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DIMINISHED JOINT COORDINATION WITH AGING LEADS TO MORE VARIABLE HAND PATHS

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Abstract

Differences in joint coordination between arms and due to aging were studied in healthy young and older adults reaching to either a fixed, central target or to the same target when it could unexpectedly change location after reach initiation. Joint coordination was investigated by artificially removing the covariation of each joint's motions with other joints' motions. Uncontrolled manifold analysis was used to partition joint configuration variance into variance reflecting motor abundance (V_{UCM}) and variance causing hand path variability (V_{ORT}). The extent to which V_{ORT}, related to the consistency of the hand path, increased after removing a joint's covariation indicated the strength of its coordination with other joints. Young adults exhibited stronger indices of joint coordination, evidenced by a larger increase in V_{ORT} after removing joint covariation than for older adults. This effect was more striking for the dominant right compared to the left arm for young adults, but not for older adults, especially with target uncertainty. The results indicate that interjoint coordination in young adults leads to less hand path variability compared to older adults.

Keywords

Coordination; Reaching; Uncontrolled Manifold Analysis; Aging

1. Introduction

The coordination of tasks like reaching, postural control, and force production has been shown to involve the use of motor abundance by the central nervous system (CNS) (de Freitas, Scholz, & Stehman, 2007; Gera, Freitas, Latash, Monahan, Schoner, & Scholz, 2010; Hsu, Scholz, Schöner, Jeka, & Kiemel, 2007; Krishnamoorthy, Scholz, & Latash, 2007; Latash, Scholz, Danion, & Schoner, 2001; Latash, Scholz, Danion, & Schöner, 2002;

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Scholz & Schöner, 1999; Scholz, Schoner, Hsu, Jeka, Horak, & Martin, 2007; Tseng & Scholz, 2005; Zhang, Scholz, Zatsiorsky, & Latash, 2008). These studies suggest that the CNS stabilizes variables most related to task success by allowing for flexible combinations of redundant degrees of freedom. A functional synergy in this context is defined as having two features, namely,1) a neural organization that determines the division of labor among elemental variables (i.e., how much each variable contributes, on average, to the value of a performance variable) and 2) their covariation to stabilize the values of important performance variables (Latash, Scholz, & Schöner, 2007). Covariation between elemental variables could either be negative or positive. However, negative covariation has a greater probability of stabilizing the task (Latash et al., 2007). For example, a task requiring generation of a total of 10-N force by pressing with two fingers can be accomplished by attempting to produce exactly 5-N by each finger on every attempt. Successful performance then requires near perfect control. A more realistic approach involves the negative covariation of finger forces, i.e., an increase in one finger's force is accompanied by an equal reduction in the other's force, thus providing more flexibility to stabilize the 10-N total force.

The second feature of functional synergies has been quantified using the uncontrolled manifold approach (UCM) to separate the across-trials or across time (depending on the task) variance of elemental variables into a component that reflects flexibility in stabilizing a performance variable (variance within the UCM subspace) from a component that leads to variability of the same variable (orthogonal subspace) (Latash et al., 2007; Schöner & Scholz, 2007). In this study, we used the framework of UCM to investigate the extent to which covariation of individual joints with other joints of the arm stabilizes the hand's three-dimensional path during reaching. Some of the UCM variance could reflect the fact that the axis of a particular joint's motion lies geometrically parallel to a dimension of the UCM in joint space. To the extent that this is true, its variance has no effect on the performance variable under consideration. Thus, even if such a joint's motion did not co-vary with that of other joints, it would contribute to UCM variance. For example, during a pointing task when the elbow is extended fully forward and shoulder flexed to 90 degrees, rotation of forearm has a minimal to no effect on the three dimensional position of the hand. That is, the hand position considered as the performance variable would have low sensitivity to this rotation.

In addition, it has been observed that proximal and distal joints play different roles in the control of reaching. Proximal joints appear to be most important for arm transport, whereas distal joints are more important for positioning and orienting the hand near the target (Jeannerod, 1999; Marotta, Medendorp, & Crawford, 2003; Wang, 1999). Differences in the role of proximal and distal joints have also been proposed by the leading joint hypothesis (Dounskaia, 2005). This hypothesis postulates that the leading joint, generally proposed to be the shoulder joint, generates the muscle torques to accelerate the limb whereas the subordinate joints (usually wrist and elbow) regulate interaction torques produced by the leading joint and create net torque resulting in motion of the end-effector (Galloway & Koshland, 2002). The effectiveness of this proposed strategy should be reflected by coordination of proximal and distal joint motion to stabilize the hands' path to a target. This hypothesis can be tested by artificially removing the covariation, a measure of coordination, between various joint motions to determine its effect on hand path stability compared to what is observed experimentally. That is, lack of coordination of proximal joint motions with those of other joints might be expected to have a greater effect on the transport phase of reaching, whereas poor coordination of distal joint motions with more proximal joints could have a greater effect as the hand approaches the target. To our knowledge, the role of covariation of different joints with others in stabilization of the hand position has not been investigated previously. Recently, the UCM approach has been used to distinguish between joint covariation and individual variation of joint motions whose axes are nearly parallel to

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one dimension of the UCM subspace of joint space as the source of UCM variance (Verrel, 2011; Yen & Chang, 2011).

The UCM approach has been used to show that motor abundance provides the ability to resolve multiple task constraints simultaneously (Gera et al., 2010; Zhang et al., 2008) and to overcome unexpected perturbations (de Freitas et al., 2007; Scholz et al., 2007). The double step paradigm has been used to investigate the effect of target uncertainty on movement planning and the control of arm movements (Freitas & Scholz, 2009; Georgopoulos, Kalaska, & Massey, 1981; Pelisson, Prablanc, Goodale, & Jeannerod, 1986; Robertson & Miall, 1997; Soechting & Lacquaniti, 1983). Soechting and Lacquaniti (1983) suggested that successful correction of a movement trajectory when reaching under a double-step paradigm occurs by using stereotypic solutions. However, this assertion has been contradicted by other data suggesting that motor abundance is used in reaching when there is uncertainty in the target location (de Freitas et al., 2007; Robertson & Miall, 1997). de Freitas et al. (2007) showed that when right hand-dominant healthy young adults reached to targets with an uncertain final target location, a greater variety of joint combinations were used than when the initial target position was fixed, without increasing performance error. This effect should result from increased negative covariation of joint motions when reaching under the former target condition. Freitas and Scholz (2009) also suggested that the right arm is better at utilizing motor abundance. Thus, the right compared to left arm is better at decoupling joint combinations that lead to task success, and are less restricted, from those that would result in hand path variability, which are strongly resisted.

Differences in the coordination of left and right arms have also been attributed to specialization of each hemisphere for different aspects of task performance (Barthelemy & Boulinguez, 2002; Boulinguez, Nougier, & Velay, 2001; Boulinguez, Velay, & Nougier, 2001; Sainburg & Kalakanis, 2000; Sainburg & Wang, 2002; Winstein & Pohl, 1995). For example, with the right hand-dominant adults, the dominant arm has been shown to be more efficient than the non-dominant at dealing with interaction torques, resulting in better trajectory control (Sainburg & Kalakanis, 2000; Sainburg & Wang, 2002). In contrast, those authors provide evidence that the left arm is better at positional accuracy because of the purported advantage of right hemisphere for online corrections. Other studies have attributed better motor planning to the right arm/left hemisphere (Freitas & Scholz, 2009; Winstein & Pohl, 1995), whereas the left arm/right hemisphere is argued to be better at movement planning because of faster reaction time for the left than the right arm (Barthelemy & Boulinguez, 2002; Boulinguez, Nougier, et al., 2001; Boulinguez, Velay, et al., 2001). The current study investigated differences in joint coordination between the arms by testing the effect of removing the covariation of specific joint motions with other joints of the arm on joint variance components, especially the component that leads to hand path variability.

The current study also investigated changes in the role of joint covariation with aging. It has been suggested that reliance on feedback control is a main factor for slowing down of movement with aging (Seidler-Dobrin & Stelmach, 1998; Verrel, Lovden, & Lindenberger, 2010). Performance of multi-joint movements also declines with aging (Seidler, Alberts, & Stelmach, 2002; Verrel et al., 2010). Elderly adults exhibit decline in the performance of reaching, e.g., increased targeting error, for reaching tasks requiring two joints as compared to those involving one joint (Seidler et al., 2002). Verrel et al. (2010) showed that elderly adults used less motor abundance (a reduced amount of joint variance within the UCM subspace of joint space) as compared to young adults, but this difference was not associated with differences in task stabilization. That is, the non-UCM component of joint variance that would lead to variability of the hand path was not different between young and older adults. If true, these results would suggest that older adults use less motor abundance to achieve equal accuracy in task performance. The current investigation explores this question further

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in a reaching task involving target uncertainty. In addition, we asked whether differences might exist in the extent to which proximal and distal joints contribute to task-variability in different phases of reaching.

The overarching aims of the present study were, therefore, (1) to investigate the extent to which the coordination of an individual joint with others contributes to hand path stabilization and (2) how that coordination changes with aging. First, we expected that removal of pertinent joint's covariation would lead to greater change in task stabilization for the unexpected target reaches as compared to when target location was fixed at onset and throughout the reach. Second, we also expected that removal of covariation among joints would lead to greater hand path variability for the right than the left arm. Third, we hypothesized that the covariation of shoulder joint motions with those of other joints would be more important to stabilize the three-dimensional hand path during the period from reach onset until peak velocity. In contrast, it was predicted that the covariation of elbow, and especially the wrist joint motions with other joints would have a greater impact on the hand path during the latter period of the reach, i.e., from peak velocity to movement termination. These hypotheses were tested by 1) performing UCM analysis to identify differences in the two components of joint configuration variance and 2) measuring actual performance variability (end-point variability). These measures were compared between the results of actual reaches and the simulation of reaches were a particular joint's motions were not coordinated with those of other joints by artificially removing the covariation of a joint's motions with those of other joints and performing again the analysis. In line with the overarching aim of this study, we predicted that elderly individuals would exhibit poorer covariation among their joints and, consequently, greater hand path variability than younger individuals, as determined by investigation of the above hypotheses.

2. Methods

2.1. Participants

Eleven young (YA: 27 ± 11 years old; 5 males, 6 females) and ten older (OA: 67 ± 5 years old; 4M, 6F) adults participated in the experiment. All participants were right-hand dominant as determined by the Edinburgh handedness questionnaire (Oldfield, 1971). They gave informed consent as approved by the University's Human Subjects Review Board prior to their participation.

2.2. Apparatus and data acquisition

An eight-camera VICON motion measurement system was used to record three-dimensional (3D) kinematics of the arm and scapula at a sampling rate of 120Hz. Rigid bodies consisting of 4 markers each were placed on the hand, lower arm, upper arm, and on the superior aspect of the upper trunk, two-thirds of the distance between the neck and the acromion process. Individual markers were placed at the sterno-clavicular joint and on the tip of a pointer attached to a custom made hand splint worn by the participant. The sternum marker served as the origin of the body-centered coordinate system used in the computations. One static arm calibration trial was recorded prior to the start of the experiment as a reference zero position for computing joint angles. For this trial, additional markers were placed on the radial and ulnar styloid processes of the wrist and on the medial and lateral epicondyles of the elbow, and their average position was used to estimate the mean position of these joints' centers. Another marker was placed lateral and just inferior to the acromion process to estimate the shoulder joint location. During the static arm calibration trial, the arm faced forward from the shoulder, with the upper arm, forearm and hand aligned and held parallel to the floor with the thumb pointing upward (see Fig. 1, (Tseng, Scholz, & Schöner, 2002)). For this position, the arm was parallel to the global Y-axis. Positive X-axis of all the joints

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pointed laterally to the right, positive Y-axis pointed forward along the long axis of the upper arm, forearm and hand, while the positive Z-axis pointed upward.

2.3. Experimental procedure

Fig. 1a provides an illustration of the experimental set-up (right arm view). Participants were seated in a height-adjustable chair to ensure that their forearm rested on the table in pronation, with the upper arm nearly vertical and the elbow flexed to approximately 90°. The subject's trunk was strapped to the chair in such a way as to minimize its motion during reaching while ensuring freedom of scapular motion. Participants started each trial from the same initial position. Consistent positioning of the initial arm and hand position was obtained by fitting a radiology vacuum air bag (Bionix, RT-7815, Toledo, OH) to the underside of the arm while resting on the table. Once positioned, the air in the bag vacuumed out to form a trough that fixed the lateral and medial sides of the elbow, the forearm and the hand in the initial position. This arrangement restricted only pure lateral or medial arm movement from the initial position. From the same initial position, participants were instructed to reach and touch a target displayed on a touch-screen computer monitor so the contact location of the pointer-tip could be recorded. The length of pointer was adjusted relative to the hand rigid body to ensure its tip was at a distance equal to the index finger's length when it was extended. The target height was set at 70% of the participant's eye level and the target was displayed on the screen of the monitor placed in a distance from the participant of approximately 95% of the functional arm length (i.e., the distance between the tips of the acromion process and the index finger of the arm when participants actively fully extended their arm forward). At the beginning of each trial, participants focused at a green 1.5-cm diameter circular target presented at the center of a computer screen. The target was aligned with subjects' midline. Participants were instructed to initiate each reach anytime after an auditory signal was provided. Once moving, they should "reach as fast as possible while still being accurate". There were no reaction time requirements.

Participants performed the task with both the right and left arms. In young adults, five participants performed the task first with their dominant right arm while six participants performed first with their non-dominant left arm, with the order randomly assigned. For older adults, five participants performed the task first with their dominant right arm and other five participants performed first with their non-dominant left arm, also randomly assigned. Each participant performed 160 reaches. The target location remained fixed at the center of the computer screen for the first block of 40 trials (certain center target, CCT; Fig. 1b). Then, during an additional block of 120 reaches, the "double-step" paradigm was employed to create target location uncertainty. During these trials, the subjects were instructed to initiate one smooth movement toward the central target and try to maintain the same movement speed as for the CCT trials. For all 120 uncertain trials, the target was displayed initially at the same location as for CCT trials. The participant's reaching hand rested on a switch in the initial position. Depending on the current state of a customized LabView™ computer program controlling the experiments, the signal could result in the target jumping 13-cm ipsliaterally (40 trials) or contralaterally (40 trials), with a delay of approximately 16-ms after switch release, or could remain at the center target location on the remaining 40 trials (uncertain central target, UCT; Fig. 1b). Only the CCT and UCT trials were analyzed here to compare differences in coordination when the initial position and final target location were identical, but the potential need to correct the reach differed. The order of trials in the uncertain block was randomized. For the uncertain trials, the subjects were instructed not to anticipate a target jump but to adjust their reaches if the target shifted from the center location. Single-step (CCT) trials served as the control trials and were performed before the double-step trials to prevent biased performance of the UCT trials. A ten-minute break was taken between the two blocks of trials. Prior to the beginning of each block, the

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participants practiced approximately 10 familiarization trials. Participants never reported being fatigued during the experiments.

2.4. Data Analysis

In the current study, only reaches performed towards the central target location under both the CCT and UCT conditions were analyzed. Kinematic data were low-pass filtered at 5-Hz using a bi-directional, second-order Butterworth filter before further processing. The marker data during dynamic trials were referenced back to the arm calibration trial to compute the 10 rotational DOFs of the arm: three DOFs each of clavicle and shoulder joint motion and two DOFs each of elbow (flexion-extension and pronation-supination) and wrist (flexion-extension and abduction-adduction) joint motion. Joint angles were calculated using the algorithm proposed by Söderkvist and Wedin (1993).

Movement onsets and terminations were defined respectively at 3% and 5% of the peak pointer-tip velocity. The determination of these instants of time were performed automatically with a Matlab™ routine and visually checked for accuracy. Movement duration was divided into two phases: 1) period of onset to peak velocity and 2) period of peak velocity to termination. Movement phases were each time-normalized separately to 100 samples to align trials for computing the across-trials variance at each percentage of the reach trajectory (Scholz & Schöner, 1999). Time normalization was performed using the cubic spline interpolation function of Matlab™ (de Boor, 1978).

2.4.1.Typical Uncontrolled Manifold Analysis (UCM) analysis—The UCM approach (Scholz & Schöner, 1999) was implemented to analyze two components of variance of 10 rotational degrees of freedom (10-DOF) in relation to stabilizing the hand's three-dimensional (3D) position. This analysis partitions the total joint variance into a component that (1) does not affect the performance variable of interest (V_{UCM}; in the present study, the stabilization of hand's three-dimensional (3D) position], therefore, reflecting motor abundant combinations of joints used to achieve a given value of the performance variable. The other component is joint variance that leads to variability in the value of the performance variable across repetitions (V_{ORT}). In the current study, a Jacobian matrix was obtained at each time point of the reach trajectory as the partial derivatives of the geometric model relating small changes in each of the ten joint angles to changes in the 3D hand position. The null space of each Jacobian matrix, computed in Matlab™, corresponded to basis vectors in joint space where different combinations of the joints had no effect on the control of hand position. The range space of the Jacobian corresponded to the direction(s) in joint space where combinations of the joints led to a change in the value of hand position. Null and range spaces were computed based on the mean joint configuration at each point in normalized time. At each normalized-time point of a given trial, the current mean-free configuration of joints was projected onto the null space and into the range space (Scholz & Schöner, 1999). The variance of the projections into each subspace across trials was then obtained and normalized to the number of DOFs of each subspace to allow comparisons across the two subspaces. For the 3D hand position, variance within the UCM was divided by 7 (V_{UCM}), whereas variance in the subspace orthogonal to the UCM was divided by 3 (10-7; V_{ORT}). Mathematical details of the method can be found elsewhere (de Freitas & Scholz, 2009; Gera et al., 2010; Reisman & Scholz, 2003).

2.4.2. UCM analysis after joint co-variances were removed—To test the hypothetical effect of the lack of a particular joint's coordination with other joints, the non-diagonal elements of its covariance matrix were zeroed prior to the UCM analysis, ensuring elimination of its covariation with other joints (Verrel, 2011; Yen & Chang, 2011). We performed this analysis separately after removing the covariation of each of the shoulder,

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elbow and wrist joints' motions with other joints. That is, for the shoulder analysis, covariation of shoulder flexion-extension, abduction-adduction and internal-external rotation with the elbow and wrist joint motions were removed, and UCM analysis was repeated.

2.4.3. Ratio of task variability before and after removing joint covariation—The ratio of the estimated task variability, i.e., 3D hand path variability, before and after removing covariation of joints was computed to determine the extent of change in the task variability as a result of removing covariation of a pertinent joint with other joints' motions. Task variability was estimated using the formulations described below (Verrel, 2011) for the typical data and the data from which covariation of pertinent joint with others was removed eq. (1) and (2).

$$TV = trace\left(JCJ^T\right) \quad (1)$$

where TV is the task variability based on the covariance matrix C of the typical data and J is the Jacobian matrix.

$$TV_0 = trace\left(JC_0J^T\right) \quad (2)$$

Where TV_0 is the task variability based on the covariance matrix C_0 of the data from which covariance of pertinent joints has been removed and J is the Jacobian matrix.

The task variability ratio was then computed as an index to define the change in the task variability after removing covariation of pertinent joints' with others. Thus, a task variability ratio of 1.0 indicates no change in the task variability after removal of covariation of a joint's motions with others and a ratio less than 1.0 indicates that that covariation with other joints was important to reduce variability of the hand path. The task variability ratio was computed after independently removing the covariation of each of the shoulder, elbow and wrist joints' motions with the other joints' motions as:

$$TV_{ratio} = \frac{TV^i}{TV_o^i}, \quad \text{where i } = \{\text{shoulder;elbow;wrist}\} \quad (3)$$

2.5. Statistical Analysis

SPSS 18.0 was used to conduct all statistical analyses. Mixed-effects analyses of variance with a between-subjects factor Group (young adults (YA) versus older adults (OA)) and repeated factors as described below were used to test the experimental hypotheses. For the first hypothesis, i.e., removal of pertinent joint's covariation should lead to greater change in task stabilization for the unexpected (UCT) versus expected (CCT) target location, and the second hypothesis, i.e., removal of covariation among joints should lead to greater hand path variability for the right than the left arm, the dependent variables were the joint variance components (V_{UCM} and V_{ORT}). The repeated factors were the arm (left versus right), target condition (CCT versus UCT; to the central target) and type of data (normal versus de-correlated). The effects were tested separately for data averaged across each of two movement phases, i.e., onset to peak velocity and peak velocity to termination. For the third hypothesis, i.e., that the covariation of shoulder joint motions with those of other joints would be most important to produce a consistent three-dimensional hand path during the period from reach onset until peak velocity, the dependent variable was the task variability ratio (TV_{ratio}), with repeated factors 1) joints (shoulder, elbow and wrist), 2) phase of movement (onset to peak velocity versus peak velocity to termination), 3) arm (left versus right) and 4) target condition (CCT versus UCT). The joint variance components and the

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task variability ratio were log transformed for the statistical analyses because the data was not normally distributed as per the tests of normality (Shapiro-Wilk Test, $p > .05$).

Although there were no hypotheses about movement time (MT), because MT was found to differ quantitatively between younger and older adults, a mixed-effect ANOVA testing differences in MT between the two groups, with repeated factors arm and condition, was performed.

The level of significance for all analyses was set at $p < .05$. Post hoc pairwise comparisons with LSD corrections were used when appropriate.

3. Results

3.1. Movement Time (MT)

The movement time of older adults was approximately 140-170-ms longer than in younger adults (Table 1; $F(1, 19) = 58.64$, $p < .001$). There was also a three-way interaction of group, arm and condition, however, $F(1, 19) = 5.83$, $p < .05$. This resulted from MT being approximately 140-ms longer, on average, for older adults for both conditions for the left arm and for the CCT condition for the right arm, while the difference between groups was greater (172-ms) for the right arm in the UCT condition.

3.2. Comparison of V_{UCM} and V_{ORT} after removing a joint's covariation with other joints (Hypothesis 1 and 2)

This analysis investigated what would happen to each component of joint configuration variance (i.e., V_{UCM}, Fig. 2, and V_{ORT}, Fig. 3) if a specific joint's motions were not coordinated with those of other joints, simulated by removing the covariation of a joint's motions with those of others. We tested whether the change in the magnitude of joint variance components after removing covariation of joint with others differed between young and older adults and how that was affected by the uncertainty of the target condition (first hypothesis) and the arm used to perform the reach (second hypothesis). In general, removal of the covariation of a joint's motion with those of other joints led to a reduction in V_{UCM} (Fig. 2) and an increase in V_{ORT} (Fig. 3). However, this pattern of results differed somewhat depending on which joint's covariation was removed.

3.2.1. Joint configuration variance reflecting motor equivalent joint combinations (V_{UCM})

Movement onset to peak velocity: When removing covariation of wrist joint movements with of other joints' motions, V_{UCM} decreased more in young than in older adults (Table 2a, group by data type interaction; Fig. 2a, top panel), irrespective of the arm used to reach ($p = .58$) or target condition ($p = .06$). Removing covariation of either the elbow (Fig. 2a, middle panel) or shoulder (Fig. 2a, bottom panel) joints' motions with those of other joints also led to a reduction in the magnitude of V_{UCM} (Table 2a, data type effect). However, this effect did not differ between young and older adults ($p > .27$), regardless of the arm used to reach ($p > .06$) or the target condition (CCT and UCT, $p > .6$).

Peak velocity to movement termination: Removing covariation of the wrist joint's motions with joint motions of the other joints led to a reduction in V_{UCM} (Table 2b; data type effect; Fig. 2b, top panel). This effect differed between young and older adults depending on the arm used to reach and the targeting condition (Table 2b, group by arm by target condition by data type interaction). Further analysis indicated that there was a significant interaction for the young adults between arm and target condition, $F(1, 10) = 5.3$, $p < .05$. Reduction in V_{UCM} after removal of covariation of the wrist with other joints motions did not differ

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between CCT and UCT conditions (*p* = .42). Removing covariation of the left wrist led to a larger decrease in V_{UCM} for the CCT condition versus the UCT condition, $F(1, 10) = 11.75$, $p < .01$. In contrast, older adults did not exhibit a reduction in V_{UCM} when removing wrist covariation ($p = .08$), regardless of the target condition ($p = .067$) or arm used to reach ($p = .75$).

Removing covariation of either the elbow (Fig. 2b, middle panel) or shoulder (Fig. 2b, lower panel) joint's motions led to a reduction in V_{UCM} (Table 2b, data type) that was not dependent on age ($p > .73$), target condition ($p > .21$), or arm used to reach ($p > .69$).

Thus, the changes in V_{UCM} after the removal of covariation of the wrist joint's motion with other joints, for both phases of the movement, supported the first and second hypotheses that greater covariation among joints is utilized in stabilizing the hand's position for the right than the left arm for the UCT condition and that coordination of the right arm results in less hand path variability during reaching than for the left arm. Moreover, it also supports the overarching aim of the study that inter-joint coordination diminishes with aging.

3.2.2. Joint variance tending to produce hand path variability (V_{ORT})

Movement onset to peak velocity: An increase in V_{ORT} after removing wrist joint movement covariation with other joints was greater for young than for older adults (Table 3a; Group by Data type; Fig. 3a, top panel), independent of the arm used to reach (Table 3a; Arm by Group by Data type interaction) or target condition (Table 3a; Group by Target condition by Data type). In contrast, although there an increase in V_{ORT} after removal of either the elbow (Fig. 3a, middle panel) and shoulder (Fig. 3a, bottom panel) joint's covariation with the other joints' motions (Table 3a; Data type effect), this effect did not differ between young and older adults (p > .5), regardless of the arm used to reach (p > .15) or the target condition (p > .8).

Peak velocity to movement termination: A significant four-way interaction was found among group, arm, target condition and type of data related to removing wrist joint covariation (Table 3b; Group by Arm by Target condition by Data type; Fig. 3b, top panel). V_{ORT} increased more for young compared to older adults when removing the wrist joint's covariation with other joints' motions (Table 3b; group by data type). For young adults, V_{ORT} increased more in the right than in the left arm, $F(1, 10) = 4.9$, $p = .05$, although there was an interaction of arm with target condition, $F(1, 10) = 7.2$, $p < .05$. This was due to a similar increase in V_{ORT} after removal of wrist covariation in the right arm for both target conditions ($p = .3$) whereas for the left arm, V_{ORT} increased more when removing wrist covariation when reaching under the CCT versus UCT condition, $F(1, 10) = 16.05$, $p < .01$. Additionally, removal of wrist joint's covariation with other joints' motions for the CCT condition led to a similar increase in V_{ORT} for both arms ($p = .36$), whereas for the UCT condition there was an interaction of arm and type of data, $F(1, 10) = 6.89$, $p < .05$. This interaction was due to the fact that 1) for UCM analysis on the actual data, V_{ORT} was greater for left than the right arm ($p < .05$; white filled bars in Fig. 3b); whereas 2) UCM analysis on simulated results after removing covariation resulted in a similar magnitude of V_{ORT} for both arms ($p = .55$). These findings suggest that the wrist joint covaried more with other joints to stabilize the hand path for the UCT condition when reaches occurred with the right compared to the left arm.

For older adults, removing wrist covariation led to an increase in V_{ORT}, $F(1, 9) = 6.4$, $p < .05$, regardless of the arm used to reach ($p = .97$), although there was a trend in the two-way interaction between condition and type of data ($p = .057$). This was because after removing wrist's covariation with other joint motions, V_{ORT} increased for the CCT condition ($p < .01$) but not so for the UCT condition ($p = .29$; Fig. 3b).

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Removing covariation of elbow's movement with motions of other joints (Fig. 4b, middle panel) was associated with a significant four way interaction among group, arm, target condition and type of data (Table 3b). V_{ORT} increased more when removing elbow covariation in the young adults compared to older adults (Table 3b; Group by Data type interaction). For young adults, the increase in V_{ORT} depended on both target condition and the arm used to reach, $F(1, 10) = 6.8$, $p < .05$. For the left arm, V_{ORT} increased, $F(1, 10) = 18.7$, $p < .01$, regardless of the target condition ($p = .83$). For the right arm, the increase in V_{ORT} with removal of elbow covariation was greater when reaching to the central target under the UCT compared to the CCT condition, $F(1, 10) = 14.9$, $p < .01$. Removal of elbow joint covariation led to increased V_{ORT} in older adults, $F(1, 9) = 33.9$, $p < .001$, that did not depend on target condition ($p = .5$) or the arm used to reach ($p = .22$).

For shoulder joint movements (Fig. 3b, bottom panel), V_{ORT} increased for both groups when its covariation with other joints' motions was removed (Table 3b; data type), but more so in young compared to older adults (Table 3b, group by data type interaction). This increase for both groups did not differ across target conditions (Table 3b, group by target condition by data type interaction) or arms used to reach (Table 3b, group by arm by data type interaction).

Removal of a joint's covariation, especially the wrist with elbow and shoulder joints, or the elbow with shoulder and wrist joints, supported the main hypothesis that inter-joint coordination deteriorates with aging. The results also supported the hypothesis that inter-joint coordination in the right arm led to less hand path variability than in the left arm for young but not for older adults. The effect of the target condition was, however, somewhat inconsistent. For the left arm, inter-joint coordination led to less hand path variability when reaching if the target location was certain in advance of the reach. In contrast, for the right arm, inter-joint coordination tended to be similar regardless of the target location's certainty prior to reaching. However, during the late phase of reaching, inter-joint coordination of wrist and elbow joint motions with the other joints of the right arm led to less hand path variability when reaching in the UCT condition.

3.3. Differences in the covariation between proximal and distal joints during early versus late phase of the movement (third hypothesis)

The previous analysis of changes in V_{ORT} with removal of a joints' covariation provides an indication of the extent to which joint configuration variance that tends to cause changes in the hand's path would increase if a particular joint's motions had not been coordinated with those of other joints. However, the extent to which a given amount of increase in V_{ORT} actually affects the hand's path depends on factors such as the geometry of the limb. That is, an equal increase in V_{ORT} in two different joint configurations can lead to different amounts of hand position variability. The task variability ratio was computed to investigate directly how the lack of coordination of a joint's motion with other joints would affect the 3D hand position. If removal of covariation of a joint does not lead to greater variability of the 3D hand position, then the task variability ratio should be 1 (see Methods, Eq.3). If removing a joint's covariation with other joints leads to increased task variability, then the ratio will be less than 1.

The effect of removing covariation of a joint's motions with those of other joints on the task variability ratio differed between young and older adults depending on the phase of the movement and joint considered, i.e., there was a group by joints by phase interaction (Table 4; Fig. 4). There was no effect of the arm used to reach ($p = .38$) or the target condition ($p = .36$). For both young and older adults, the task variability ratio differed between phases depending on which joint's covariation with others was removed (YA: $F(2, 20) = 11.3$, $p < .01$, OA: $F(2, 18) = 37.6$, $p < .01$; Fig. 4). Post-hoc tests revealed that for both young and

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older adults, removal of wrist as well as elbow joint's covariation with other joints led to a lower task variability ratio for the period from peak velocity to movement termination compared to the period from movement onset to peak velocity (all comparisons, $p < .05$). Thus, coordination of wrist joint's motions with those of the shoulder and elbow, and coordination elbow joint's motions with those of the wrist and shoulder tended to stabilize the hand path more during the late than during the early phase of reaching. In contrast, removal of the covariation of shoulder joint motions with those of the other joints led to increased hand path variability that did not differ between the two periods of reaching. This was true for both age groups ($p > .14$). Also, for young adults, the value of the task variability ratio was smaller for the shoulder than the elbow than the wrist, regardless of the phase of reaching (both phases, shoulder and elbow: $p < .05$; wrist: $p < .001$).

For older adults during the early phase of reach, the task variability ratio also was smaller for the shoulder than the elbow than the wrist (all comparisons, $p < .001$). However, for the late phase of reaching the task variability ratio for the shoulder and elbow joints were similar in magnitude ($p = .53$), although still greater than that of wrist joint ($p < .001$).

Thus, in line with our prediction, the elbow and wrist distal joints covaried with other joints to stabilize the hand's path (i.e., lower TV_{ratio}) more during the late than the early phase of reaching whereas the shoulder joint's covariation with other joints was similar throughout the movement. In addition, the shoulder's coordination with other joints had more of an impact on reducing the hand path variability than did elbow and wrist joint coordination, as evidenced by a lower TV_{ratio} for the shoulder compared to the other joints when that joint's covariation was removed selectively.

4. Discussion

The primary goal of this study was to investigate the extent to which coordination of each of the shoulder, elbow and wrist joint motions with other joints contributes to stabilization of the hand's three-dimensional path during reaching and how that differs, if at all, between the arm used to reach, the phase of the reach and, of greatest interest, between young and older adults. Simulated data were analyzed relative to actual data using the framework of UCM approach to address this question (Scholz & Schöner, 1999; Verrel, 2011; Yen & Chang, 2011). It is important to emphasize that the simulation involved removal of only the covariation among joints to simulate the lack of joint coordination. The variability of individual joints was not removed. Thus, comparison of V_{UCM} and V_{ORT} between the actual data and the data from which covariation of pertinent joints with others was removed is expected to reveal the extent to which coordination of that joint with others stabilizes the hand path.

The current results support the hypothesis that inter-joint coordination of reaching diminishes with aging, as do differences between the arms used to perform the reach. The degree of inter-joint coordination also appears to depend, to some extent, on whether the target of reaching is fixed or uncertain in advance of the reach. Removing a joint's covariation with other joints resulted in a greater increase of V_{ORT} in young than in older adults, especially during the later half of the reach. Young adults also displayed stronger inter-joint coordination of the right compared to the left arm, indicated by the increase in V_{ORT} when removing a joint's covariation. This was particularly true when the target's final location was uncertain. However, older adults showed minimal arm differences. Thus, in general, our results supported the first two hypotheses that the right arm has stronger inter joint coordination than the left arm, although mainly in young adults and especially when there was an uncertainty in the target location. The finding that young adults are better coordinated than the older adults and that the right arm is more coordinated than the left may

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seem trivial at the outset. The contribution of this study was to quantitatively reveal the role of each of the shoulder, elbow and wrist joints in inter-joint coordination that stabilizes the hand path.

In previous studies, it has been shown that the CNS stabilizes the value of important performance variables by using flexible joint combinations, reflected by V_{UCM}, while minimizing V_{ORT} (de Freitas et al., 2007; Gera et al., 2010; Reisman & Scholz, 2006; Zhang et al., 2008). Minimizing the V_{ORT} variance component is more crucial for task stabilization because it reflects combinations of joint angles that lead to unwanted hand path variability. Interestingly, findings of the present study suggest that removal of a joint's covariation led to a greater increase in V_{ORT} than to a reduction in V_{UCM}. This indicates that the joints were co-varying to keep the variance that would lead to inconsistency of the hand path to a minimum. These findings suggest that the smaller amount of V_{ORT} for the right than the left arm for the period from peak velocity to reach termination observed by de Freitas et al. (2007), is accounted for by different contributions to inter-joint coordination of the shoulder, elbow and wrist joint that stabilize the hand's path in young versus older adults. Furthermore, the apparently better inter-joint coordination of the right compared to the left arm observed in young adults, especially when reaching in the uncertain target condition, could be a consequence of subjects' inexperience with such tasks using their non-dominant limb (Tseng et al., 2002).

Results of recent studies provide support for our findings. Although a joint torque analysis was not performed in this study, the observed differences between right and left arms of young adults are consistent with the dynamic-dominance hypothesis (Sainburg, 2005; Sainburg & Kalakanis, 2000). This hypothesis suggests that the dominant-arm/dominant hemisphere controls complex biomechanical interactions, e.g., interaction torques, that arise between moving limb segments in a more efficient manner than the non-dominant limb by better coordinating muscle actions. In contrast to young adults, older adults did not exhibit differences between the arms. Thus, the right arm/left hemisphere does not seem to have an advantage for controlling limb dynamics in older adults, suggesting reduced lateralization of this feature (Wang, Przybyla, Wuebbenhorst, Haaland, & Sainburg, 2011).

A possible explanation of age-related differences in our findings across arms could be provided by a model of reduced hemispheric asymmetry in older adults (HAROLD), as proposed for cognitive tasks by Cabeza (2002). This model was based on the observation of greater bilateral activations of brain regions for older than young adults. Recently, Wang et al. (2011) observed a reduction in hemispheric asymmetry related to performance of motor tasks. They found that, for a reaching task involving visuomotor adaptation, older adults were able to exhibit transfer of direction from non-dominant limb to dominant limb as well as vice-versa, whereas young adults exhibited poorer transfer from dominant to the non-dominant limb.

Moreover, in another study by the same group, older adults were shown to be more accurate and precise in reaching a target, with straighter hand paths, when reaching with the left arm compared to young adults (Przybyla, Haaland, Bagesteiro, & Sainburg, 2011). These findings suggest that older adults actually learn better control of left arm dynamics (Wang et al., 2011) and motor performance (Przybyla et al., 2011). Unlike the study of Przybyla et al. (2011), however, our findings do not suggest improved coordination of the left arm for older adults. Rather, the findings suggest that older adults did not coordinate their distal joints with others to the same extent as younger adults to adjust to the unexpected change in target location, as evidenced by no differences in the magnitude of V_{ORT} after removal of wrist covariation between certain and uncertain target conditions for older adults.

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Cabeza et al. (2002) have suggested that a reduction in hemispheric asymmetry for cognitive tasks with age is a reflection of increased activity of bilateral prefrontal cortex, which compensates for the deleterious unilateral hemispheric activity. Thus, it is conceivable that if the task complexity increases above a threshold, this compensatory activity may not be enough to retain similarly good performance across arms in task execution. This increased complexity may explain the poorer coordination of the wrist joint with other joints' motions in older adults, especially for the unpredictable target condition. The task investigated by Przybyla et al. (2011) required less complex coordination, involving reaching to central targets with only three planar joint motions, compared to the three-dimensional reaching task involving ten joint motions in the current study. Moreover, uncertainty of target location in the uncertain target condition added an additional cognitive component to the task, increasing its complexity. Another plausible explanation for symmetrical performance across arms and even better performance for older adults than younger adults in the study of Przybyla et al. (2011) could be that their older adults reached at a comfortable speed. In contrast, the current study had participants reach as fast as possible while being as accurate as possible. Thus, in the Przbyla et al. (2011) study, reaching at a comfortable speed likely provided older adults more time to correct their movement, which may account for their better performance than in the current study.

Covariation among proximal and distal joints differed between phases of the reach. In line with our prediction of the third hypothesis, we observed that distal joints covaried more with other joints during the late phase of the reach as compared to the early phase. This result supports the findings from the studies suggesting greater role of distal joints during the final adjustment phase of the reach (Jeannerod, 1999; Marotta et al., 2003; Wang, 1999). Simulating the lack of shoulder joint covariation with other joints increased hand path variability the most, however, followed by the lack of elbow and then wrist coordination with other joints' motions. This finding is not surprising given the larger contribution of proximal joint motions to overall hand path excursion. This finding is consistent, for example, with the leading joint hypothesis (Dounskaia, 2005) and the results of a study by Galloway and Koshland (2002). Both studies defined shoulder-centered reaching movements as those for which the shoulder produces most of the muscle torque for movement execution, whereas elbow-centered movements are those for which the elbow produces most of the muscle torque required for hand transport. In the present study, reaching to the central target involved greater shoulder joint excursion during the early phase of reaching, with elbow motion contributing more, later in the reach. Reaches were, therefore, primarily shoulder-centered. The fact that removal of shoulder joint covariation increased hand path variability the most is thus in line with the expectation for movements that are shoulder-centered. Also, for both the early and late phase of the reach, the arm differences in young adults were present mainly at the elbow and wrist joints. Given that the distal arm joints are more subject to the influences of interaction torques generated at the shoulder, diminished inter-joint coordination would make it more difficult to overcome these interaction torques, leading to greater hand path variability, as observed in older adults.

Diminished feedback processes with aging

Coordination differences in older compared to young adults also were more pronounced during the second half of the reach. This suggests poorer closed-loop processes with aging, important for online processing when the hand gets closer to the target. This would be consistent with diminished online control of the right hemisphere with aging (Elliott, Chua, & Pollock, 1994; Winstein & Pohl, 1995). Although our subjects did not have explicit visual deficits, subtle changes in sensory feedback processes due to aging could account for the observed findings (Sosnoff & Newell, 2007). Moreover, that older adults seemed to perform

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better when the target was fixed in advance compared to having an uncertain final location further suggests older adults have more difficulty in performing more complex tasks (Newell, Mayer-Kress, & Liu, 2009; Verrel et al., 2010).

5. Conclusion

The current investigation suggests that older adults have diminished joint coordination compared to young individuals, which affects the consistency of their hand paths. This was evidenced by a decrease in hand path stability in simulated data after removal of pertinent joints' covariation with others, and more so when rapid adjustments in the reach were required. The method used in the study provides a tool to distinguish the contribution of each joint to the stabilization of hand path.

Acknowledgments

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Age-related differences in performance of a double-step reaching task was studied Inter-joint coordination was investigated by simulated removal of joint covariation Better coordination = greater handpath variability with covariation (CV) removal

- CV removal resulted in greater hand path variability in younger than older adults
- Young adults had greater hand path variability for right than left arm with removal

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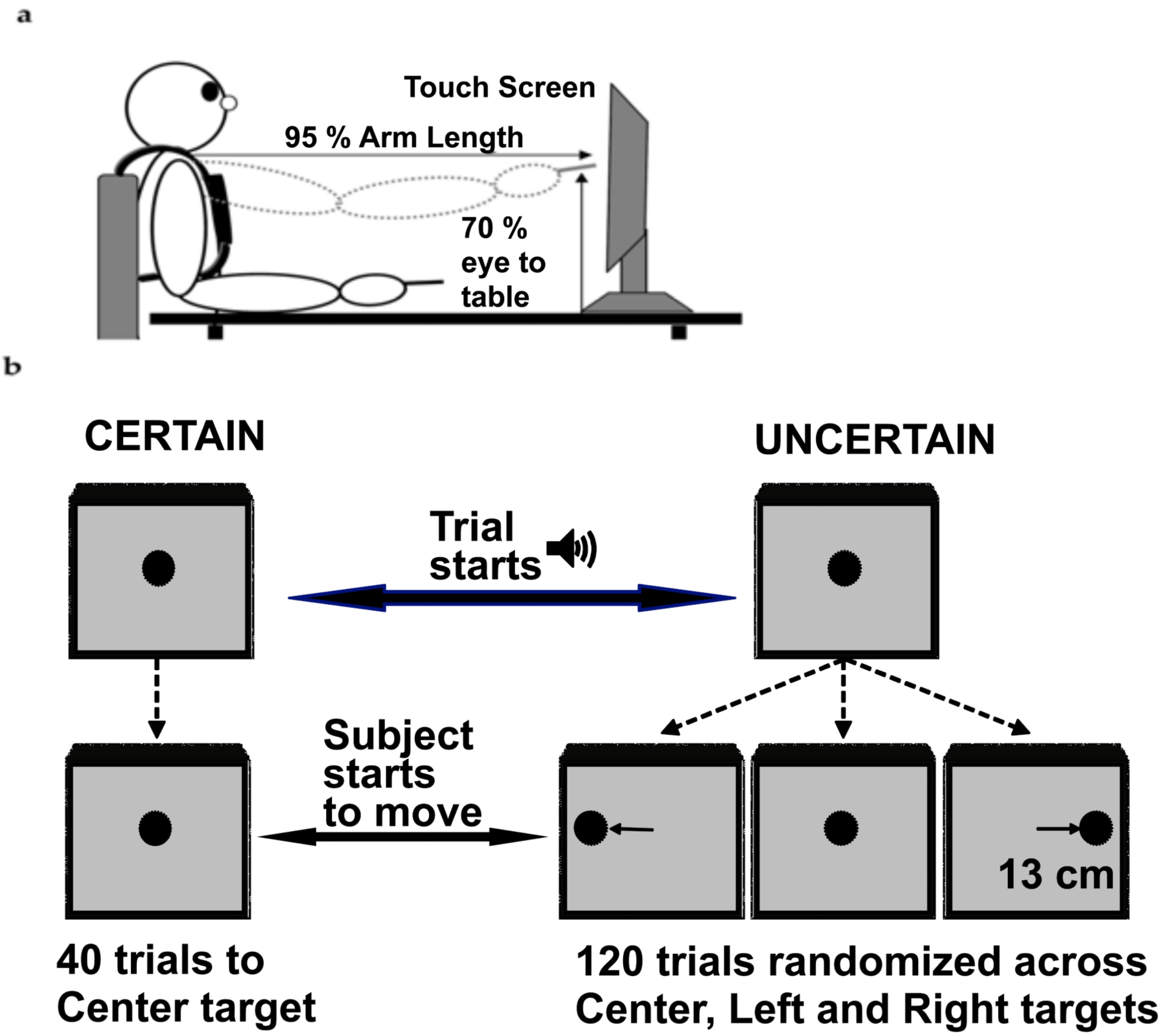

Fig. 1.
Experimental set-up when the young and older subjects performed the movements with right arm (a) and target position (b) presented at the beginning of the trial and immediately after the subjects' hand started to move for certain (left panels) and uncertain target (right panels). The experimental set-up was similar for left arm.

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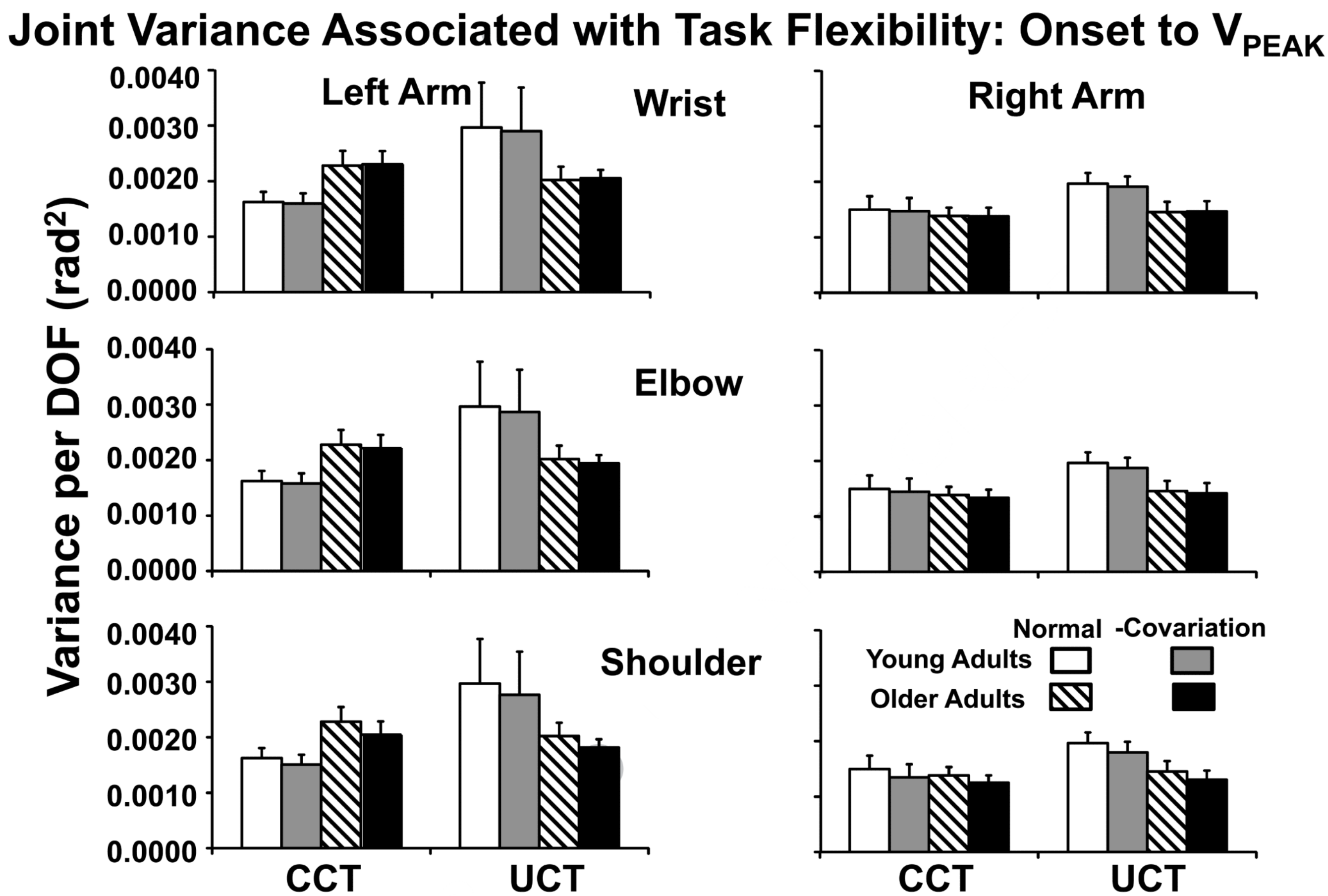

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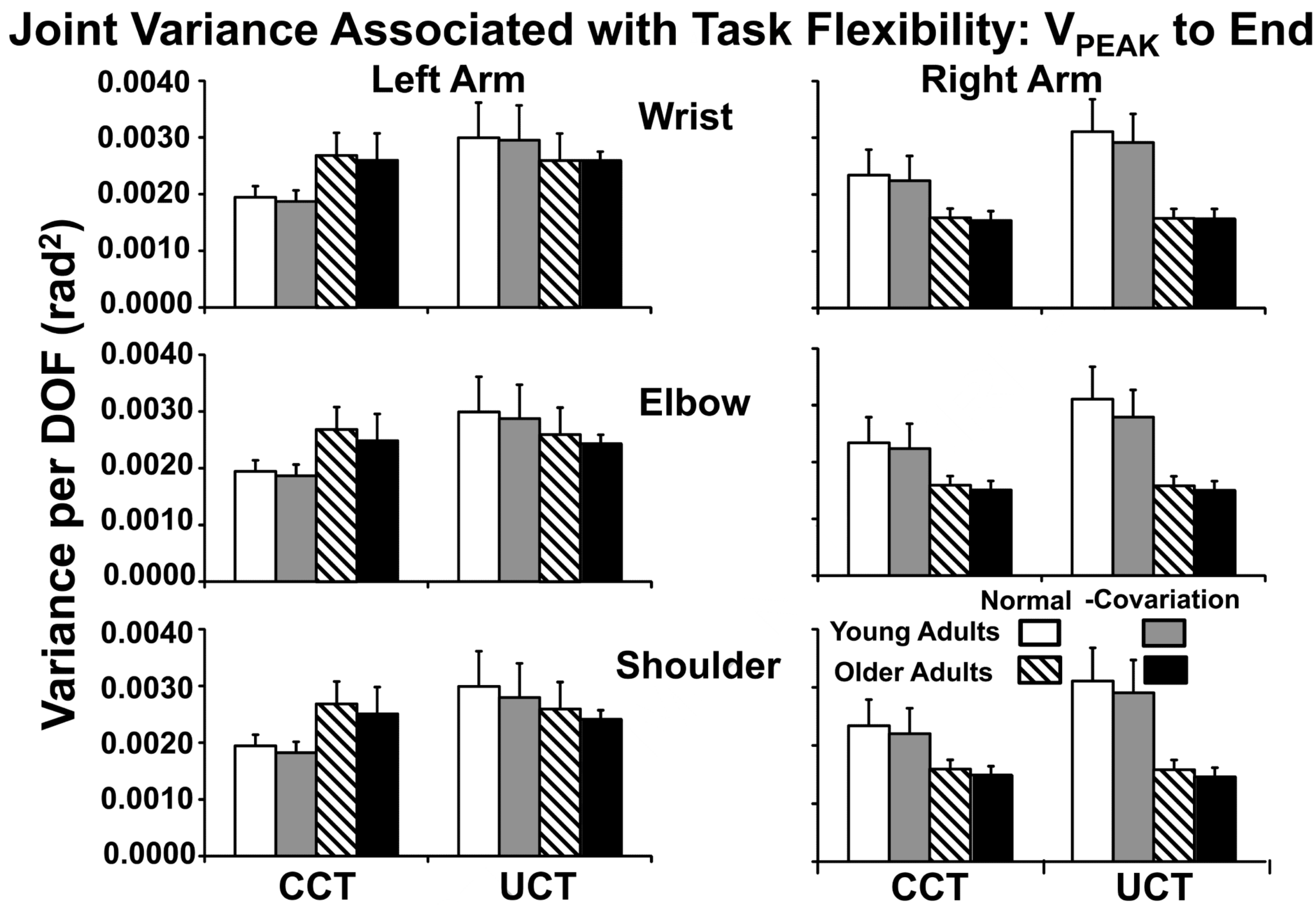

Fig. 2.

Averaged (across subjects) components of joint configuration variance within the uncontrolled manifold (V_{UCM}), averaged during the period (a) from movement onset to peak velocity and (b) from peak velocity to reach termination, computed from normal experimental data (white fill = young adults and diagonal fill = older adults) and after removing joint covariation (-Covariation; gray fill = young adults and black fill = older adults).

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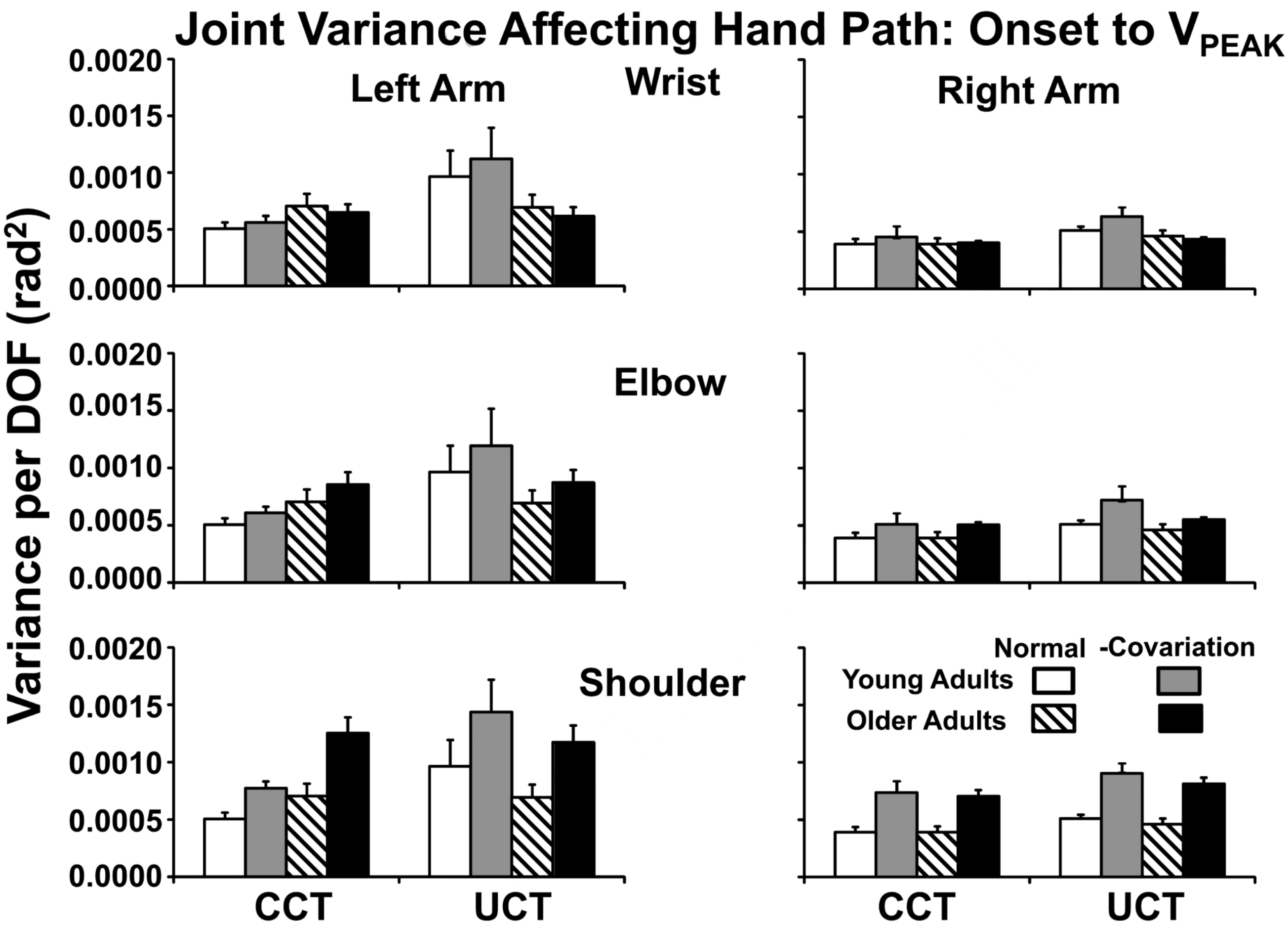

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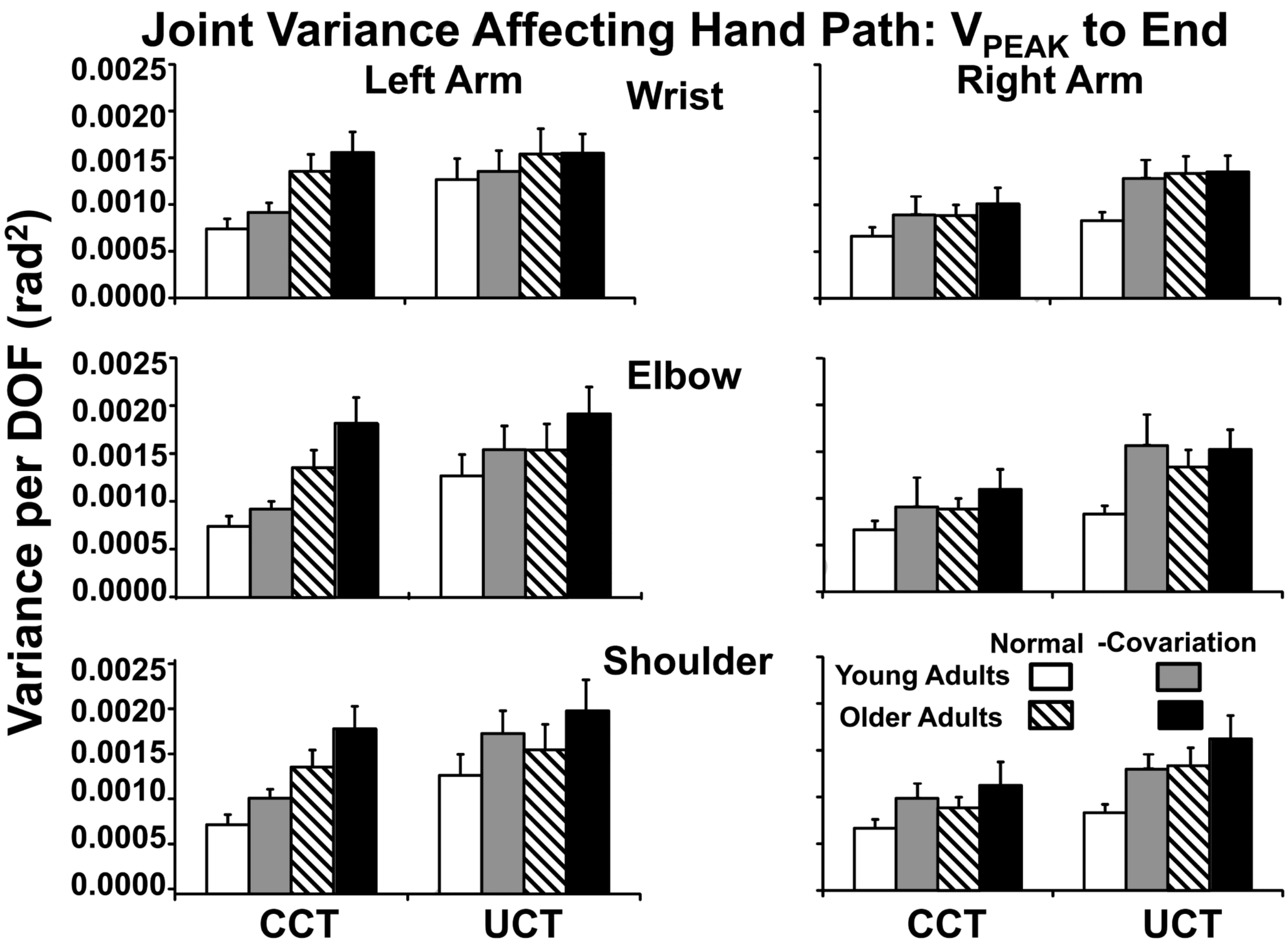

Fig. 3.

Averaged (across subjects) components of joint configuration variance orthogonal to the uncontrolled manifold (V_{ORT}), leading to hand path variability, averaged during the period (a) from movement onset to peak velocity and (b) from peak velocity to reach termination, computed from normal experimental data (white fill = young adults and diagonal fill = older adults) and after removing joint covariation (-Covariation; gray fill = young adults and black fill = older adults).

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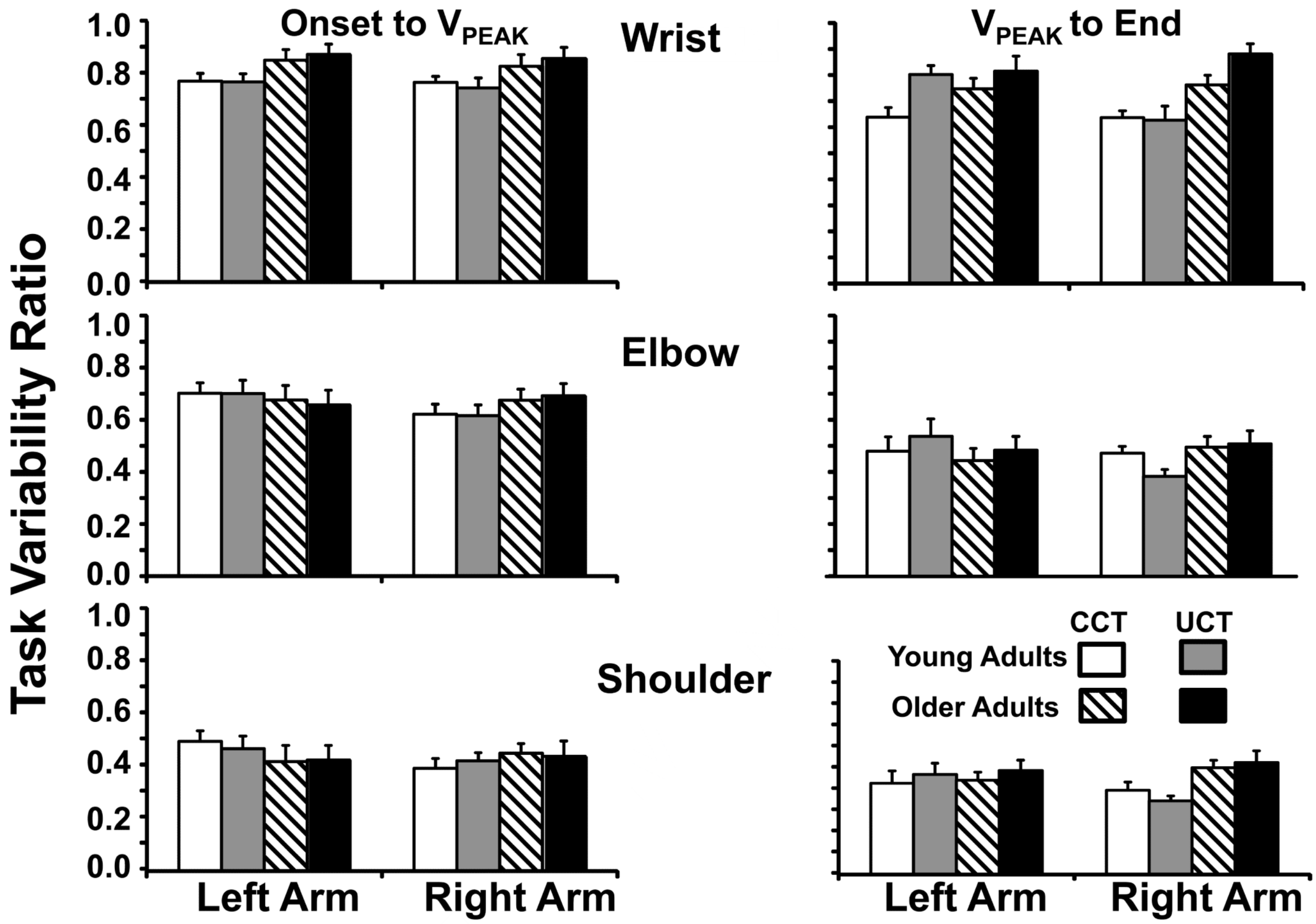

Fig. 4.

Mean, across each onset to peak velocity and peak velocity to termination phase, of the ratio of the estimated task variability (TV), i.e., $TV_{ACTUAL\ DATA}/TV_{COVARIANCE\ REMOVED}$, averaged across subjects (±*SEM*), related to control of the 3D hand position for each experimental target condition.

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Table 1

Movement time (± standard deviation) for the left and right arms of young and older adults when reaching under the two target conditions (CCT = certain center target; UCT = uncertain center target).

	Left Arm		Right Arm	
	CCT	**UCT**	**CCT**	**UCT**
Young Adults	431 ± 0.053-ms	443 ± 0.056-ms	433 ± 0.041-ms	424 ± 0.045-ms
Older Adults	573 ± 0.049-ms	582 ± 0.051-ms	580 ± 0.051-ms	596 ± 0.056-ms

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Table 2a

Onset to peak Velocity (UCM variance component)

Statistical analyses related to the UCM variance component for the period of a) onset to peak velocity and b) peak velocity to termination.

	Wrist			Elbow			Shoulder		
	$F_{(1,19)}$	**p**	**Effect size**	**$F_{(1,19)}$**	**p**	**Effect size**	**$F_{(1,19)}$**	**p**	**Effect size**
Data type	8.79	<0.01	0.32	92.73	<0.001	0.83	234.1	<0.001	0.93
Data type × Group	31.19	<0.001	0.63	0.009	0.93	0.0001	1.26	0.27	0.06
Arm × Data type	**2.08**	**0.17**	**0.09**	**0.71**	**0.41**	**0.04**	**0.62**	**0.44**	**0.03**
Target Condition × Data type	**0.74**	**0.40**	**0.04**	**0.03**	**0.87**	**0.002**	**0.18**	**0.68**	**0.01**
Target Condition × Data type × Group	4.14	0.06	0.18	0.06	0.81	0.003	0.21	0.60	0.01
Arm × Target Condition × Data type × Group	1.39	0.25	0.07	2.26	0.15	0.11	1.42	0.25	0.07

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Table 2b

Peak velocity to termination (UCM variance component)

Statistical analyses related to the UCM variance component for the period of a) onset to peak velocity and b) peak velocity to termination.

	Wrist			Elbow			Shoulder		
	$F_{(1,19)}$	**p**	**Effect size**	**$F_{(1,19)}$**	**p**	**Effect size**	**$F_{(1,19)}$**	**p**	**Effect size**
Data type	23.13	<0.001	0.55	60.14	<0.001	0.76	123.5	<0.001	0.87
Data type × Group	1.31	0.27	0.07	0.12	0.73	0.006	0.004	0.95	0.0002
Arm × Data type	**2.53**	**0.13**	**0.12**	**0.16**	**0.69**	**0.008**	**0.04**	**0.85**	**0.002**
Arm × Data type × Group	1.30	0.26	0.06	1.84	0.69	0.09	0.001	0.97	0.0001
Target Condition × Data type	**7.72**	**0.012**	**0.29**	**1.64**	**0.22**	**0.08**	**1.78**	**0.19**	**0.09**
Target Condition × Data type × Group	1.29	0.27	0.06	2.52	0.21	0.18	0.0002	0.99	0.000001
Arm × Target Condition × Data type × Group	4.65	0.04	0.20	1.52	0.23	0.074	0.99	0.33	0.05

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Table 3a

Onset to peak velocity (Orthogonal variance component)

Statistical analyses related to the orthogonal variance component for the period of a) onset to peak velocity and b) peak velocity to termination.

	Wrist			Elbow			Shoulder		
	$F_{(1,19)}$	p	Effect size	$F_{(1,19)}$	p	Effect size	$F_{(1,19)}$	p	Effect size
Data type	11.31	<0.01	0.37	133.8	<0.001	0.87	276.03	<0.001	0.93
Data type × Group	24.9	<0.001	0.57	0.086	0.77	0.005	0.45	0.50	0.02
Arm × Data type	**2.79**	**0.11**	**0.13**	**1.41**	**0.25**	**0.07**	**1.07**	**0.32**	**0.053**
Arm × Data type × Group	0.0004	0.90	0.00001	2.16	0.16	0.102	2.2	0.15	0.10
Target Condition × Data type	**0.47**	**0.49**	**0.024**	**0.004**	**0.95**	**0.0001**	**0.62**	**0.44**	**0.03**
Target Condition × Data type × Group	2.98	0.10	0.14	0.072	0.80	0.004	0.0001	0.99	0.00001
Arm × Target Condition × Data type × Group	0.94	0.34	0.047	1.64	0.22	0.08	0.48	0.49	0.025

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Table 3b

Peak Velocity to Termination (Orthogonal variance component)

Statistical analyses related to the orthogonal variance component for the period of a) onset to peak velocity and b) peak velocity to termination.

	Wrist			**Elbow**			**Shoulder**		
	$F_{(1,19)}$	**p**	**Effect size**	$F_{(1,19)}$	**p**	**Effect size**	$F_{(1,19)}$	**p**	**Effect size**
Data type	51.19	<0.001	0.73	116.5	<0.001	0.86	187.2	<0.0001	0.91
Data type × Group	9.07	<0.01	0.32	4.7	<0.05	0.2	10.9	<0.01	0.37
Arm × Data type	**3.47**	**0.08**	**0.15**	**0.62**	**0.44**	**0.03**	**0.49**	**0.49**	**0.03**
Arm × Data type × Group	3.58	0.07	0.16	3.60	0.073	0.16	2.37	0.14	0.11
Target Condition × Data type	**5.91**	**0.03**	**0.24**	**1.6**	**0.22**	**0.07**	**0.05**	**0.82**	**0.003**
Target Condition × Data type × Group	1.08	0.31	0.05	6.44	<0.05	0.25	1.08	0.31	0.05
Arm × Target Condition × Data type × Group	4.7	<0.05	0.2	5.1	<0.05	0.21	2.46	0.13	0.12

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Table 4

Task variability ratio

Statistical analyses related to the task variability ratio involving comparison of measure during the period of onset to peak velocity and peak velocity to termination by treating phase as a factor.

	F(2,38)	p	Effect size
Joints × Phase × Group	4.9	<0.05	0.21
Joints × Phase × Arm × Group	0.97	0.38	0.05
Joints × Phase × Condition × Group	1.04	0.36	0.05
Joints × Phase × Arm × Condition × Group	1.19	0.31	0.06