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RESEARCH ARTICLE

Expectation of volitional arm movement has prolonged effects on the grip force exerted on a pinched object

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Abstract
Humans closely coordinate the grip force exerted on a hand-held object with changes in the load arising from the object's dynamics. Recent work suggests the grip force is responsive to the predictability of the load forces as well. The well-known grip-force–load-force coupling is intermittent when the load arising from volitional movements fluctuates predictably, whereas grip force increases when loads are unpredictable. Here, we studied the influence of expected but uncertain volitional movements on the digit forces during a static grasp. Young, healthy participants used a pinch grasp to hold an instrumented object and track visual targets by moving the object. We quantified the mean grip force, the temporal decline in grip force (*slacking*), and the coupling between the pressing digit forces that yield the grip force during static prehension with no expectation of movement, and during the static phase of a choice reaction time task, when the participant expected to move the object after a variable duration. Simply expecting to move the object led to sustained (for at least 5 s) higher magnitude and lower slacking in the grip force, and weaker coupling between the pressing digit forces. These effects were modulated by the direction of the expected movement and the object's mass. The changes helped to maintain the safety margin for the current grasp and likely facilitated the transition from static to dynamic object manipulation. Influence of expected actions on the current grasp may have implications for manual dexterity and its well-known loss with age.

Keywords Anticipatory control · Prehension · Slacking · Stability–dexterity tradeoff

Introduction

The study of fingertip forces during object manipulation is a classic paradigm for understanding human motor control processes. While manipulating objects, grip forces are tightly coupled to the loads that the manipulation generates (Johansson and Westling 1984; Flanagan and Wing 1993, 1995; Flanagan and Tresilian 1994). This occurs despite significant sensorimotor transmission delays in the motor system (Johansson and Westling 1988a, 1988b), indicating that there is a feedforward component to the control of object manipulation that accounts for the anticipated loads. This key observation has catalyzed the development of several accounts of feedforward control of motor actions, e.g., efference-copy-driven forward models of force control (Wolpert and Flanagan 2001; Nowak et al. 2013), control with referent coordinates (Pilon et al. 2007; Ambike et al. 2015b), and anticipatory synchronization (Grover et al. 2021).

Our knowledge of predictive grip-force control, however, continues to evolve. According to recent reports, the grip force is not as tightly coupled to the load force magnitude as previously thought. Rather, grip-force predictions incorporate uncertainty in ongoing object manipulation. Grover and colleagues report that while moving a grasped object to track visual targets, the grip–load force coupling is not continuous, but intermittent when the expected changes in the load are regular and predictable (Grover et al. 2019, 2020). Furthermore, when the actor must contend with loads exerted by the environment, the grip force is more responsive to the uncertainty in loads than their expected value (Hadjiosif and Smith 2015).

Here, we explored another novel aspect of grip-force control in situations that involve movement uncertainty. In previous studies, the nature of prehensile tasks was typically

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predefined (e.g., grasp and lift, perturb the grasped object by the other hand, oscillate the object, etc.) (Johansson and Westling 1984; Flanagan and Wing 1993; Danion 2004; Shim et al. 2006; Hermsdorfer and Blankenfeld 2008; Johansson and Flanagan 2009; Fu et al. 2010; Jo et al. 2015; Grover et al. 2018; Kuling et al. 2019). Less studied, however, is how control of digit forces is influenced due to uncertainty in the transition from one object manipulation pattern to another. In isometric finger pressing tasks, when participants changed their total finger force at a self-selected time, preparation in the form of altered covariation in the finger forces is evident 300 ms before the total force changed (the so-called anticipatory synergy adjustments, cf. Olafsdottir et al. 2005). However, preparation is evident much earlier (about 2 s before total force changed) when the timing of the change is unknown (Tillman and Ambike 2018a), indicating that preparation is influenced by uncertainty. We investigated if similar uncertainty effects are evident in digit forces prior to changes in patterns of object manipulation.

Specifically, we quantified changes in digit forces exerted on an object that was stabilized in one configuration, due to expected but uncertain voluntary movement in the near future. It is well known that the grip force on a static handheld object increases about 50 ms before the object is moved upward in anticipation of the increased load arising from the object's movement (Flanagan and Tresilian 1994). Our primary goal here was to determine whether uncertainty in the upcoming transition from static grasp to object movement leads to earlier and prolonged increase in grip-force magnitude and weaker coordination between the thumb and index finger pressing forces. Influence of uncertainty on the characteristics of the current grasp may have implications for manual dexterity and its well-known loss with age and pathology (Cole and Rotella 2001, 2002; Cole et al. 2010; Santisteban et al. 2016).

Our secondary goal was to explore whether any anticipatory changes in grip characteristics are associated with functional gains in the execution of the subsequent object movement (quantified using throughput, as explained below). It has long been argued that features of the ongoing movement should change, typically stability should be lowered, when the actor anticipates quick changes in movement (Riley and Turvey 2002; Hasan 2005). This so-called stability–dexterity tradeoff has been studied in animal locomotion (Dickinson et al. 2000). In human behaviors, the stability reduction aspect of the tradeoff has received attention (Olafsdottir et al. 2005; Degani et al. 2007; Krishnan et al. 2011, 2012; Tillman and Ambike 2018a; Cui et al. 2020), but few studies quantify the subsequent impact on dexterity (Huang and Ahmed 2011; Togo and Imamizu 2016; Tillman and Ambike 2018b). Rapidly transitioning between patterns of object manipulation is a key component of manual dexterity (Santisteban et al. 2016). Therefore, identifying mechanisms that facilitate manual dexterity is an important open problem.

In the present study, participants held an object in a precision grip. In different trials, they held the object stationary either while expecting no voluntary movement (steady task), or while expecting to quickly move the object in different directions in response to a visual cue (choice reaction time (CRT) task). In different CRT tasks, the participant expected to move the object in the anterior or posterior direction, or in the inferior or superior direction. We characterized forces during the steady task, and during the stationary epoch before the object's movement in the CRT task (known as the *fore period*). During the fore period, the state of the object is the same as that during the steady task, but the expected future movements are different in the two tasks. During the fore period, object movement is expected but its direction and timing are uncertain, and furthermore, different changes in the digit forces are required for movement in each direction. The forces must change from being equal during static grasp to being unequal for anterior–posterior movement; but which digit force should be larger will depend on the direction. During vertical motion, the digit forces increase equally, per the grip–load force coupling. However, the time course of the force increase depends on direction: the forces increase before upward movement commences, but after downward movement commences (Flanagan and Tresilian 1994).

During the steady task and during the fore period, we computed the mean grip force and the slope of the best liner fit to the grip-force–time data to quantify the temporal changes in the grip force within a 5-s analysis windows in both tasks (see Methods). Although a relatively constant grip force is maintained during static prehension (Johansson and Westling 1987, 1988b), there is also scattered evidence that grip force sometimes declines while holding a static pinch grasp for several seconds (Cole and Beck 1994; Burstedt et al. 1997); cf. Figure 5 in (Johansson 1991)). We investigated if such downward grip-force drift existed (termed *grip-force slacking* cf. (Smith et al. 2018)), and if it was influenced by anticipated actions. Finally, in contrast to previous work that quantified the coordination between grip and load forces, we quantified the stability of the coupling between the pressing forces exerted by the index finger and the thumb that yield the grip force. We focused on the between-digit coupling, because our main interest is to identify force changes in preparation to and prior to the change in load, similar to the studies on isometric finger pressing tasks mentioned earlier (Olafsdottir et al. 2005; Tillman and Ambike 2018a). We did not analyze the grip–load force coupling, because the object was static with almost invariant load force when we analyzed the forces. In contrast, we expected the grip force to slack; therefore, interpreting any grip–load coupling could be problematic.

To address our primary goal, we hypothesized that the grip force would be higher in the fore period of the CRT task compared to the steady task, since the grip force is known to increase with movement uncertainty (Hadjiosif and Smith 2015; Grover et al. 2019). We also hypothesized that there would be downward slacking in the grip force over time; however, slacking would be smaller during the fore period, so that the mean grip force remains elevated for the CRT task compared to the steady task. Finally, we hypothesized that the between-digit coupling will be less stable during the fore period; the weaker coupling will facilitate the transition from a between-digit coordination pattern suited for static prehension to another pattern suited for object movement (see below), consistent with the stability–dexterity tradeoff. This expectation is also supported by the evidence of weaker coupling between the opposing digits in a prismatic grasp prior to a transition between two dynamic movements (Naik and Ambike 2020), and the finding that several features of grip control generalize across grip types (Flanagan and Tresilian 1994).

The direction of the expected movement will modulate the influence of the task type on the grip characteristics. Here, our predictions for the mean and the slacking of the grip force arose from our prediction for the between-digit coupling. For CRT tasks, we hypothesized that the mean will be higher, and the slack in grip force will be lower while expecting horizontal compared to vertical movement. We also hypothesized that the between-digit force coupling will be less stable while expecting horizontal compared to vertical movement, and the hypothesized grip-force characteristics will help offset any inadvertent decline in grip force due to the weaker coupling. The weaker coupling represents greater preparation for transitioning to horizontal movement. This greater preparation may be essential, since transitioning from static prehension to horizontal movement requires a larger change in the force pattern compared to the transition to vertical movement. During static prehension, the opposing forces of the thumb and the index finger must be equal and in phase to maintain the object stationary. During vertical movement, the forces remain equal and in phase, but the magnitudes change according to the imposed or expected loads. In contrast, during horizontal movement, the forces are unequal and out of phase (Gao et al. 2005). Thus, only the transition to horizontal movement requires a change from an in-phase to out-of-phase force coordination pattern.

Finally, we explored the effect of object mass on the grip-force characteristics. It is well-known that heavier objects are grasped using higher grip force, and the overall grip-to-load ratio is proportional to the slip ratio during static grasps (i.e., the minimum grip–load ratio essential to prevent object slip; load = object weight for static grasps; (Westling and Johansson 1984)). This means that the difference in the exerted grip force and the minimum grip force required to prevent slip is larger for heavier objects, and there is greater opportunity for the grip force to slack while grasping heavier objects. Therefore, we hypothesized that the grip-force slack will be higher for a heavier object. Similar slacking occurs when visual feedback on the isometric pressing forces produced by fingers is removed; the slacking is higher for higher initial forces (Vaillancourt and Russell 2002). We did not have a prediction for the effect of mass on between-digit force coordination, and quantifying this effect is our first exploratory goal.

To address our second exploratory goal—the stability–dexterity tradeoff—we explored whether the change in the stability of the between-digit coupling in the CRT relative to the steady tasks was related to the performance of the rapid movements in the CRT tasks. We quantified performance of the movements in the CRT tasks by computing *throughput*—a composite measure of speed and accuracy (see Methods). A higher value of throughput indicates better performance. A correlation between reduced coupling between the digit forces and increased throughput would support the stability–dexterity tradeoff in prehension.

Methods

Participants

Sixteen healthy, young individuals [6 females; age = 23.8 ± 4.5 years; weight = 74.3 ± 16.8 kg; height = 173.2 ± 8.2 cm; hand length measured from hand base to the tip of middle finger = 18.9 ± 0.9 cm; hand breadth measured across distal ends of metacarpal bones = 8.6 ± 0.7 cm (mean ± standard deviation)] volunteered to participate in the study. All participants were right-hand dominant by self-report, and no participant had any history of neurological disease or musculoskeletal disorder or injury in the upper arm. All participants provided informed consent in accordance with the procedures approved by the institutional review board of Purdue University.

Equipment

Participants grasped an instrumented object in a pinch grasp with their right hand (Fig. 1A). Two six-component force transducers (Nano 17-E, ATI Industrial Automation, Garner, NC) mounted on the object measured the forces produced by both digits along the three coordinate axes. Sandpaper (100C medium grit) was glued to the surface of both transducers to increase the coefficient of friction between the transducer and the digits. At the start of each experimental session,

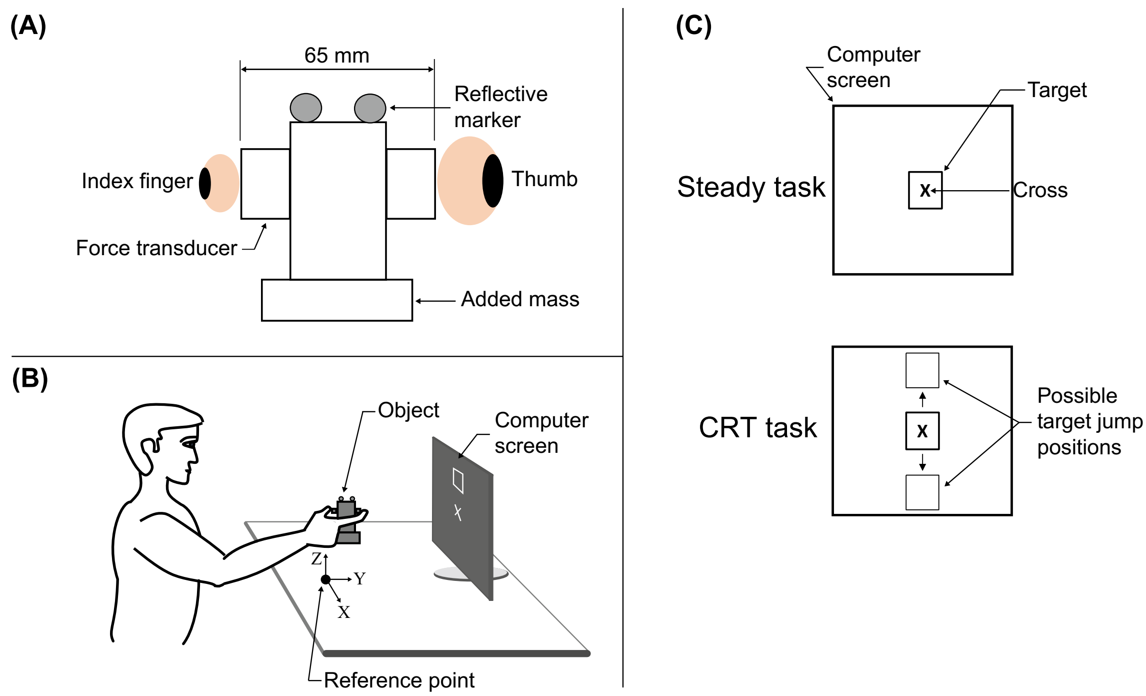

Fig. 1 Panel **A** shows an illustration of the instrumented object with force sensors for recording digit forces. A motion capture system tracked the positions of four reflective markers fixed to the object. Panel **B** shows the experimental setup. Participant sat in front of a computer screen, grasped the object in a pinch grasp, and tracked visual targets by moving the object. Panel **C** shows the visual feedback. Target represented by a square, and object position represented by 'X'-shaped cursor. Target stayed in one position for the steady task, and it jumped up or down for the choice reaction time (CRT) task. The target and cursor moved vertically for both vertical and horizontal object movements. The number of upward and downward jumps of the target were equal and randomized within each task block

the force transducers were zeroed with the object resting vertically on the table, and no digits contacting the sensor surfaces. The distance between the ends of force transducers was 65 mm.

To record the position of the object, we attached four reflective markers to the object (Fig. 1A) and used a four-camera motion capture system (Vicon Vero VE22-S, Oxford, UK) to track their positions. The motion capture system was calibrated for each participant and the tracking error was less than 1 mm inside the capture volume.

We used the MotionMonitor software (Innovative Sports Training Inc.) to synchronize and collect output signals from the force transducers (sampled at 1000 Hz) and the motion capture system (sampled at 200 Hz).

Experimental setup

Before the start of the experimental session, participants cleaned the digit tips of their right-hand using alcohol wipes to normalize the skin condition. Then, they sat upright on a piano bench facing a computer screen placed on a table (Fig. 1B). A reference point was marked on the table as the origin for the world co-ordinate system (Positive X axis along the lateral direction, positive Y axis along the anterior direction, and positive Z axis pointing vertically upward). The computer screen displayed a rectangular target and an 'X'-shaped cursor that identified the current position of the object (Fig. 1C). The centroid of the four markers defined the position of the object. The target and the cursor were restricted to move vertically on the screen.

Experimental procedure

All participants performed target tracking tasks, in which they had to place the cursor into the target by moving the object. At the beginning of each trial, the participant grasped the object by placing their right-hand thumb and index fingertip on the transducers, lifted the object off the table in the vertical direction, and held it vertical and stationary at a comfortable height above the reference point (Fig. 1B). Data collection began after the experimenter verified that the object's initial position was above the reference point. Each trial began when the initial target and a cursor indicating the object's current position appeared on the screen. Participants were instructed to move the object quickly either in the anterior–posterior or in the vertical direction to place the cursor into the target and hold the object stationary in that location. Participants were required to stabilize the cursor inside the target within 2 s after the feedback first appeared on the screen. At the end of each trial, participants replaced the handle on the reference point and released the grasp.

There were eight blocked experimental conditions (2 *task types* × 2 *directions* × 2 *masses*), with repeated trials in each experimental block. Conditions were blocked by *mass* and the order was balanced across participants. Within each *mass* block, the order of the *task type* and *direction* blocks were balanced across participants. There were two types of tasks: steady and choice reaction time (CRT) task. In the steady task, the target remained at the center of the screen, and participants were required to maintain the cursor inside the target (Fig. 1C). In contrast, in each trial of the CRT task, the target jumped once either up or down, after staying at the center of the screen for a random fore period (Fig. 1C). Participants were instructed to track the target by moving the object as quickly and as accurately as possible. The target jumped the same distance in either direction for all participants. However, the object movement required to match the target jump was standardized to 25% of the participant's arm length. Arm length was the distance from the acromion to the tip of the middle finger, measured when the participant held their right arm horizontal in front of them with the elbow fully extended.

Participants performed tracking tasks by moving the object along two *directions* (horizontal and vertical) and using objects of two *masses* (160 g—heavy, and 110 g—light). The feedback on the current position of the object was manipulated across *directions*. For the horizontal movements, moving the object in the anterior or posterior directions controlled the up or down movement of the cursor, respectively. For the vertical movements, moving the object up or down controlled the up or down movement of the cursor, respectively. Thus, for the CRT tasks, although the target always jumped vertically from the same initial position on the screen, the tracking was accomplished by moving the cursor vertically by either anterior–posterior or inferior–superior movement of the object in different *direction* conditions. The *mass* of the object was altered by adding or removing a 50 g mass at the bottom of the object (Fig. 1A).

In each condition involving the steady task (in two *directions* and with two *masses*) participants performed 20 trials, each lasting 12 s. Similarly, in each condition involving the CRT task, there were 20 12-s trials in which the target remained stationary in the initial position for anywhere between 9 and 11 s, then jumped vertically, remained in the new position for 1 s, and then vanished for the remainder of the trial. We limited the visibility of the jumped target to elicit rapid responses from the participants. Finally, to minimize the likelihood of participants accurately predicting the time of target jump, we included 20 sham trials of shorter durations. These trials were 5–9 s long, with fore periods of 4 s to 8 s. Thus, in each condition involving the CRT task there were 40 trials, the number of trials with target jump upward and downward were equal, and all trials were randomized. However, only the 20 trials lasting 12 s were used for further analyses.

At the start of each condition, participants were informed about the *task type* (steady or CRT task), *direction* (whether to move the object horizontally or vertically), and object *mass* (heavy or light). Before the start of each block of trials, participants were given six to eight practice trials. We ensured that the participants were acquainted with the relation between the direction of object movement and the direction of the feedback (especially for the anterior–posterior movements, since the feedback was rotated by 90^{o} relative to the object motion). None of the participants reported difficulty understanding the rotated feedback.

Participants rested for 15 s between trials, and for 60 s between conditions. Additional rest periods were provided if participants felt fatigue in their arm or digits. Furthermore, they were encouraged to ask for additional rest whenever required. None of the participants requested additional rest, and none of the participants reported fatigue during the protocol.

Data analysis

We wrote MATLAB programs for data analyses (R2020b, The MathWorks Inc). We analyzed the data from the 20 trials for the steady tasks (4 conditions: 2 *directions* × 2 *masses*) and 20 trials for the CRT tasks (4 conditions: 2 *directions* × 2 *masses*). All finger force and kinematic data were low-pass filtered at a cutoff frequency of 10 Hz using a fourth-order, zero-lag Butterworth filter. We then isolated the data in an *analysis window* from the 4th second to the 9th second after the start of each trial (Fig. 2). This analysis window ensures that the dynamics associated with moving the object into the initial target location have died out and provides sufficient data to obtain reasonable estimates of digit force coupling measures (Marwan et al. 2002). Note that the participant always held the object stationary and in the same location during this period. However, they expected no further object movement in the steady conditions but expected to move the object in the CRT conditions during this period. Therefore, any differences in the outcome measures obtained from this data can be attributed to difference in the expectation of movement across the two *task types*.

Out of total 2560 trials performed by all participants, in 76 trials (3% of all trials), the participant did not stabilize the object in the initial position, and the cursor moved outside the stationary target while within the analysis window. Hence, we excluded these trials from further analyses. From the remaining trials, the minimum number of trials available

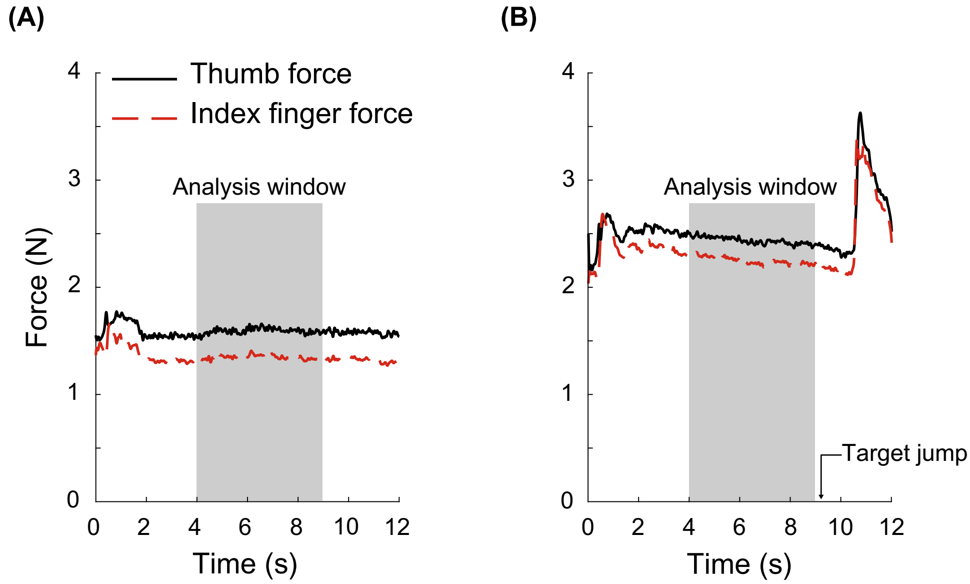

Fig. 2 Representative time series for the pressing forces of the thumb (black solid line) and index finger (dashed red line) for the steady task in panel **(A)** and for the choice reaction time task in panel **(B)**. The data in the shaded analysis window was used for analysis. The normal forces of the thumb and the index finger show a small mismatch because the sensor cables exert a small force on the object. This difference does not influence our key results because it is small, it is consistent across all conditions, and it is irrelevant for the temporal structure between the two force time series

for all eight conditions across all participants was 15. Hence, we randomly selected 15 trials for each condition and participant from the available good trials for further analyses ($n = 1920$ trials).

Basic performance measures

To determine whether the participants stabilized the object within the initial target within 2 s of feedback presentation, we computed the duration between the instant when the feedback appeared on the screen and the instant when the object movement velocity along the feedback direction dropped below 2% of the peak velocity of the initial movement. To characterize task performance within the analysis window, we quantified the object's kinematics by computing the mean and variance of the object tilt about the vertical, and the variance in object displacement along the direction of feedback. We computed the mean ± standard deviation for each measure across all 1920 trials.

Grip-force characteristics

We computed grip force as the sum of the magnitude of the thumb and the index finger normal forces. Then, we computed the mean grip force and the slope of the best linear fit in the least-squared sense to the grip force–time data within the analysis window.

Analysis of stability of coupling between thumb and index finger normal forces (cross-recurrence quantification analysis)

Conventionally, the coupling between digit forces during object manipulations have been inspected using linear cross-correlational and power spectral analyses on force trajectories that are averaged across multiple repetitions (Flanagan et al. 1993; Blank et al. 2001; Danion 2004; Danion et al. 2007). Although effective in capturing gross features of grip–load coupling, these methods fail to identify temporal variations in the grip–load coupling (Grover et al. 2018, 2019) as well as in the normal forces exerted by the thumb and all four opposing fingers (Naik and Ambike 2020). Therefore, we used a non-linear time-series analysis technique called cross-recurrence quantification analysis (CRQA) to quantify the stability of the coupling between the normal pressing forces applied by the thumb and the index finger during the analysis window.

CRQA quantifies how two processes unfold together and interact over time by computing how often their time series come close to each other in a common reconstructed phase space (Webber and Zbilut 1994). This technique proceeds in three steps. First, a common phase space for both time series is constructed using time-delayed versions of both series (Marwan et al. 2007). Second, instances when the phase-space trajectories of the two time series are within a pre-defined distance (known as radius) from each other are identified. These instances, called recurrence points, are used to create a cross recurrence plot. Third, the patterns in the cross recurrence plots are characterized by computing the appropriate outcome measure(s) as explained below.

To construct the phase space and the cross recurrence plot for the digit forces, we used the maximum (L_∞) norm (Marwan et al. 2007), and identified three input parameters required for this technique—the embedding dimension (Abarbanel et al. 1993), time delay (Hasson et al. 2008), and radius (Zbilut et al. 2002). We used an embedding dimension equal to 6, a time delay equal to 16 samples, and a radius equal to 0.2, for every trial.

We consistently observed vertical line structures in the cross recurrence plots (see Fig. 3 for a representative plot). Presence of vertical structures suggest that the state of one process does not change or changes slowly relative to the other, i.e., one time series gets trapped at a location, while the other varies about that location (Marwan and Webber 2015). This implies the coupling between the two processes is intermittent (Marwan et al. 2002; Grover et al. 2018), and the degree of intermittency can be used to quantify the stability of the coupling. In particular, the stability of the coupling is inversely proportional to the length of the vertical lines. To quantify the occurrence of vertical lines we used *trapping time*, which is equal to the average vertical line length, and reflects the average amount of time one time series is trapped relative to the other (Marwan et al. 2002). We computed other vertical line measures (laminarity and maximum vertical line length). However, they yielded the same results as trapping time, and hence, we excluded them from this manuscript for brevity.

Finally, we computed relative stability of coupling between the thumb and the index finger normal force pair, as the difference between trapping time for the steady and the CRT tasks for a given object *mass* and movement *direction*. A negative value of this measure means the stability of coupling reduced for the CRT task relative to the steady task.

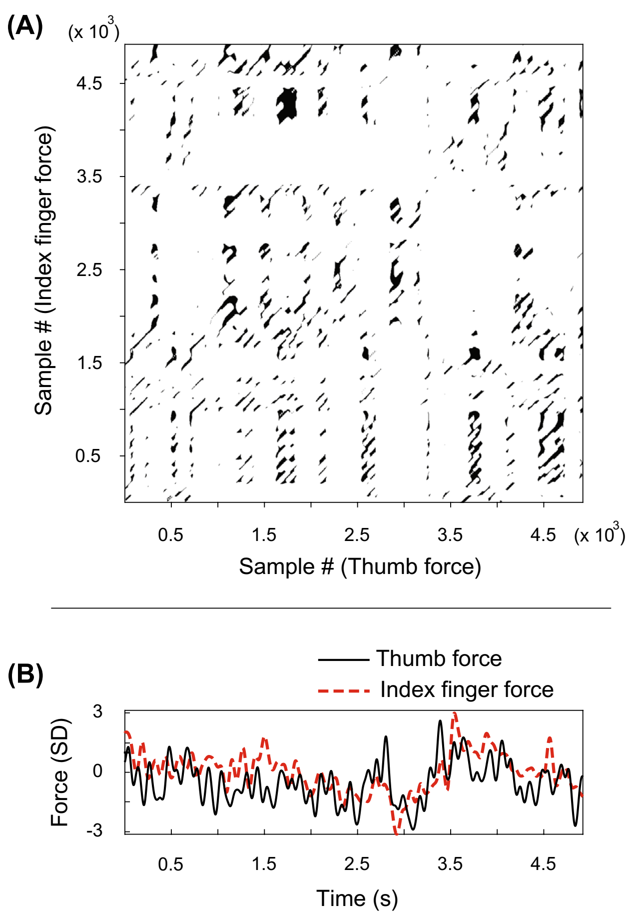

Fig. 3 Panel **A** shows a representative cross recurrence plot for the thumb and index finger pressing forces. Panel **B** shows the normalized time series of the two forces that are used to obtain the cross recurrence plot in **A**

Dexterity analysis

We computed *throughput* as the measure of dexterity. Since we instructed participants to perform the tracking task as quickly and as accurately as possible, different participants may prioritize either speed or accuracy. Therefore, throughput is an appropriate measure to quantify dexterity; it is a composite of both speed and accuracy, and it bears no prejudice towards either (MacKenzie 2015).

Throughput is computed as

$$\text{Throughput} = \frac{ID_e}{MT} = \frac{log_2(\frac{A_e}{4.133*SD} + 1)}{MT},$$

where ID_e is the effective index of difficulty. MT is the mean of movement time, A_e is the mean of movement amplitude, and SD is the standard deviation of the final position of the object, all computed across trials (MacKenzie 2015). Throughput was computed in bits/s, with a higher value indicating better performance. We computed movement amplitude as the difference between the object's final position at the end of the movement and its initial position at the time of target jump. We computed MT as the duration from the object's movement initiation to termination. We identified movement initiation as the first instant when the object's velocity increased above 2% of its peak velocity, and movement termination as the first instant when the velocity dropped below 2% of peak velocity after reaching peak velocity. Out of total 960 CRT trials across all participants, 7 trials (0.7%) were rejected and not used while computing throughput, because the movement began 500 ms or more after the target jumped.

Statistics

The data are presented as mean ± standard errors (SE) in the Results section, unless mentioned otherwise. To meet normality and constant variance requirements, we log transformed the trapping time. However, non-transformed data are presented in the Results. We fit a linear mixed-effects (LME) model (Pinheiro and Bates 2000) to the mean grip force, the slope of the grip force–time relation (slacking) and the (log-transformed) trapping time. We included the three experimental factors, and their two- and three-way interactions as fixed effects, participants as a random effect, and all trials within a condition as repeated measures. Although the LME model has been used in the motor control literature (Taylor Tavares et al. 2005; Holtzer et al. 2012; Codol et al. 2020), it seems to be relatively new to the field. In contrast to the traditional repeated measures (rm)ANOVA, the LME model considers both fixed and random effects and does not assume that the observed data are uncorrelated; hence the sphericity assumption—required in rmANOVA—is not essential in LME models.

We used Tukey–Kramer tests to perform post-hoc pairwise comparisons when significant main or interaction effects were observed. We calculated effect sizes by computing Cohen's *d*. To study the stability–dexterity tradeoff, we performed linear regressions between throughput and relative trapping time. All statistics were performed using the SAS statistical software (version 9.4; SAS Institute, Cary, NC), with an α-level of 0.05.

Results

Basic performance measures

We report the object stabilization time and object kinematics during the analysis window (when the object was held stationary), computed across all trials ($n = 1920$). The mean ± standard deviation of the stabilization time was 0.9 ± 0.3 s, the mean object tilt was 4.8° ± 2.9°, the object tilt variance was 0.1 ± 0.1 (°)^2, and the variance in object displacement along the feedback direction was 0.2 ± 0.2 mm^2. Overall, participants performed the tasks as instructed: the object stabilization time was less than 2 s and the object was held vertical (with minimal tilt) and stationary (with low variability in position and orientation).

Grip-force characteristics

We found a significant *task type x direction x mass* interaction ($F_{(1,15)} = 10.3$; $p < 0.01$) for the mean grip force (Fig. 4A). Post hoc analyses revealed that for the light object, the grip force increased for the CRT task (4.0 ± 0.3 N) relative to the steady task (3.6 ± 0.2 N) when movement was expected in the horizontal direction (Cohen's $d = 0.4$). Similarly, the grip force increased for the CRT task (4.2 ± 0.3 N) relative to the steady task (3.7 ± 0.2 N) when movement was expected in the vertical direction (Cohen's $d = 0.5$). The grip force was higher for the heavy object compared to the light object, and in contrast to the light object, the grip force increased for the CRT task (5.4 ± 0.3 N) compared to the steady task (4.6 ± 0.2 N) only when movement in the horizontal direction was expected (Cohen's $d = 0.9$).

The slope of the grip-force time linear fit was significant for 98% of all trials. The median and the inter-quartile range of the R^2 values for the fits across all trials was 0.4 and 0.5, respectively. All 15 trials within a block showed significant slopes for 106 out of the 112 blocks (8 blocks × 16 participants), and all blocks showed at least 12 trials with significant slope. The slope was not always negative, however. For 8 out of the 16 participants, at least 60% of the trials across all blocks had negative slope, and the slope was negative for 63% of all trials. Finally, the linear mixed-effects model for the slopes revealed main effects of *task*

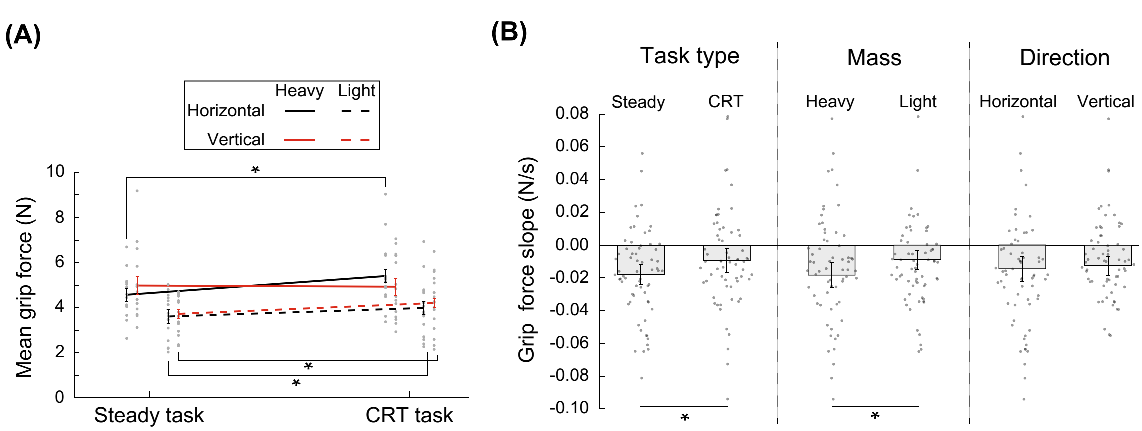

Fig. 4 Panel **A** shows the mean grip force during the analysis window with individual data points for each trial for all participants. Panel **B** shows the slopes of the best fit line to the grip-force–time data within the analysis window with individual data points for each trial for all participants. Negative slope indicates slacking in grip force (see text). '*' indicates significant differences ($p < 0.05$)

type ($F_{(1,15)}=7.57$; $p=0.01$; Cohen's $d=0.1$) and *mass* ($F_{(1,15)}=9.22$; $p<0.01$; Cohen's $d=0.1$; Fig. 4B). Post hoc analyses showed that the slope was more negative (indicating greater slack) for the steady task (− 0.02 ± 0.01 N/s) compared to the CRT task (− 0.01 ± 0.01 N/s), and for the heavy object (− 0.02 ± 0.01 N/s) compared to the light object (− 0.01 ± 0.01 N/s). The slopes for horizontal and vertical directions were not significantly different (− 0.01 ± 0.01 N/s).

Stability of coupling between thumb and index finger normal forces (cross-recurrence quantification analysis)

We found main effects of *task type* ($F_{(1,15)}=6.23$; $p=0.02$; Cohen's $d=0.1$), *direction* ($F_{(1,15)}=9.44$; $p=0.01$; Cohen's $d=0.1$), and *mass* ($F_{(1,15)}=20.6$; $p<0.01$; Cohen's $d=0.2$) on trapping time. Post hoc analyses revealed that trapping time was higher for the CRT task (32.7 ± 4.7 ms) compared to the steady task (30.7 ± 4.8 ms), while expecting movement in the horizontal direction (34.0 ± 5.1 ms) than in the vertical direction (29.4 ± 4.3 ms), and for the heavy object (32.1 ± 3.5 ms) compared to the light object (31.3 ± 5.7 ms), as shown in Fig. 5.

There were statistical outliers in our outcome measures (Figs. 4 and 5). However, there were no scientific reasons to exclude these datapoints. Note that we already excluded trials, where participants did not follow the instructions (see Methods). Moreover, the statistical results with and without the outliers yielded similar overall results and did not change our interpretations.

Stability–dexterity tradeoff

We found no significant regression ($p>0.05$ for the slope of the regression) between throughput and relative trapping time for any condition. Statistical results from the linear regression analysis between throughput and relative trapping time are summarized in Table 1.

Discussion

The primary objective of our study was to investigate the effect of expected voluntary movement of a hand-held object on the digit forces involved in grasping the object. We observed that the expectation of upcoming movement influenced force characteristics of the current, static grasp, although not all specific hypotheses were supported.

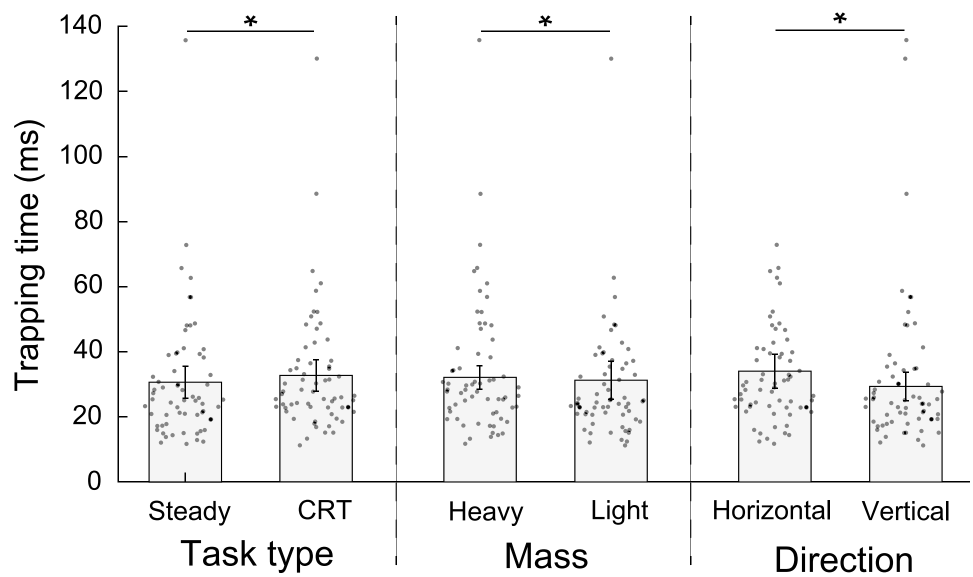

Fig. 5 Trapping time obtained from the cross recurrence plots for the thumb and the index finger pressing forces with individual data points for each trial for all participants. Higher value indicates weaker coupling between the forces. '*' indicates significant differences (**p** < 0.05)

Table 1 Statistical results for linear regression between throughput and relative trapping time

Mass and direction condition	Slope (mean ± SE)	Goodness of fit (R^2)	$t_{(1,14)}$ (*p* value for slope)
Heavy and horizontal	0.01 ± 0.01	0.02	0.51 (0.63)
Heavy and vertical	0.00 ± 0.01	0.00	0.09 (0.93)
Light and horizontal	0.00 ± 0.01	0.04	− 0.76 (0.46)
Light and vertical	− 0.01 ± 0.01	0.00	0.27 (0.79)

Compared to the steady task, the mean grip force was higher while expecting object movement in all *mass* and *direction* conditions except while expecting vertical motion with the heavy object. In partial support of our hypothesis, we observed less slacking in grip force during the CRT compared to the steady task, and less slacking for the light compared to the heavy object. The direction of the expected movement in the CRT task did not influence slacking. Next, consistent with our hypotheses, the between-digit force coupling was weaker for the CRT compared to the steady task, and when horizontal compared to vertical movement was expected. Finally, the between-digit coupling was weaker while grasping the heavier object (exploratory goal).

With respect to the secondary goal of this paper, we observed no evidence to support the stability–dexterity tradeoff in our prehensile movements. Although the stability of the between-digit coupling was lower during the fore period of the CRT task, this decline was not associated with improved throughput of the subsequent object movement. We discuss these findings below.

Anticipatory control of digit forces

The increase in grip force during *static grasp—when the load is invariant*—is in stark contrast with the well-known coupled changes in grip and movement and/or environment induced loads (cf. Westling and Johansson 1984; Flanagan et al. 1993; Jordan and Newell 2004; Hadjiosif and Smith 2015; Grover et al. 2019). In addition, notable is the extended duration of the grip-force change. In the CRT task, slacking was observed over a 5-s analysis window indicating that grip-force changes arose at least 5 s before movement initiation, and the slacking was lower in the CRT task compared to the steady task. In contrast, in most previous work, the lag between the grip and load forces ranges from a few to a few hundred ms (Flanagan and Tresilian 1994; Grover et al. 2018). In addition, we note that the higher mean grip force for the CRT compared to the steady task was not only due to less slacking, but also because participants applied greater grip force in that task. This is evident from the intercepts of the linear fits to the grip-force–time data; this data show patterns almost identical to those in the mean grip force (Fig. 4A; data on intercept not included for brevity).

It is plausible that the increased magnitude and lower slack in grip force during the fore period of the CRT tasks was a compensatory mechanism to guard against object slip due to inadvertent decline in grip force that will arise from the reduced stability of the between-digit force coupling. This interpretation is compatible with the view that the central nervous system (CNS) maintains a constant statistical confidence level of grip force to ensure sufficient safety margin (i.e., the excess grip force beyond the minimum required to avoid slip) depending on the level uncertainty in the task (Hadjiosif and Smith 2015).

In addition to guarding against slip, the increased grip force during the fore period could be aimed at efficient transition to object movement. The plan for anterior movement would be to produce greater force with the thumb than the index finger, and vice-versa for posterior movement. The plans for up vs. down movement would be to increase grip force with a short and a long latency, respectively (Flanagan and Tresilian 1994; Hager-Ross et al. 1996). However, irrespective of the direction, both digit normal forces eventually increase. Since all possible movements in our task require an increase in grip force, the CNS may be preparing for these movements by increasing the force in advance.

The grip force increase during the fore period can be discussed in the context of two competing hypotheses on motor planning under uncertainty. The first hypothesis is that the CNS prepares multiple competing motor plans when upcoming movements are uncertain (Cisek and Kalaska 2005), and also prepares a set of actions that address any common features of these plans, which is called motor averaging (Gallivan et al. 2015, 2016). Since the increased grip force addresses a common component of the upcoming movements in our work, the strategy can be called motor averaging. In contrast, the performance optimization hypothesis suggests that the brain prepares a single motor plan that is optimized for task performance under movement uncertainty (Dekleva et al. 2016; Haith et al. 2016). Since the grip force increases for subsequent movement in any direction, the increased grip force during the fore period could also be interpreted as part of a single optimized motor plan. Our experimental paradigm does not allow distinguishing between these hypotheses.

Finally, increasing the overall grip force and reducing the stability of coupling between digit forces could be a strategy for increasing the activity of afferents in the digit tips. Activity of the SA afferents increases with grip-force intensity (Wheat et al. 2010), and when the contact force creates more dynamic patterns of skin deformation (Birznieks et al. 2001). The so-called inverse models that determine the motor commands appropriate for a given action require an estimate of the current state of the system. The enhanced feedback will provide a better estimate of the current state and assist in generating the appropriate motor commands to execute the desired object movement. Such enhancement may be critical when the movement patterns change significantly, such as the transition from static prehension to dynamic object movement (Johansson and Flanagan 2009; Gale et al. 2021).

We note that the mean grip force did not change when expecting vertical movement compared to the steady task for the heavier object. This result was unexpected, and it is not compatible with the other results. Further work should identify whether higher loads alter the nature of preparation.

Slacking in grip force

We have quantified for the first time small temporal declines (around 0.01–0.02 N/s) in the grip force during a naturalistic, static, pinch grasp of an object. Although there is scattered evidence of this phenomenon in classic works (Johansson 1991; Burstedt et al. 1997), a systematic quantification seems to be missing. The drop in grip force is an example of *slacking*: the reduction in muscular effort during goal-directed behaviors. Slacking has been observed during assisted reaching and gait movements during robot-assisted therapy (Reinkensmeyer et al. 2009; Secoli et al. 2011) and in force tracking tasks with isometric digit forces (Cole and Beck 1994; Vaillancourt and Russell 2002; Ambike et al. 2015a, 2016b, 2016a; Parsa et al. 2016; Smith et al. 2018). In both these scenarios, slacking occurs when visual access to performance errors is absent. During robot-assisted movements, slacking occurs only when the robot compensates for the lower muscular effort to accomplish the task, so that kinematic errors are small. During isometric force-tracking tasks, slacking occurs after the visual feedback on the force is removed, suggesting that visual feedback on action outcomes assists in maintaining muscular effort and to prevent slacking.

In the absence of such feedback, it is possible that slacking occurs continuously (Smith et al. 2018), likely due to the nature of tactile feedback driven control of grip. Stable grasp is maintained mainly via rapid force corrections driven by tactile feedback arising from small slips at the digit–object interface (Johansson and Westling 1987). The grip force may be slacking, because these corrections are intermittent (Edin et al. 1992; Burstedt et al. 1997), suggesting that the magnitude of slacking is determined, at least in part, by the frequency of tactile-feedback-based corrections.

The nature of the task affected slacking as well. We observed that, when future movements are expected, slacking is reduced, perhaps through more frequent feedback-based corrections. Furthermore, starting from the same initial force, the magnitude of slacking would likely be lower for a grasping task compared to a pressing task (with fingers pressing down isometrically on sensors). Slacking while pressing can be high—up to 40% of the initial force over 15–20 s, for high initial forces (Ambike et al. 2015b). This is unlikely to occur during grasping. The consistent tangential deformations of the digit tips due to the object's weight may improve the efficacy of tactile-feedback-based corrections of grip force. However, this modality of correction may be weaker in pressing tasks, where the tangential deformations are likely inconsistent. This will lead to greater reliance on visual feedback for maintaining pressing force, and why slacking increases when it is removed.

We observed consistent slacking only while grasping the heavy object, when the grip force was higher. This observation is compatible with slacking during isometric pressing tasks (Vaillancourt and Russell 2002) and may reflect the fact that there is a larger range for the force to slack before the object slips. This relation also helps explain why slacking was less consistent in our data overall (63% of all trials displayed slacking) compared to previous studies; this inconsistency is due to the low grip force used to hold the light object. Slacking is likely affected by other factors as well and investigating how slacking influences aging-related decline in manual dexterity is an important direction for future research.

Between-digit coupling and the stability–dexterity tradeoff

The coupling between the thumb and index finger pressing forces declined in anticipation of a change from a static grasp to a discrete dynamic movement. This decline could arise from increased grip force, or it could be an independent action in service of dexterity that accompanied and perhaps interacted with the increase in grip force.

While holding the heavy object, the grip force was larger, and the coupling was weaker. Similarly, higher grip forces and lower coupling co-occur for the CRT tasks. Larger digit forces are also more irregular due to recruitment of more and larger motor units (Kamen et al. 1995; Slifkin and Newell 1999). Hence, the weaker between-digit coupling could be a byproduct of the increased grip force. In addition, the hypothesized greater frequency of grip-force corrections during the fore period may also contribute to the weaker coupling.

However, there is evidence that the grip-force magnitude may be dissociated from the between-digit coupling. When grasping the heavy object, coupling was lower while expecting vertical movement compared to the steady task, but the grip force did not change across these conditions (Fig. 4A). Furthermore, the decoupling was greater while expecting horizontal vs. vertical movements, although there was no effect of movement direction on mean grip force or slacking, at least for the light object (Figs. 4 and 5). Finally, if the coupling depended *only* on the noise in grip force associated with its mean value, we would expect a *task type* × *mass* interaction for trapping time. We observed main effects instead, further indicating that changes in coupling are at least partly dissociated from the noise in the pressing forces. There was also evidence of weaker coupling between the pressing forces of the thumb and the four fingers engaged in a prismatic grasp in an earlier study, where the overall load, and hence grip force was not expected to change across conditions (Naik and Ambike 2020). More broadly, in isometric multi-finger force production tasks, the between-finger coordination weakens prior to a quick volitional increase in the total force, even with static values of the current force, showing clearly that dissociation between force magnitude and coordination is possible (Olafsdottir et al. 2005; Togo and Imamizu 2016; Tillman and Ambike 2018a, 2020).

There may be a virtuous circle of causes and effects at play in which force magnitude (and slacking) and coupling interact. The grip-force magnitude may have increased for reasons discussed earlier that are independent of the weaker coupling. However, the increased force may also protect from the inadvertent declines in grip force due to the weaker coupling. The coupling was weakened to enhance dexterity, independent of the effects of increased force. However, some of the reduced coupling may also arise from higher variability due to higher forces.

At the physiological level, the weaker between-digit coupling may occur due to changes in central and peripheral processes. The decoupling may be a downstream, peripheral consequence of central changes, such as the well-known readiness potentials (Herrmann et al. 2008). Other peripheral changes may also contribute. Muscle tone increases (Sherrington 1906) and sustained augmentation in the Hoffman and tendon-jerk reflexes has been observed for up to 4 s before movement during the fore period (Scheirs and Brunia 1985). These changes could have led to more irregular digit forces, and hence weaker inter-digit coupling.

We note that our results are similar to previous work by Latash and colleagues. The so-called anticipatory synergy adjustment (ASA) describes changes in digit force coordination prior to moving a grasped object (Kim et al. 2006; Shim et al. 2006; Latash et al. 2010; Jo et al. 2015). However, a key difference between ASAs and this paper is the presence of uncertainty. ASAs were observed in self triggered object movements, where the direction and timing of the movement are known to the participant. Here, we report changes in coordination when information about the direction and timing about the movement is unknown. Our results may be viewed as extending this prior work on anticipatory control of grip via altered coordination.

We argued that the reduced stability of coupling facilitates the transition from static to dynamic object movement. Although participants reduced the stability of coupling for the CRT task, we failed to see its benefits in terms of increased throughput across subjects. The lack of effect may be because the participants in this study were healthy, young adults, and there is a ceiling effect on the benefits of stability reduction on movement efficacy. Furthermore, different participants may interpret our instruction to move as quickly and accurately as possible by prioritizing speed and accuracy differently. We used throughput as a measure of dexterity to account for this phenomenon (MacKenzie 2015), but this measure does not seem immune to ceiling effects either. We also considered correlations between the coupling change and reaction time or accuracy separately but did not find consistent correlations.

Limitations

The main limitation of this study was that we restricted our analysis to grip forces and digit pressing forces. A soft-contact model is a better description of the digit-object contact dynamics (Singh and Ambike 2015, 2017), with the digits exerting forces in the tangential direction as well as a free moment on the object. Analysis of coupling between other pair of forces and moments will provide a more complete picture of stability modulation of the precision grasp. Finally, our participant pool was homogeneous. It is likely that the gains in dexterity from stability reduction will become apparent in other populations (e.g., older adults), and provide a better picture of this tradeoff in prehensile behaviors.

Conclusions

We have demonstrated that young healthy adults change their grip-force characteristics during static grasp in anticipation of quick volitional movements. The grip force increased and was maintained for at least 5 s prior to movement. Simultaneously, the coupling between the digit forces weakened. These changes were sensitive to task-specific factors, namely, mass of the object and the direction of the expected movement. We did not observe a relation between reduced coupling and the efficacy of the object movement or dexterity, likely due to the homogeneity of our participant pool. Nevertheless, the expectation of movement had a prolonged effect on the current grasp, and this phenomenon may have significant implications for understanding the loss of dexterity with age.

Data availability statement The data sets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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