stage-2 ASA

UCM

Input variable space

their stability, even as the gait variability increases (Dingwell and Marin 2006), and individuals with Parkinson's disease demonstrate low variability in upright stance, and yet, they are at an increased risk of falling (Horak et al. 1992). These observations suggest a direct relation between stability and variability. For the YA in the present study, the dexterous tasks were associated with lower stability because, even though the total variability was lower for those tasks, a larger proportion of the total variability resulted in errors in the task performance.

We propose two possible reasons for the reduction in V_{UCM} for the dexterous tasks in YA (Tillman and Ambike 2018). Both explanations assume that V_{UCM} is reduced to enhance the agility of the system. First, we hypothesize that there exist smaller subspaces within the UCM that are better suited for rapid transitions away from that UCM. These optimal subspaces will be characterized by the mean of the data projected onto the UCM. We are currently working toward identifying these preferred locations. YA are successful at restricting the individual finger forces to lie within these subspaces when they expect to change F_T. This idea was proposed earlier in the context of reaching movements (de Freitas et al. 2007). It is also a downstream version of the optimal subspace hypothesis proposed by (Churchland et al. 2006) who recorded neural firing rates from the dorsal premotor cortex in monkeys, and demonstrated a significant decrease in across-trial variability during the foreperiod of a delay-reach task. Second, for isometric finger-force production tasks, voluntary and perturbation-induced movements have significant components along the UCM (Wilhelm et al. 2013; Mattos et al. 2015; Ambike et al. 2016a, b). This component, known as self-motion, is a consequence of negative covariation in the individual finger forces, which simply fails to change F_T. We hypothesize that the reduction in V_{UCM} during the static portion of our tasks will translate to less self-motion during the subsequent dynamic tracking of the F_T target, thereby making it more efficient.

The second way to destabilize a motor state is by increasing V_{ORT} and V_{UCM}, as seen in the behavior of the OA. Since the increase in V_{ORT} is directly related to the error in the task variable (total force, F_T), this observation is consistent with a traditional view that variability and stability are inversely related (Gabell and Nayak 1984; van Emmerik and van Wegen 2000). It is also consistent with the dynamical system view of movement stating that heightened fluctuations are not only a key feature of an impending transition in behavior (Kelso et al. 1986; Kelso 1995), but they facilitate upcoming transitions (Kelso 1995; Collins et al. 1998; van Emmerik and van Wegen 2000; Riley and Turvey 2002).

It is plausible that OA are unable to minimize V_{UCM} in response to an expectation to move. Therefore, the strategy used by the OA may be an adaptive response to this coordination deficit. It is well known that aging leads to a decrease

in finger enslaving—the characteristic of human fingers in which force production by one finger inadvertently leads to forces produced by other fingers (Zatsiorsky et al. 2000; Shinohara et al. 2003b). That is, the fingers become more independent with aging, and this may prompt the central nervous system to switch from a synergic mode of control (where the fingers are combined into functional units) to a more element-based mode of control (Kapur et al. 2010; Park et al. 2011; Latash and Zatsiorsky 2016). This may be responsible for the higher V_{UCM} for OA for all task types (Figs. 5b, 6a, b). Unable to use the strategy used by the YA, OA resort to the destabilization of the attractor for the current behavior (Kelso 1995; Riley and Turvey 2002) through other mechanisms (we do not speculate on these), which also results in increased variability in the task performance (V_{ORT}).

However, we note that some increase in V_{ORT} may be an inescapable consequence of advanced age, rather than an adaptation. This is evident from force production studies involving a single finger. Aging-related changes in neuromuscular architecture (e.g., increased size of motor units due to progressive death of α−motoneurons) and cognitive abilities (Enoka et al. 2003) lead to more variable fingertip force, and altered structure of the variability in the that force (Galganski et al. 1993; Vaillancourt and Newell 2003; Temprado et al. 2017).

Therefore, although OA and YA show a similar magnitude of Stage-1 ASA, the mechanism utilized by the OA may be interpreted as an adaptation to a coordination deficit. The adaptive response is clearly inferior, since it affects the accuracy of the current behavior. It may also contribute to the slower reaction time demonstrated by the OA (Fig. 7), although this is speculative.

Generalized motor preparation

The analysis window for the dexterous tasks (Fig. 2b) is the foreperiod of a choice reaction time (CRT) task. In a typical CRT task, an initial warning cue is provided, followed by a blank interval (foreperiod), followed by a 'go' signal that singles out one action from a predefined set that the participant must execute as fast as possible. Including a foreperiod in CRT tasks leads to faster RT and lower movement errors (Goodman and Kelso 1980; Jahanshahi et al. 1992; Brunia 1993). The psychological literature posits that generalized motor preparation that is somehow common to all the possible upcoming actions occurs during the foreperiod and leads to these improvements in task switching (Niemi and Naatanen 1981; Jahanshahi et al. 1992; Brunia 1993). These general preparations may occur centrally: cortical involvement is suggested by the slow negative wave in the electroencephalogram (Brunia et al. 2012), known as the readiness potential, that accompanies an expectation of

movement, even when the participant cannot determine the exact movement to be performed (Herrmann et al. 2008). The cortex may receive sub-cortical motor information gated through the thalamus during the foreperiod (Brunia 1993). The preparations may also occur peripherally: the gain of the spinal reflexes could be modulated supra-spinally during the foreperiod. Muscle tone increases in anticipation of movement (Sherrington 1906), and so do reflexes in the agonist muscles (Prochazka 1989). In particular, consistent with the prolonged decrease in ΔV during the foreperiod in this study, sustained augmentation in the Hoffman and tendon-jerk reflexes has been observed for up to 4 s during the foreperiod (Scheirs and Brunia 1985).

If the behavioral model used to study these processes involves redundant sets of actuators, then there is a possibility that the neuromuscular changes outlined above will manifest in the kinetics (forces and/or movements). Consequently, in the present work, we were able to observe the modulation in the stability of a kinetic variable produced by a redundant set of inputs during the foreperiod. This may not be possible when the behavioral model uses single or homologous bilateral actuators (e.g., button presses with the right and left index finger). We speculate that the anticipatory changes observed in reaching, prehensile, or locomotor tasks performed with redundant input sets (de Freitas et al. 2007; Freitas and Scholz 2009; Huang and Ahmed 2011; Wu et al. 2015), and Stage-1 ASA observed in this work, in particular, are the kinetic manifestations of the generalized motor preparations (Tillman and Ambike 2018).

Limitations

One limitation of this study is that for the dexterous tasks, the history of the total force trajectories may influence the synergy variables computed during the steady portion. Then, our results reflect hysteresis effects rather than the influence of anticipatory, feed-forward mechanisms. However, note that the total-force histories during the stable task are more uniform than those during the dexterous tasks. Therefore, if the system state when the UCM analysis was performed is influenced by behavior history only, one would expect greater rather than smaller V_{UCM} (and total variance) for the dexterous tasks. Since our results for YA show smaller V_{UCM}, this is more reason to suspect anticipatory control processes (Stage-1 ASA) at work. In case of the OA, however, the main result is an increase in the variability. In this case, we cannot unambiguously state an influence of Stage-1 ASA. Our future work will address this issue.

Our designs for the slow and fast dexterous tasks were likely responsible for two further limitations of this study. First, the design of the two dexterous tasks was meant to alter the expectation (perceived difficulty) of upcoming movement. Rather than have an explicit variable to measure

this change across the two dexterous tasks, we used total force rate as a surrogate measure. Perhaps due to this drawback, we were unable to demonstrate that Stage-1 ASA is a graded process that scales with the perceived difficulty of the upcoming state change. The magnitude of Stage-1 ASA was similar for both dexterous tasks (Fig. 5a).

Second, we were unable to demonstrate that reduced stability was accompanied by improved agility, i.e., we were unable to demonstrate that Stage-1 ASA leads to reduced RT, either across task type or age group. We found that the RT was greater for the fast dexterous task (Fig. 7), contradicting our hypothesis. There were more number and types of target jumps in the fast dexterous task compared to the slow dexterous task. Therefore, the increase in RT for the fast dexterous task is consistent with the Hick–Hyman law, which states that the RT in a choice reaction time task increases logarithmically with the number of possible choices (Hick 1952; Hyman 1953). Furthermore, RT was longer for OA compared to YA, despite both age groups having similar ΔV_{z} prior to resuming dynamic force tracking (Fig. 5a). We did identify a possible adaptation to a coordination deficit in OA. However, we cannot quantify the efficacy of this adaptation. It is unclear how the increased variability (V_{ORT} and V_{UCM}) relates to the longer RT demonstrated by the OA (Fig. 7).

Finally, we did not measure or control for any cognitive and sensory factors, which likely contribute to the RT obtained from our data.

Conclusion

Young and old adults responded in a similar fashion to a cue to produce a force change in the future by reducing the stability of their current state by similar amounts. However, young adults achieved this reduction by reducing UCM variability (~ 42%) while simultaneously maintaining the accuracy of their performance, whereas the older adults *increased* both their UCM variability (~ 38%) and performance error (~ 267% increase in V_{ORT}). Furthermore, older adults were about 120 ms slower than young adults in an ensuing choice reaction time task. How the different strategy used by OA relates to their slower reaction time remains unclear.

We have established the existence of Stage-1 ASA in isometric force production tasks in young and older adults. We have argued that Stage-1 ASA is a new feed-forward phenomenon, separate from the traditional (Stage-2) ASA reported in the literature over the past decade [cf. (Latash and Huang 2015)]. Studying redundant systems have allowed us to observe kinetic changes during the foreperiod of a choice reaction time task. We speculate that these changes are downstream effects of central processes associated with

generalized motor preparations (Brunia 1993) in response to an expectation to move at an unknown time and in an unknown direction.

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