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Limb Position Drift: Implications for Control of Posture and Movement

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Abstract

In the absence of visual feedback, subject reports of hand location tend to drift over time. Such drift has been attributed to a gradual reduction in the usefulness of proprioception to signal limb position. If this account is correct, drift should degrade the accuracy of movement distance and direction over a series of movements made without visual feedback. To test this hypothesis, we asked participants to perform six series of 75 repetitive movements from a visible start location to a visible target, in time with a regular, audible tone. Fingertip position feedback was given by a cursor during the first five trials in the series. Feedback was then removed, and participants were to continue on pace for the next 70 trials. Movements were made in two directions (30° and 120°) from each of three start locations (initial shoulder angles of 30°, 40°, 50°, and initial elbow angles of 90°). Over the 70 trials, the start location of each movement drifted, on average, 8 cm away from the initial start location. This drift varied systematically with movement direction, indicating that drift is related to movement production. However, despite these dramatic changes in hand position and joint configuration, movement distance and direction remained relatively constant. Inverse dynamics analysis revealed that movement preservation was accompanied by substantial modification of joint muscle torque. These results suggest that proprioception continues to be a reliable source of limb position information after prolonged time without vision, but that this information is used differently for maintaining limb position and for specifying movement trajectory.

INTRODUCTION

Perception of limb position with respect to both the body and the external world depends on information provided by vision, proprioception, and touch (Graziano 1999; van Beers et al. 1998, 1999). Hand position matching experiments, in which the participant indicates the location of an occluded hand by matching its location with the other hand, show that without vision, the accuracy with which finger location is reported declines over repeated matches such that perception of limb position appears to drift (Paillard and Brouchon 1968; Wann and Ibrahim 1993; Wolpert et al. 1998). Drift is attenuated, however, when passive or active movements are performed with the target limb between matching trials (Paillard

and Brouchon 1968) or when brief isometric contractions are performed with the target limb between reports (Wann and Ibrahim 1993). These results suggest that the efficacy with which proprioception conveys information about limb position is altered during prolonged periods without vision or without movement.

Two findings call this explanation into question, however. First, Desmurget et al. (2000) showed that with a hand position-matching task, drift distance did not grow over time when only two matching reports were made in a 20-s period. This finding is inconsistent with a proprioceptive decay account because participants' ability to indicate limb position did not decrease as a function of time. Second, several researchers have shown that when shapes are drawn continuously without vision, shape position drifts but shape form is preserved (Brown and Rosenbaum 2001; Brown et al. 2003; Verschueren et al. 1999; Zelaznik and Lantero 1996). Shape form preservation coupled with shape position drift appears inconsistent with proprioceptive decay because preserved movement production depends on knowledge of current limb position.

Previous studies have shown that initial limb position information influences performance of both movement trajectory and endpoint accuracy. Reaching accuracy is degraded when vision of the limb is removed prior to movement onset (Desmurget et al. 1997; Ghez et al. 1995; Ghilardi et al. 1995; Prablanc et al. 1979; Vindras et al. 1998; Vindras and Viviani 1998), and reaching accuracy is systematically affected by dissociations between visual feedback about limb position and somatosensory feedback about limb position (Lateiner and Sainburg 2003; Rossetti et al. 1995; Sainburg et al. 2003). Moreover, single-unit recording studies have shown that limb position information influences the neural coding of movement parameters. In the macaque primary motor and premotor cortex the population vector, the weighted average of single-cell movement direction selectivity, reflects movement direction in relation to the start position of the hand in extrinsic space (Georgopoulos et al. 1986). With regard to single-unit activity, preferred directions are modified as the hand adopts new starting postures (Caminiti et al. 1990, 1991) even when initial hand location, movement trajectory, and end position are held constant (Scott and Kalaska 1996; Scott et al. 1997). This implies coding of movement in relation to both intrinsic and extrinsic representations of initial hand position. The importance of such information is further underscored by the finding that pointing errors accumulate over the course of a movement sequence while movement amplitude is preserved, such that end position errors mirror start position errors (Bock and Arnold 1993; Bock and Eckmiller 1986). Taken together, these studies emphasize the importance of initial hand location information in planning and executing accurate movement trajectories.

The experiment reported here was designed to investigate the source of limb position drift and to determine whether drift affects movement production. The possibility that drift results from the accumulation of movement-dependent error was tested by asking participants to perform repetitive back-and-forth movements along axes that were 30° or 120° relative to the coronal axis and to do so in the absence of visual feedback. The two directions required different relative amounts of shoulder and elbow motion resulting in movement-dependent differences in both the dynamic interactions between the segments and the inertia that had to be overcome to initiate and produce the movements (Gordon et al. 1994b; Gribble and

Ostry 1998; Sainburg et al. 1995). If position drift is dependent on such dynamic factors, the drift associated with 120° movements should be different from the drift associated with 30° movements. We also tested the possibility that the hand might drift toward an attractor position. We did this by varying start location. If drift is position-dependent such that the limb drifts toward an attractor (either a specific spatial location or a posture), both drift distance and direction should vary with start location. Finally, we tested the hypothesis that drift is due to proprioceptive decay. We addressed this issue by analyzing kinematic and kinetic features of the movement trajectories produced. We reasoned that if drift is the result of decay in the usefulness of proprioceptive information concerning start position when vision is absent, then movement distance and direction should vary as the hand drifts away from its initial position.

Portions of this research were presented at the 2002 meeting of the Society for the Neural Control of Movement, Naples, Florida, and the 2002 meeting of the Society for Neuroscience, Orlando, Florida.

MEHODS

Participants performed blocks of 75 back-and-forth movements along axes in each of two directions (30° and 120° with respect to the right-pointing horizontal) from three start locations in time with a metronome. Hand location information was shown during the first five movements but was removed for the following 70 movements. Movements were restricted to the horizontal plane, involved elbow and shoulder motion only, and were carried out with the arm supported by a frictionless air sled system.

Participants

Five healthy students (3 female, 2 male), aged 21–25 years, participated. All were right-handed according to the Edinburgh Handedness Questionnaire (Oldfield 1971) and had normal or corrected-to-normal vision. All participants gave informed consent prior to participation.

Apparatus

Each participant was seated securely at a table such that its horizontal surface was positioned just below shoulder height. The participant's trunk was fit snugly against the table's edge. As touch is a powerful signal for preventing the misalignment of extrinsic and intrinsic reference frames (Lackner and DiZio 2000), this contact between the trunk and the table reduced the likelihood that hand drift would arise from progressive misalignment of trunk-centered and table-centered frames of reference. The participant's fingers, hand, and wrist were immobilized with a splint, and the forearm was secured to a custom-made air-jet sled that allowed the arm and hand to float over the table surface without friction. Movements of the arm and forearm were monitored with a Flock of Birds (Ascension-Technology) magnetic motion recording system controlled by a Macintosh computer. One 6-DOF sensor was mounted on a plastic cuff and secured to the upper arm, and a second sensor was mounted on the air sled. These sensors transmitted position and orientation data, digitized over time at 103 Hz, to the computer where they were stored for later analysis.

Custom-designed software controlled both the presentation of experimental conditions to the participant and data collection.

A horizontal back-projection visual display system was suspended above the table surface (Fig. 1). The back-projection screen was suspended 21 cm above a mirror that was in turn suspended 21 cm above the table surface. This arrangement gave participants the impression that the visual display was in the same horizontal plane as the table surface. The start locations, targets, and cursor representing fingertip location were presented within the resulting virtual-reality environment.

Three start locations, defined by initial shoulder angles of 30°, 40°, and 50° and an initial elbow angle of 90°, were customized for each individual. All joint angles were defined with respect to the extension of the more proximal limb. Target locations were defined such that movement direction was 30° or 120° with respect to the rightward horizontal at each start location. The start and target circles were 2 and 4 cm in diameter, respectively, and were separated by 15 cm.

Start and target circles were presented on a white rectangular display (91 × 67 cm) that was projected onto the framed, rectangular (87 × 154 cm) back projection screen. The mirror through which the participant viewed the display (also 87 × 154 cm) was framed by dark green fiberglass. The room lights were extinguished. Light from the display was sufficient to keep the mirror's frame illuminated. The continuous visibility of the frame reduced the likelihood that hand drift would arise from drift in their visual reference frame (Adams 1912).

Experimental design

We used a 3 start locations × 2 movement directions × 75 movement trials within-participants design. Each participant performed two practice blocks of 25 trials prior to performing six blocks of 75 repetitive movement trials. Each of the six combinations of start location and movement direction was presented randomly.

Experimental task

Participants performed blocks of 75 trials involving repetitive movements to the target and back to the start location in time with a computer-generated metronome. Each block was self-initiated and lasted 120 s. During the first five trials of each block, the participant viewed a 1-cm-diam cursor that reflected the continuous location of the index fingertip. The participant initiated the trial by aligning the cursor with the start circle, at which time a 50-ms tone sounded. This tone recurred at 1.6-s intervals for the remainder of the block and did not depend on hand location. Participants were instructed that on hearing each tone, they should move quickly and accurately to the target and back to the start location. The participants were further instructed that they should return to the start location in enough time to treat the next tone as a signal to begin the next movement. The participant was informed in advance that cursor feedback would be removed after the fifth trial. In addition, the participant was instructed to continue to perform the task on-pace and as accurately as possible for the remainder of the block.

Kinematic analysis

Data were analyzed off-line using custom-designed software developed with IgorPro (Wavemetrics) and Matlab (Mathworks). Prior to data collection, the three-dimensional (3D) positions of the index fingertip, elbow, and shoulder with respect to the fixed arm and forearm sensors were measured with a calibration stylus. This allowed us to calculate the 3D positions of the index finger, elbow, and shoulder from sampled sensor position and orientation data. Position data were filtered with a third order, dual-pass Butterworth filter (cutoff frequency = 8 Hz) and differentiated over time to obtain measures of linear velocity and acceleration at the fingertip, elbow, and shoulder. All velocity profiles were visually inspected to determine movement initiation and termination. Movement initiation was defined as the velocity minimum closest in time and preceding peak velocity that fell below a 12% peak velocity cut-off threshold. Movement termination was defined as the first velocity minimum that both followed peak velocity and fell below a 12% peak velocity cut-off threshold.

To characterize hand start location changes over the block of trials (hand drift), we calculated both cumulative and instantaneous hand drift extent and direction for the first 70 trials in each block. *Cumulative drift* was defined as the Euclidean distance between the start location adopted during trial 1 and each successive start location ($\text{location}_i - \text{location}_1$, $i = 1-70$), whereas *instantaneous drift* was defined as the Euclidean distance between each start location and the previously adopted start location ($\text{location}_i - \text{location}_{i-1}$, $i = 2-71$). These distances are shown in Fig. 2. Shoulder and elbow angular cumulative and instantaneous drift were calculated in a similar way except with respect to joint angles rather than spatial positions. Cumulative and instantaneous drift direction was defined as the angle subtended by the line joining the initial start location with the final start location with respect to the horizontal.

Hand movement distance and direction were measured for movements from the start location to the target. Movement distance was defined as the Euclidean distance between the hand location at movement initiation and the hand location at movement termination. Movement direction was defined as the angle subtended by the line joining the two locations with respect to the horizontal.

Kinetic analysis

Joint torques were calculated for the shoulder and elbow using the equations detailed in the APPENDIX. We assumed that the upper extremity consisted of two interconnected rigid links (upper arm and forearm) with frictionless joints at the shoulder and elbow. The shoulder was allowed to move freely, and the torques resulting from linear accelerations of the shoulder were included in the equations of motion for each joint as detailed in the APPENDIX (Bagesteiro and Sainburg 2002). The inertia and mass of the forearm support were 0.0247 kgm^2 and 0.58 kg , respectively. Limb segment inertia, center of mass, and mass were computed from regression equations using participants' body mass and measured limb segment lengths (Winter 1990).

It is important to note that computed joint muscle torque cannot be considered a simple proxy for the neural activation of muscles acting at the joint. Muscle torque does not distinguish muscle forces that counter one another during co-contraction and it includes the passive effects of soft tissue deformation. In addition, the force generated by muscle in response to a given neural input signal is dependent on muscle length, velocity of muscle length change, and recent activation history (Abbot and Wilkie 1953; Wilkie 1956; Zajac 1989).

Shoulder and elbow torque profiles were integrated over time from time of movement initiation to time of peak tangential hand velocity to obtain measures of initial shoulder and elbow torque impulses. Torque impulse was calculated to provide a summary measure of the magnitude of torque applied during the defined time period.

Simulations

We used a simulation to estimate what the movement trajectory would look like if participants were to apply the same torque strategy both early and late in the trial. We solved the equations of motion for a two segment, two frictionless pin-joint system, and then forward integrated using a fixed 1-ms time step. Inputs to each simulation were initial shoulder and elbow angles, participants' limb dimensions and inertial values, and the joint torque histories calculated from a recorded movement trial. Thus we were able to predict the effects of an ideal open-loop controller by using the muscle torques computed for a movement made from a given initial position to drive the simulation originating from a new initial position. We calculated the forward integration error by comparing a simulated hand path to that of the actual trial, beginning with the same initial conditions. The maximum error was 0.61 mm (see Sainburg et al. 1999).

Statistical analysis

Most dependent measures reported here were submitted to a start location (30°, 40°, and 50° shoulder angle) × movement direction (30°; 120°) × trial number (1–70) repeated-measures ANOVA ($\alpha = 0.05$). We removed the final five movement trials from the analysis to eliminate artifacts associated with the end of the block. Significant interactions were decomposed by computing simple main effects. Significant main effects of start location were analyzed further using Bonferroni-corrected pairwise comparisons. Significant main effects involving trial number were further analyzed using planned comparisons (*t*-test) between mean vision-present performance (mean of trials 1–5), mean early vision-absent performance (mean of trials 6–10), mean mid-block vision-absent performance (mean of trials 35–40), and mean late vision-absent performance (mean of trials 65–70). Drift direction means and variances were calculated using circular statistics (Fisher 1993). Differences between conditions for cumulative drift direction were assessed by conducting pairwise Watson's *F* tests. Statistical analysis of cumulative and instantaneous drift direction variance over time was conducted by submitting the arcsine transformation of angular variance to a repeated-measures ANOVA.

RESULTS

When participants performed the task without visual feedback, hand location at the initiation of each movement gradually drifted away from the visible start location. Figure 3 shows the series of 70 hand paths produced by one participant (P5) in each start location and movement direction. In each plot, the prescribed start location is shown as a black ring, and the target location is shown as a closed circle. Thirty-degree movement paths are shown on the *top row* and 120° movement paths are shown on the *bottom row*. Progression of the block over time is represented by the gray shade of the movement paths. In all of the plots, although hand position drift is evident, movement extent and direction appear relatively preserved over time. To quantify the drift, we computed both cumulative and instantaneous drift over trials. The results are shown in Fig. 4.

Without visual feedback, drift accumulates over time

Figure 4A shows the mean instantaneous hand drift, reflecting the change in hand start locations between each successive outward movement, for each start position and target direction separately. Data were averaged across every 10 movements for graphical clarity, whereas the statistical analysis was conducted using individual trials. As seen in the figure, instantaneous hand drift (1.37 ± 0.1 cm) remained constant across successive trials [$F(69, 276) = 1.19$; not significant (ns)]. Instantaneous drift varied reliably with movement direction [$F(1, 4) = 96.63$, $P = 0.001$], such that it was consistently greater for movements to the 120° target (1.49 ± 0.1 cm) than for movements to the 30° target (1.26 ± 0.1 cm; see Fig. 4B). There was also a main effect of start location [$F(2, 8) = 8.21$, $P = 0.012$], such that average instantaneous drift was larger at start location 3 (1.45 ± 0.1 cm) than at either start location 1 (1.34 ± 0.1 cm) or 2 (1.33 ± 0.1 cm). There were no other significant main effects or interactions.

Average cumulative hand drift, representing the distance of the hand from the original start position, is presented in Fig. 4C. Hand position drift increased early in the trial block, reaching an apparent plateau near trial 40. The increase was confirmed by a main effect of trial number [$F(69, 276) = 12.69$, $P < 0.001$]. Cumulative drift increased abruptly when vision was removed (vision-present versus early vision-absent, $P < 0.001$), and continued to accumulate to mid-block (early vision-absent vs. mid-block vision-absent, $P = 0.005$). However, drift did not accumulate appreciably beyond mid-block (mid-block vision-absent vs. late vision-absent, $P = 0.424$). On average, hand position drifted 7.9 ± 0.2 cm from the initial start location by trial 40, but position changes did not accumulate significantly beyond this point.

Cumulative hand drift was affected by movement direction but not by manipulations of start location. Figure 4D shows the rate of drift accumulation early in the block (between trials 6 and 40) and late in the block (between trials 41 and 70). A significant interaction between movement direction and trial number [$F(69, 276) = 1.42$, $P = 0.027$] showed that drift accumulated more quickly for 120° movements than for 30° movements early in the block, but there was no effect of movement direction on drift accumulation rate late in the block. Furthermore, total drift distance was not different for the two movement directions

($P = 0.269$). Finally, there were no significant main effects or interactions involving start location.

Figure 5 shows vectors representing the mean cumulative drift distance (vector magnitude) and the mean cumulative drift direction (vector angle) for each participant (symbols), from each start position, for both the 30° and 120° targets (black and gray, respectively). Cumulative drift direction did not vary as a function of movement direction ($P = 0.60$). Pairwise comparisons of mean cumulative drift direction as a function of start location showed that start location 2 differed significantly from both start location 1 ($P < 0.001$) and start location 3 ($P < 0.05$). Start location 1, however, did not differ significantly from start location 3 ($P = 0.86$), indicating that there was no systematic tendency to modify drift direction as a function of start location. There was a tendency for hand position to drift outward from the body and to the left of the initial start location, taking the shoulder and elbow joints away from the middle of the range of motion. We quantified cumulative drift direction variability over time by computing SD in moving windows of 10 points from trial 6 (the first vision-absent trial) through trial 70. Analysis of within-trial cumulative drift direction SD, shown in the *inset* of Fig. 5, indicated that cumulative drift direction variability was relatively consistent over a block of trials.

We analyzed the time course of instantaneous drift direction variability to determine how cumulative drift could increase and then plateau while instantaneous drift remained constant over time. The results of this analysis are presented in Fig. 6. Figure 6A shows the path produced by plotting the series of movement start positions adopted by one participant (P4) in each condition. For clarity, we plotted start positions from vision-absent trials only. Moreover, only every third start location is plotted. Early in the trial, as the participant began to drift away from the initial start location (represented by cross-hairs), instantaneous (movement-to-movement) drift vectors tended to fall along a particular direction, allowing drift to accumulate, whereas later in the trial the drift vectors were more random. Late in the trial, instantaneous drift direction variability increased dramatically such that changes in position no longer took the hand away from the initial start location, and cumulative drift plateaued. We quantified this increase in variability over time by computing instantaneous drift direction SD in moving windows of 10 points from trial 6 (the first vision-absent trial) through trial 70. The results of this calculation across participants, presented in Fig. 6B, resemble the single participant data shown in Fig. 6A. Instantaneous drift direction variability was relatively low early in the series, but then increased later in the series [$F(54,216) = 5.02$, $P < 0.001$]. This increase in instantaneous drift direction variability curtailed the further accumulation of cumulative drift.

To summarize, participants' hand position drifted during performance of this repetitive reaching task in the absence of visual feedback. Although instantaneous drift remained small and constant over time, hand position drift accumulated substantially during the early portion of the block and then reached an apparent plateau at mid-block (around trial 40).

Movement distance and direction were preserved as hand position drifted

We reasoned that if drift was the result of decay in the usefulness of proprioception when vision was absent, movement distance and direction would vary considerably as the hand

drifted away from its initial position. By contrast, if proprioception remained a reliable source of limb configuration information, then movement distance and direction would be preserved even though the hand drifted.

Data bearing on these predictions appear in Fig. 7, A and B. Figure 7A shows hand movement distance from the start location to the target, and Fig. 7B shows direction from the start location. For this figure, every 10 trials were averaged for graphical clarity, but the actual statistical analyses were conducted using individual trials. Because hand position drift reached a plateau by trial 40, we looked for changes in movement distance and direction over the first 40 movements only. This strategy increased the likelihood that the effects of hand drift on production of movement distance and direction would be detected.

Movement distance increased significantly as a function of movement direction and trial number [$F(39, 156) = 3.63, P < 0.001$]. This interaction, however, could be attributed more to the removal of visual feedback than to hand position drift. Figure 7A shows that for 30° movements, movement distance increased abruptly when visual feedback was removed, but movement distance did not change significantly thereafter ($M_{\text{early}} = 0.189 \pm 0.014$ vs. $M_{\text{mid-block}} = 0.207 \pm 0.018$ m, ns). In contrast, for 120° movements, movement distance was not affected by the removal of visual feedback and did not change significantly thereafter ($M_{\text{early}} = 0.175 \pm 0.007$ vs. $M_{\text{mid-block}} = 0.170 \pm 0.015$ m, ns). On the whole, the results show that movement distance was preserved as hand position drifted.

Although the target movement distance was 15 cm, the performed movement distance was generally >15 cm, even when vision was available. This hypermetria was greater for movements in the 30° direction (0.199 ± 0.001 m) than for movements in the 120° direction [0.173 ± 0.001 m; $F(1, 4) = 8.19, P = 0.046$]. Similar accounts of direction-dependent hypermetria have been described in previous studies of horizontal reaching (Gordon et al. 1994a,b; Sainburg et al. 1995).

Mean movement direction produced over time is summarized in Fig. 7B. Most importantly, movement direction did not vary significantly with trial number [$F(39, 156) = 0.953$, ns], indicating that movement direction was preserved over the portion of the block when hand position drifted most rapidly. Not surprisingly, observed movement direction varied significantly with prescribed movement direction [$F(1, 4) = 674.96, P < 0.0001$]. Observed movement direction also varied significantly with manipulated start location [$F(2, 8) = 10.29, P = 0.006$]. Movement directions produced at start location 1 ($73.44 \pm 2.54^\circ$) showed clockwise direction errors with respect to movement directions produced at start locations 2 ($78.15 \pm 2.01^\circ$) and 3 ($79.09 \pm 2.83^\circ$). Thus there was a clockwise rotation error that varied directly with the rightward eccentricity of the prescribed start location, consistent with observations of Ghilardi et al. (1995).

The evidence presented in this section demonstrates that while hand position drifted approximately 8 cm from its original location, movement distance and direction were preserved over time. This pattern of results suggests that 1) proprioception remained a reliable source of limb position information over time, and 2) participants were able to

use this proprioceptive information to adjust motor commands such that movement was preserved as the hand drifted.

Movement dynamics changed to preserve movement distance and direction

To preserve movement distance and direction as hand position drifted, torques generated at the shoulder and/or elbow must have changed. We calculated the necessary muscle torque generated at the elbow and shoulder for each participant. Results for a typical participant (S3) are shown in Fig. 8, A–D. In this example, movements were performed in the 120° direction from start location 3. In Fig. 8A, the movement path for a trial generated early in the block, immediately after vision was removed (*right*), is juxtaposed with a movement path generated late in the block, after the participant reached the cumulative drift plateau (*left*). Although this participant drifted 9.1 cm to the left and toward the body as the block progressed, the late movement path appears similar to the early movement path in both distance and direction.

Using drift, movement distance, direction, and peak velocity as measures, we compared the mean of the first five postvision movements (“early-block” trials) with the mean of five consecutive postplateau movements (“late-block” trials) using an independent-samples *t*-test. Figure 8B demonstrates that while early-block hand position was significantly different from late-block hand position ($P < 0.001$), movement distance ($P = 0.241$), movement direction ($P = 0.206$), and peak velocity ($P = 0.774$) were preserved.

Figure 8C shows the shoulder (*left*) and elbow (*right*) muscle torque profiles from movement initiation to peak tangential velocity for the same early- and late-block movements. Values greater than zero represent flexor muscle torque, and values less than zero represent extensor muscle torque. Whereas the difference between the early- and late-block elbow muscle torque profiles was minimal, shoulder flexor torque generated for the early-block movement was notably greater than that generated for the late-block movement. To obtain measures of initial shoulder and elbow torque impulse, we integrated the shoulder and elbow muscle torque profiles from movement initiation to peak velocity. Mean shoulder and elbow torque impulse are presented in Fig. 8D and Table 1. Positive impulse values represent flexor muscle torque impulse, whereas negative values represent extensor muscle torque impulse. While the comparison of early- and late-block elbow muscle torque impulse did not turn up a significant difference ($P = 0.070$), early-block shoulder muscle torque impulse was consistently different from late-block shoulder torque impulse ($P = 0.019$).

This analysis was repeated for each participant individually. Because drift varied in extent and direction across participants, we expected drift-dependent modifications of torque also to vary across participants. The details are presented in Table 1. All participants showed differences between early- and late-block shoulder torque impulse, and two of five participants showed differences between early- and late-block elbow torque impulse. Therefore according to this analysis, all of the participants modified their muscle torque strategy as hand position drifted.

As stated in our description of the kinetic analysis, joint muscle torque does not directly reflect the neural activation of muscles acting at the joint. Muscle torque includes forces

generated during co-contraction and the passive effects of soft tissue deformation, and both active and passive force generation depends on muscle length, velocity of muscle length change, and recent activation history (Abbot and Wilkie 1953; Wilkie 1956; Zajac 1989). Nonetheless, it is highly unlikely that the shoulder muscle torque changes reported here reflect passive changes to muscle and tendon stiffness and viscosity. To begin with, the likelihood that the observed position changes were perfectly compensated by passive changes in muscle properties is very small. This possibility becomes even more unlikely when one considers that movement trajectory was preserved at all levels of our two-direction by three-start position design.

If movement dynamics had not changed, movement direction might not have been preserved

We next asked how the movement trajectory would have changed if participants had *not* modified their muscle torque strategies as hand position drifted. We implemented a simple two-segment rigid body simulation (Sainburg et al. 1999). The muscle torques calculated from an early trial, with minimal position drift, were used as inputs to the forward dynamic equations of motion. The forward simulation was performed with the inertial values and geometric parameters of the participant, but was initiated from a new hand position that reflected the start position of the first postdrift plateau trials in the trial block. In effect, this simulation predicted what would have happened to movement direction if early, predrift torque profiles were applied at late, postdrift hand positions.

Figure 9A shows the results for typical trials to the 120° and 30° targets for participant S3. On the *left* are shown the 120° movement hand paths from an observed early trial, an observed late trial, and a simulated trial. The distance and direction of the early and late trial are similar, although the late trial was initiated some 9 cm medial and posterior to the early trial. In contrast, the simulated trial predicted a 33° counterclockwise shift in movement direction compared with the actual late-block trial. Thus the simulation shows that using the same torque profiles to drive the limb from the drifted position would have rotated movement direction substantially. The torque profiles in Fig. 9B show a 50% reduction in shoulder flexor muscle torque between the early and late movement. This reduction did not occur in the simulation, leading to a large counterclockwise direction error in the simulated trial.

The *right panel* of Fig. 9A shows the 30° hand paths for an observed early trial, an observed late trial, and for a simulated trial. The early and late trials were similar in direction and amplitude, although the late trial was initiated 10 cm medial to the early trial. Application of the early trial torque profiles to drive the simulation from the late start position resulted in an 8.4° counterclockwise error. Torque profiles in Fig. 9B (*right*) show a near 20% increase in shoulder extensor torque between the early and late movements. In the simulation, this extensor torque increase did not occur, resulting in a clear counterclockwise direction error.

It should be emphasized that this simulation was implemented through torque actuators and thus does not consider muscle and tendon properties and geometries. It simply predicts, for a two-segment, rigid body system, how application of the same torque to a “drifted” limb configuration would produce substantial errors in movement direction. Our kinematic

analysis revealed that movement direction errors did not occur, whereas our inverse dynamic analysis revealed that substantial changes in muscle torque were associated with the drifted limb positions. We therefore conclude that participants systematically adjusted their dynamic control strategies in accord with drift-induced changes in initial limb configuration.

Joint angular cumulative drift depends on posture maintenance and movement production

As the foregoing discussion indicates, our results show that movement trajectory was preserved while limb position drifted. We next examined how drift was distributed across the shoulder and elbow joints. Mean angular excursions and mean final cumulative drift for 120° and 30° movements are presented in the *left* and *right panels* of Fig. 10, respectively. Figure 10A shows that for 120° movements, the elbow and shoulder contributed both to movement production and posture maintenance. Figure 10C shows that there was significant drift accumulation both at the elbow ($P=0.019$) and the shoulder ($P=0.022$). Figure 10B shows that for 30° movements, there was a well-defined division of labor between the shoulder and elbow joints. Movement occurred primarily through elbow motion, while the shoulder served to stabilize limb position. Figure 10D shows that for 30° movements, there was significant angular drift accumulation at the shoulder ($P=0.045$), but not at the elbow ($P=0.367$). This pattern of results supports the idea that two features of control may be independent: 1) maintaining general postural location for the arm and 2) moving the hand along a preferred distance and direction.

DISCUSSION

The purpose of the experiment reported here was to examine how limb position drifts during a series of movements and to determine how this drift affects movement performance. Participants performed blocks of 75 repetitive movements. Movements were restricted to the horizontal plane and involved flexion and extension movements about the elbow and shoulder only. Within each block, movements were performed in one of two directions (30° and 120°) from one of three start locations, in time with a metronome. Visual feedback about fingertip location was provided during the first five movements and was then removed for the remainder of the block. The results showed that although instantaneous (movement-to-movement) hand position drift remained constant over time, cumulative drift increased rapidly during the early portion of the block before reaching an apparent plateau at mid-block. Both instantaneous and cumulative drift varied consistently with movement direction, suggesting that drift is related to movement production. Although hand position drifted on average 8 cm from its original location, movement distance and direction were preserved over repeated trials. Inverse dynamic analysis showed that muscle torque strategies changed substantially so as to preserve movement distance and direction prescribed by the visually presented target vector. Forward simulations predicted large changes in movement direction without such modifications in joint torque. The results as a whole suggest that proprioception continues to be a reliable source of limb position information after prolonged time without vision and that this information is used in different ways by separate position and movement controllers.

The latter conclusion suggests a paradox: proprioceptive information about limb position was used to update and produce appropriate movement trajectories but was not used to maintain the limb's spatial position that defined the starting location of each successive movement. If proprioception was useful for movement, why was it not useful for position? We sought to answer this question by posing four other, more detailed questions.

Is drift driven by an attractor?

One possibility is that drift resulted from attraction to or repulsion from specific positions defined intrinsically (postures) or extrinsically (locations in space). Theoretically, this possibility is plausible because some positions may afford higher levels of comfort, control, stability, or sensory or perceptual resolution than others. Those positions that have one or more of these properties might serve as attractors, whereas those positions that have none of these properties might serve as repellers.

The attractor hypothesis predicted that cumulative drift distance and direction would vary with manipulated start location and that drift would converge on a common spatial or postural region. These predictions were not supported. Drift distance was not affected by start location, drift did not converge on any one position in space, and drift was often directed away from the center of joint range of motion.

An alternative version of the attractor hypothesis, based on the possibility that participants drifted toward positions or postures at which joint stiffness was balanced, predicted that instantaneous drift distance would vary directly with distance from the attractor because larger forces would occur when the limb was furthest from the attractor. This hypothesis was also not supported. Instantaneous drift did not vary over time or with the position of the limb.

The notion that start positions acted as repeller locations was also not supported because participants often drifted toward other start locations. Although there was a tendency for participants to avoid drifting toward their bodies, we found no other evidence that drift was driven by an attractor or repeller.

Does drift reflect a growing state estimation error?

Wolpert et al. (1998) proposed an account of limb position error accumulation that provides a second possible explanation for our data. According to this account, perception of limb position involves both an updating procedure that establishes the current spatial relationship between the visual and the proprioceptive state of the limb (Redding and Wallace 1996) and a mechanism that stores past limb position estimates (Wolpert et al. 1998). Estimates of the current state are based both on available information and on the integrity of the stored state estimate. Therefore any error introduced into the current limb-position estimate, due to faulty or absent sensory information, is incorporated into subsequent estimates and allowed to accumulate. In our experiment, visual information about limb position was absent, and so errors in limb-position estimation could have accumulated. This account may explain how drift accumulates with respect to the visually presented initial start position. However, it does not account for the fact that participants were able to update limb position information

as required for maintaining accuracy of the movement trajectory in terms of the distance and direction covered.

Does drift reflect differential salience of static and dynamic proprioceptive information?

A third possibility is that the proprioceptive signals providing limb position and movement information—static and dynamic proprioceptive information, respectively—are different and perhaps unequally available in this task. Type Ia (large-fiber) muscle spindle afferents respond both to changes in static muscle length and rate of change of muscle length. Thus they are sensitive both to static position and movement. By contrast, type II afferents respond most effectively to changes in static muscle length (Matthews 1972). Thus they are sensitive primarily to position. Psychophysical evidence suggests that these two channels of proprioceptive information support independent perception of limb movement and limb position (Clark et al. 1985; Sittig et al. 1985; Taylor and McCloskey 1990).

Most of the evidence for independent perception of position and movement has been acquired under conditions in which the participant's only task was to monitor position. Under these conditions, participants were able to detect excursions at the elbow and shoulder that produced fingertip position changes of under 5 mm with 70% accuracy (Hall and McCloskey 1983). In our task, by contrast, participants were required to monitor both position and movement trajectory. This dual-task situation may have raised the threshold for position change detection, allowing position errors not only to go undetected but also to accumulate. Indeed, Clark et al. (1985) showed with a single participant that instruction to attend to joint position rather than movement lowered her position change detection threshold at low rates of rotation. Therefore although instantaneous drift is well above the position change detection thresholds reported by McCloskey (Hall and McCloskey 1983; Taylor and McCloskey 1990) and by Clark et al. (1985), it is possible that limb position drift accompanied by the relative preservation of movement may be attributable to differences between static and dynamic proprioception.

Whereas it is likely that the current differences in regulation of limb position and movement trajectory are related to differences in static and dynamic proprioceptive information, we do not expect that these findings result from disparities in salience between these two modes of proprioceptive information. In fact, we recently tested this hypothesis in an experiment designed to manipulate the magnitude of instantaneous drift (Brown et al. 2003). In that experiment, subjects performed blocks of repetitive movements at different speeds. According to the information salience hypothesis stated above, relatively large position changes should be more salient than small position changes, and therefore the participant should be able to compensate for drift more effectively when position changes were large than when they were small. Thus this hypothesis predicted that drift would accumulate more slowly, and plateau at a smaller drift extent, when fast movements were performed than when slow movements were performed. However, our data contradicted this prediction. Whereas drift accumulated more quickly during faster movements, drift extent (plateau) remained the same under both speed conditions, indicating equivalent position regulation. If the salience of static limb position information was different under fast and slow movement

conditions, this did not lead to differences in regulation of limb posture over repeated movements.

Does drift reflect differential use of proprioception by separate position and movement controllers?

Finally, preservation of movement trajectory coupled with hand position drift suggested that proprioception continued to be a reliable source of limb position information after prolonged periods without visual limb position feedback, but that this information was used differently by separate position and movement controllers. According to this separate controllers hypothesis, the movement control system tracks small changes in limb position and uses this information to produce and maintain movement distance and direction. The position control system relies more heavily on visually-specified limb position information and is fairly indifferent to small position errors, although it triggers corrections when larger, more categorical changes in limb position are sensed. Drift may arise because the two controllers are differentially sensitive to small position errors, or it may arise because the two controllers are sensitive to different kinds of limb position information. The movement controllers may track intrinsic limb posture and the position controller may track extrinsic hand location. The transformation of intrinsic limb postures to extrinsic hand locations is likely not perfect when vision of the limb is absent, and the resulting errors may contribute to drift. Among the hypotheses that we have considered, we find the *separate controllers hypothesis* the most satisfactory. Not only does it provide a parsimonious account of our data; it also fits with the findings of a number of other studies.

In one of the clearest demonstrations of the separation of limb position control limb movement control, Sittig et al. (1985) asked participants to track a moving target with their finger while also being exposed to elbow flexor vibration. The participants, unaware of the discrepancy between target and finger position, reported that they were tracking accurately even though they lagged behind the target in a way consistent with the vibration illusion. When they were asked to stop tracking and point to the target location, they did so accurately.

Several motor learning experiments have likewise shown independent acquisition and transfer of position and movement information. DiZio and Lackner (1995) showed that exposure training with Coriolis forces produced differential movement trajectory and endpoint position aftereffects in the trained and untrained arm. Whereas the trained arm showed both trajectory curvature and endpoint aftereffects, the untrained arm showed only endpoint aftereffects, suggesting that learned end position and trajectory information are distinct. This conclusion is strengthened by observations that, during exposure to Coriolis force perturbations, training reduced movement path curvature more than endpoint error when endpoint finger contact was either absent (Lackner and DiZio 1994) or abnormal (DiZio and Lackner 2001).

Further support for the hypothesis that position and movement are controlled independently comes from Sainburg and Wang (2002), who showed that information about these features of movement transfers differentially between limbs following adaptation to novel visuomotor rotations. When participants first adapted to a 30° rotation of the visual

projection of hand position with their nondominant arm, the first movements made with the dominant arm demonstrated transfer of information used to specify trajectory direction. However, when participants first adapted to the visuomotor rotation using the dominant arm, information used to specify final position accuracy, but not trajectory direction, transferred to nondominant arm performance. These findings are consistent with earlier reports that the dominant arm controls intersegmental dynamics more efficiently than the nondominant arm, whereas the nondominant arm controls final position accuracy better than the dominant arm (Sainburg and Kalakanis 2000).

Yet another line of work that supports the separate controllers hypothesis pertains to memory for position versus memory for movement. Memory for position is better than memory for movement (Marteniuk and Roy 1972; Smyth 1984). Rosenbaum et al. (1999) showed that memory for posture is dissociable from memory for spatial location. In related computational modeling, Rosenbaum et al. (2001) showed that motor planning and control works well when one assumes distinct representations for postures and movements.

The only study we know of which has explicitly disputed the separate controllers hypothesis is by Vindras et al. (1998). These authors showed that endpoint error vectors measured during an aiming task were correlated with position drift vectors measured during a separate, but concurrently run, limb-position perception task. Vindras et al. did not directly assess the interplay of position drift and movement production as we have done, however. In fact, they tried to prevent drift during their movement task by allowing participants to see their hand until it was within 4 cm of the start location and by passively moving the participant's hand between both movement and position perception trials. The relevance of the findings of Vindras et al. to our study is therefore questionable.

Aside from this last reservation, the present findings, along with many other findings in the literature, suggest that limb position and movement are controlled separately. We have shown here that this separate controller model accounts for the remarkable fact that position drifts with movement repetition whereas the distance and direction of movement remain surprisingly stable.

DISCLOSURE

We thank J. Lateiner and L. Bagesteiro for help with data collection and analysis.

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APPENDIX

The arm was modeled as a two-segment link with the shoulder joint free to move in the $x - y$ horizontal plane. The length of each segment is denoted by l . Each segment is homogeneous, and the segment mass m is assumed to be concentrated in the center of mass CM (located

at r distance from the joints) with its respective moment of inertia I . The position for the center of mass of each segment in the base coordinate system is denoted by $p(x, y)$. Each joint generates a torque T , which tends to cause a rotational movement, and each segment is affected by forces F and moments M .

The Newton-Euler equations for the shoulder (s) segment are given by

$$F_s - F_c + m_s \ddot{p}_0 - m_s \ddot{p}_{sCM} = 0$$

$$M_s - M_c + (p_1 - p_{sCM}) \times F_c - (p_0 - p_{sCM}) \times F_s - I_s \dot{\omega}_s = 0 \quad (\text{A1})$$

and similarly to the elbow (e) joint

$$F_c + m_e \ddot{p}_0 - m_e \ddot{p}_{eCM} = 0$$

$$M_e - (p_1 - p_{eCM}) \times F_c - I_e \dot{\omega}_e = 0 \quad (\text{A2})$$

To obtain the dynamic equations, we first eliminate the joint forces and separate them from the joint torques to explicitly involve the joint torques in the dynamic equations. For the planar two-segment link, the joint torques T_s and T_e are equal to the coupling moments, M_s and M_e , respectively. Eliminating F_c in Eq. A2 and subsequently eliminating F_s in Eq. A1, we obtain

$$T_e - (p_1 - p_{eCM}) \times m_e \ddot{p}_{eCM} + (p_1 - p_{eCM}) \times m_e \ddot{p}_0 - I_e \dot{\omega}_e = 0 \quad (\text{A3})$$

$$T_s - T_e - (p_0 - p_{sCM}) \times m_s \ddot{p}_{sCM} - (p_0 - p_1) \times m_e \ddot{p}_{eCM} + (p_0 - p_{sCM}) \times m_s \ddot{p}_0 + (p_0 - p_1) \times m_e \ddot{p}_0 - I_s \dot{\omega}_s = 0 \quad (\text{A4})$$

Rewriting the angular and linear velocities for shoulder and elbow joints, and the position vectors, using joint displacement angles (θ_e and θ_s), which are independent variables, we have

$$\omega_s = \dot{\theta}_s$$

$$\omega_e = \dot{\theta}_s + \dot{\theta}_e \quad (\text{A5})$$

$$p_{sCM} = \begin{bmatrix} r_s \cos(\theta_s) \\ r_s \sin(\theta_s) \end{bmatrix} p_{eCM} = \begin{bmatrix} l_s \cos(\theta_s) + r_e \cos(\theta_s + \theta_e) \\ l_s \sin(\theta_s) + r_e \sin(\theta_s + \theta_e) \end{bmatrix}$$

$$\dot{p}_{sCM} = \begin{bmatrix} -r_s \dot{\theta}_s \sin(\theta_s) \\ r_s \dot{\theta}_s \cos(\theta_s) \end{bmatrix}$$

$$\dot{p}_{eCM} = \begin{bmatrix} -\{I_s \sin(\theta_s) + r_c \sin(\theta_s + \theta_e)\} \dot{\theta}_s - r_c \sin(\theta_s + \theta_e) \dot{\theta}_e \\ \{I_s \cos \theta_s + r_c \cos(\theta_s + \theta_e)\} \dot{\theta}_s + r_c \cos(\theta_s + \theta_e) \dot{\theta}_e \end{bmatrix} \quad (A6)$$

Substituting Eqs. A5 and A6 along with their time derivatives into Eqs. A3 and A4, we obtain the dynamic equations in terms of joint angles and shoulder position

$$T_s = \alpha \ddot{\theta}_s + \beta \ddot{\theta}_e - \gamma \dot{\theta}_e^2 - 2\gamma \dot{\theta}_s \dot{\theta}_e + \delta$$

$$T_e = \varepsilon \ddot{\theta}_e + \beta \ddot{\theta}_s + \gamma \dot{\theta}_s^2 + \varphi \quad (A7)$$

where $\alpha = m_s r_s^2 + I_s + m_e [l_s^2 + r_c^2 + 2l_s r_c \cos(\theta_e)] + I_e$; $\beta = m_e l_s r_c \cos(\theta_e) + m_e r_c^2 + I_e$; $\gamma = m_e l_s r_c \sin(\theta_e)$; $\delta = [m_s r_s \cos(\theta_s) + m_e (r_c \cos(\theta_s + \theta_e) + l_s \cos(\theta_s))] \ddot{y} - [m_s r_s \sin(\theta_s) + m_e (r_c \sin(\theta_s + \theta_e) + l_s \sin(\theta_s))] \dot{y} + I_e$; $\varepsilon = m_e r_c^2 + I_e$; $\varphi = [m_e r_c \cos(\theta_s + \theta_e)] \ddot{y} - [m_e r_c \sin(\theta_s + \theta_e)] \dot{y}$; m_s and m_e = masses of upper arm and forearm, respectively; r_s and r_e = distances from the proximal joint to center of mass of upper arm and forearm, respectively; l_s and l_e = lengths of upper arm and forearm, respectively; I_s and I_e = moments of inertia at center of mass of upper arm and forearm, respectively; θ_s and θ_e = orientation angles at proximal end of segment for upper arm and forearm, respectively; x = x position of the shoulder; and y = y position of the shoulder.

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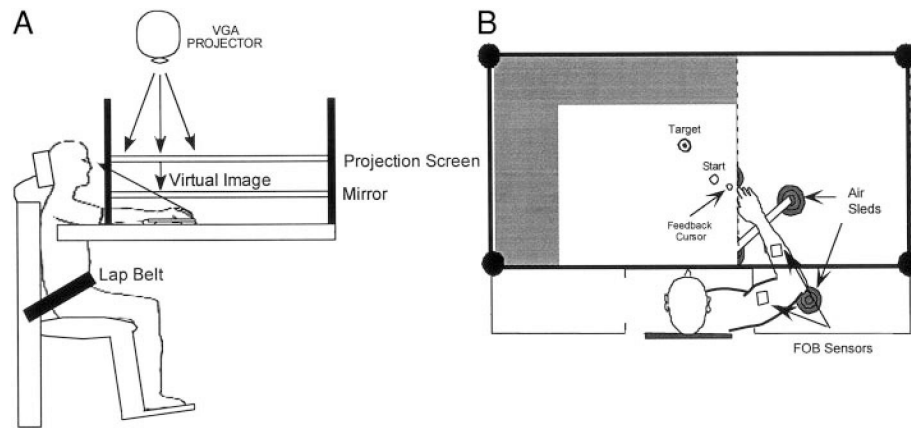
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**FIG. 1.**

The experimental setup. *A*: a back projection screen was suspended above a 1-way mirror suspended above a glass-covered table surface. This arrangement provided the impression that the display was in the same depth plane as the table surface. *B*: forearm was secured to a custom-made air-jet sled. Flock of Bird sensors (shown as open squares) were fixed to the sled and the upper arm.

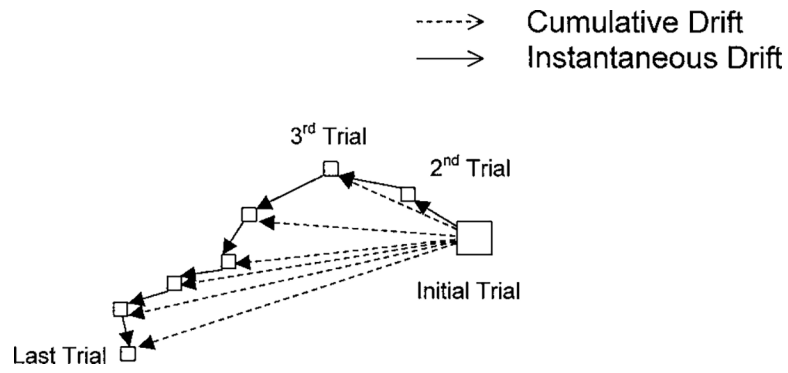


FIG. 2. Calculation of cumulative (dashed lines) and instantaneous drift (solid lines). Cumulative drift was defined as the Euclidean distance between the start location adopted on the initial trial and each successive start location. Instantaneous drift was defined as the Euclidean distance between each start location and the previously adopted start location.

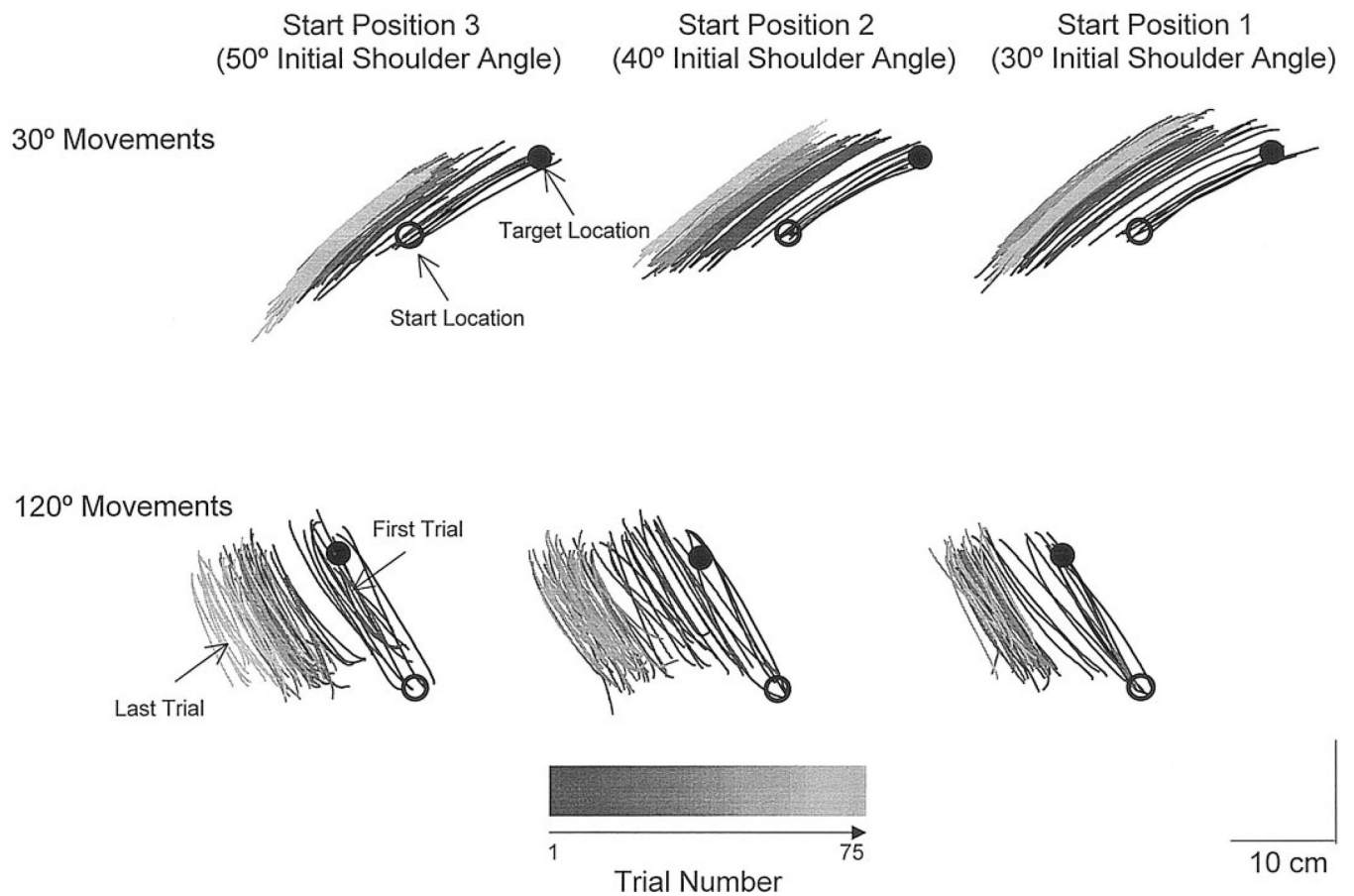
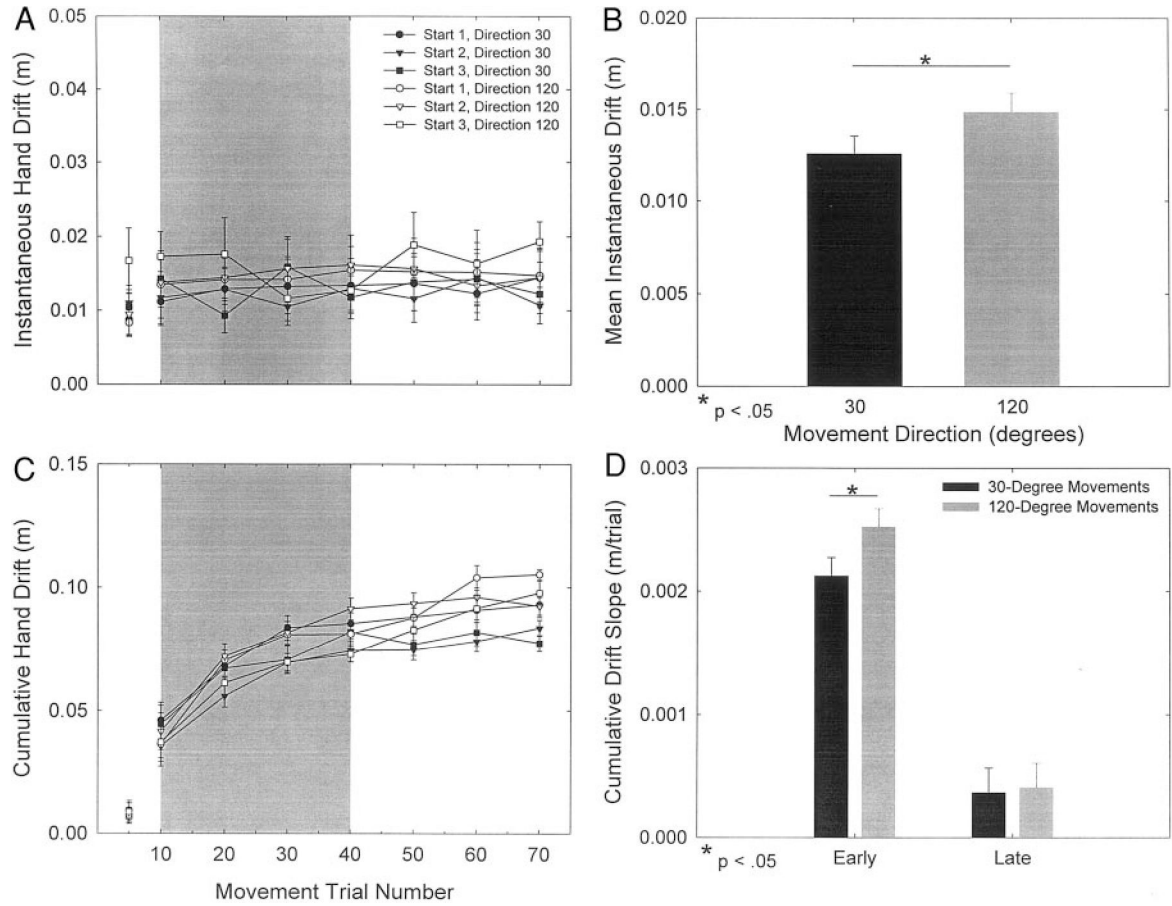


FIG. 3. Series of 70 hand paths produced by 1 participant (S5) in each start location and movement direction. *Top:* 30° movement paths. *Bottom:* 120° movement paths. In each plot, the prescribed start location is shown as an open circle, and the target location is shown as a closed circle. Progression of trials over time is represented by the gray shade of the path, where early trials are darker than late trials. Movements with visual feedback about fingertip position are drawn in black.

**FIG. 4.**

Mean instantaneous and cumulative hand position drift. *A*: mean instantaneous drift (m) as a function of trial number, start location, and movement direction. Error bars represent inter-subject SE. Shaded area represents the portion of the block during which drift accumulated rapidly. *B*: mean instantaneous drift collapsed across trial number and start location. Mean instantaneous drift was greater for 120° than for 30° movements. *C*: mean cumulative drift as a function of trial number, start location, and movement direction. Error bars represent inter-subject SE. Drift accumulated rapidly over the 1st 40 trials and then reached a plateau. Shaded area in both *A* and *C* highlights the rapid accumulation portion of the block. *D*: drift accumulation rate for 30° and 120° movements. Early bars reflect drift accumulation rates between trials 6 and 40, and late bars reflect drift accumulation rates between trials 41 and 70. Early drift accumulation rate was greater for 120° movements than for 30° movements.

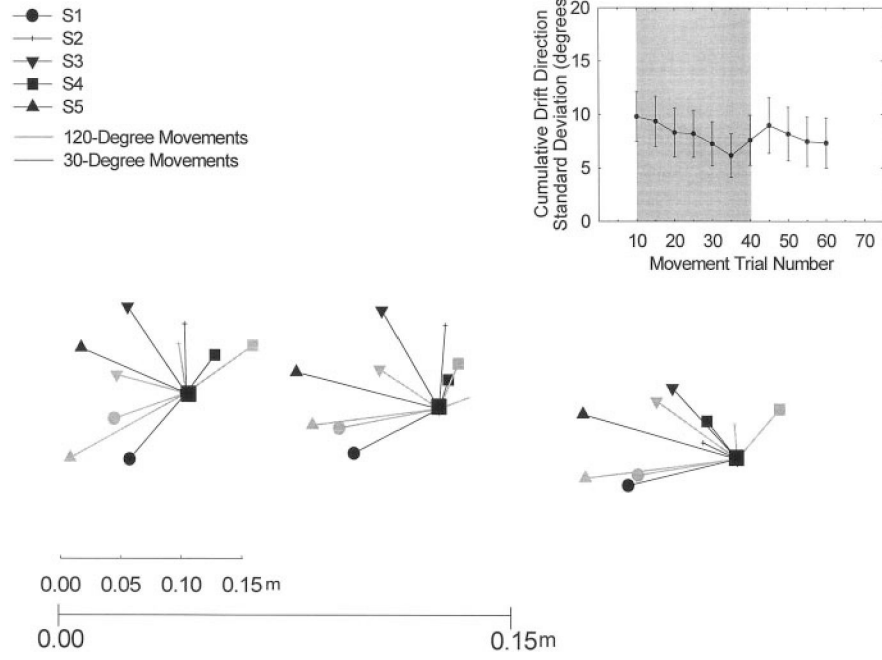


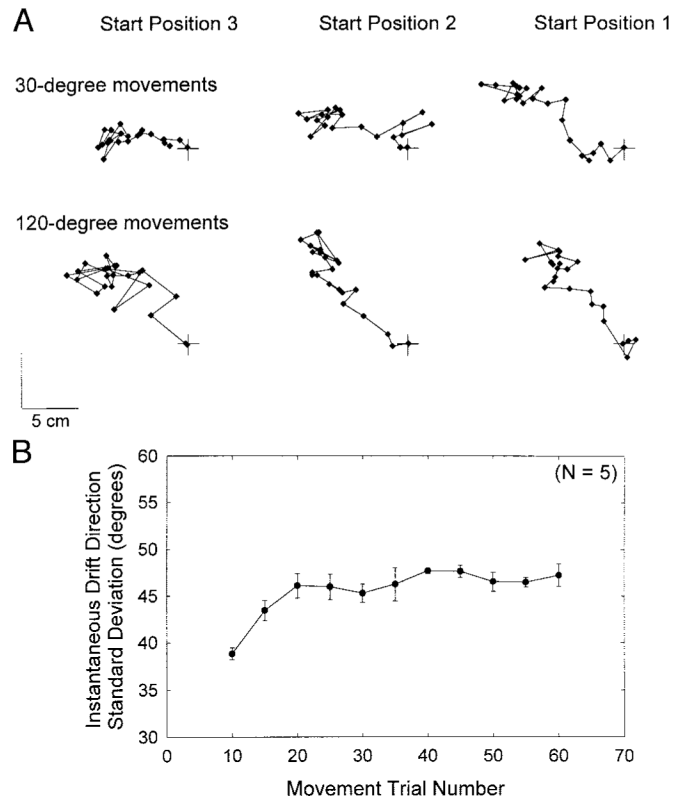
FIG. 5. Vectors representing mean drift distance and direction for each participant. Outer scale shows the relative positions of the 3 start locations. Inner scale reflects the distances of the drift vectors. These drift vectors show that, although participants did not drift toward their body, there was no one direction toward which drift was directed. *Top right:* mean within-trial drift direction variance, as a function of trial number, start location, and movement direction. This plot indicates that participants drifted consistently after vision was removed.

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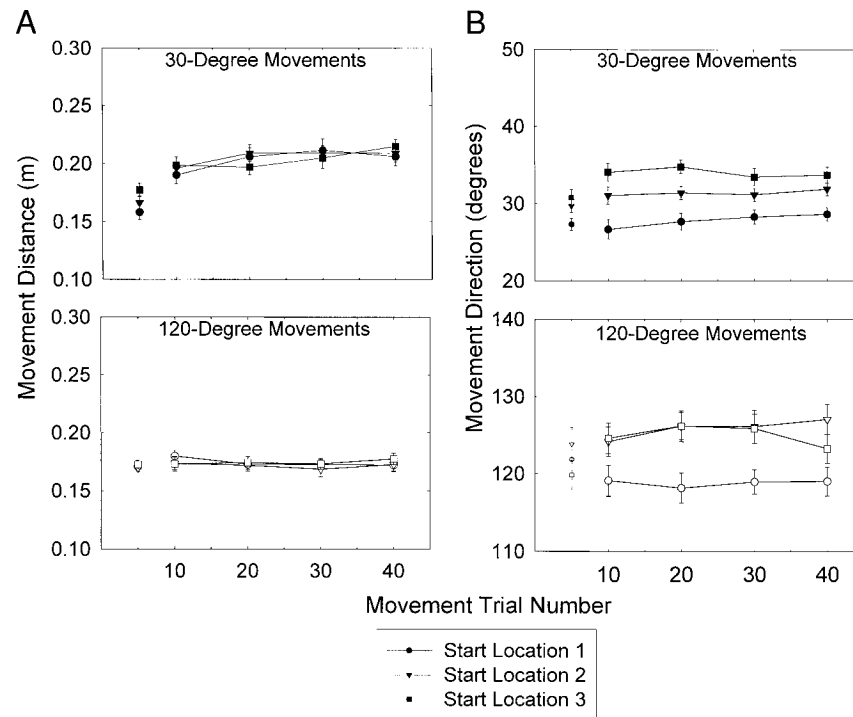
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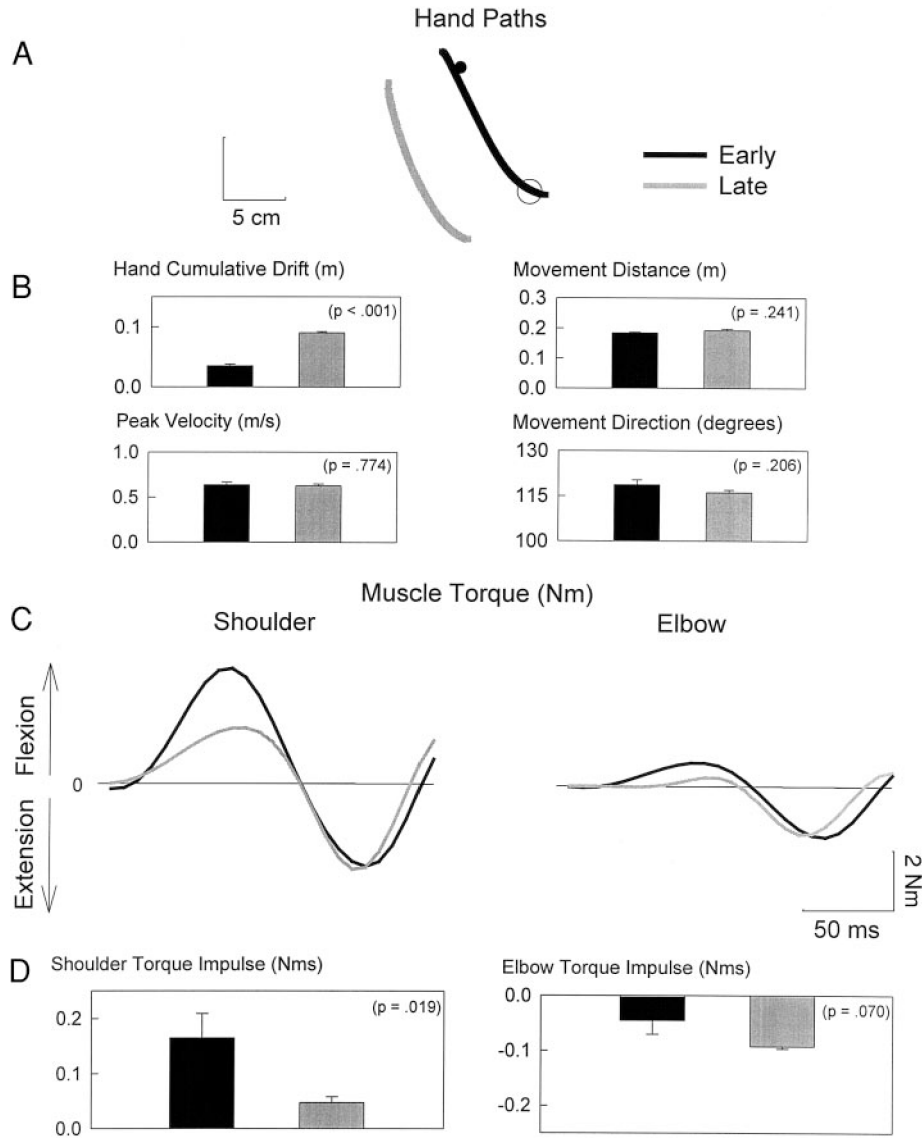
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**FIG. 6.**

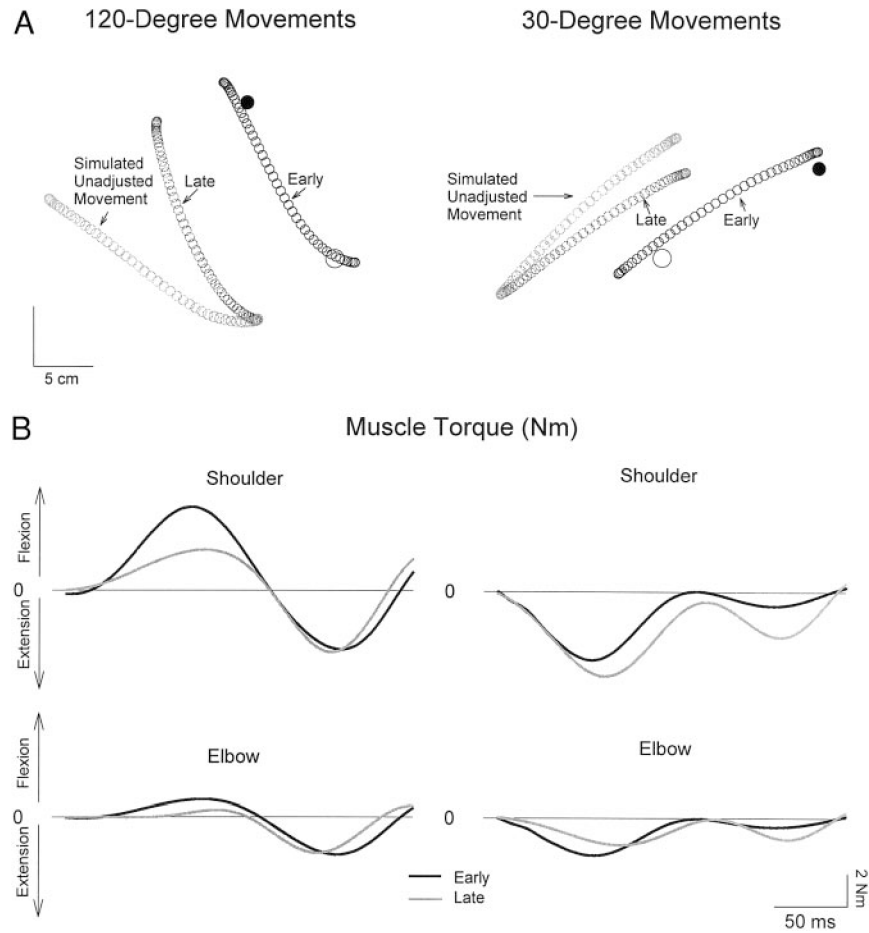
A: paths produced by plotting the series of movement start positions adopted by 1 participant (S4) in each condition. For clarity, we plotted start positions from vision-absent trials only and only every 3rd start location is plotted. Initial starting position is represented by crosshairs (+). *B:* instantaneous drift direction variance as a function of movement number. Only vision absent trials were included in this analysis.

**FIG. 7.**

Hand movement distance (*A*) and direction (*B*) as a function of trial number, start location, and movement direction. Results are shown for the trials over which drift accumulated most rapidly. Error bars represent inter-subject SE.

**FIG. 8.**

A: representative hand paths from a single participant (S3). Start location and target are indicated by an open and closed circle, respectively. The early-block hand path is the 1st no-feedback movement, and the late-block path is one performed after the participant had reached the drift plateau. *B:* comparisons of early and late cumulative drift, movement distance and direction, and peak velocity. The hand drifted significantly but movement distance, movement direction, and peak velocity were preserved. Error bars represent inter-movement SE. *C:* shoulder (*left*) and elbow (*right*) muscle torque profiles during the 1st 250 ms of the same early- and late-block movements. Values greater and less than 0 reflect flexor and extensor muscle torque, respectively. *D:* comparisons of early- and late-block shoulder (*left*) and elbow (*right*) muscle torque impulse. Error bars represent inter-movement SE.

**FIG. 9.**

A: simulation results for representative 120° (*left*) and 30° (*right*) movement paths. Observed early (black) and late (gray) paths are shown next to paths predicted by the simulation (light gray). Predicted paths represent the movement path that would have been performed had participants not modified muscle torque profiles as the hand drifted. *B:* observed early (black) and late (gray) shoulder and elbow muscle torques for the 120° (*left*) and 30° (*right*) movements depicted above. Simulated movements show the movement path that would have been performed if the early muscle torque profiles had been used at the late movement start location.

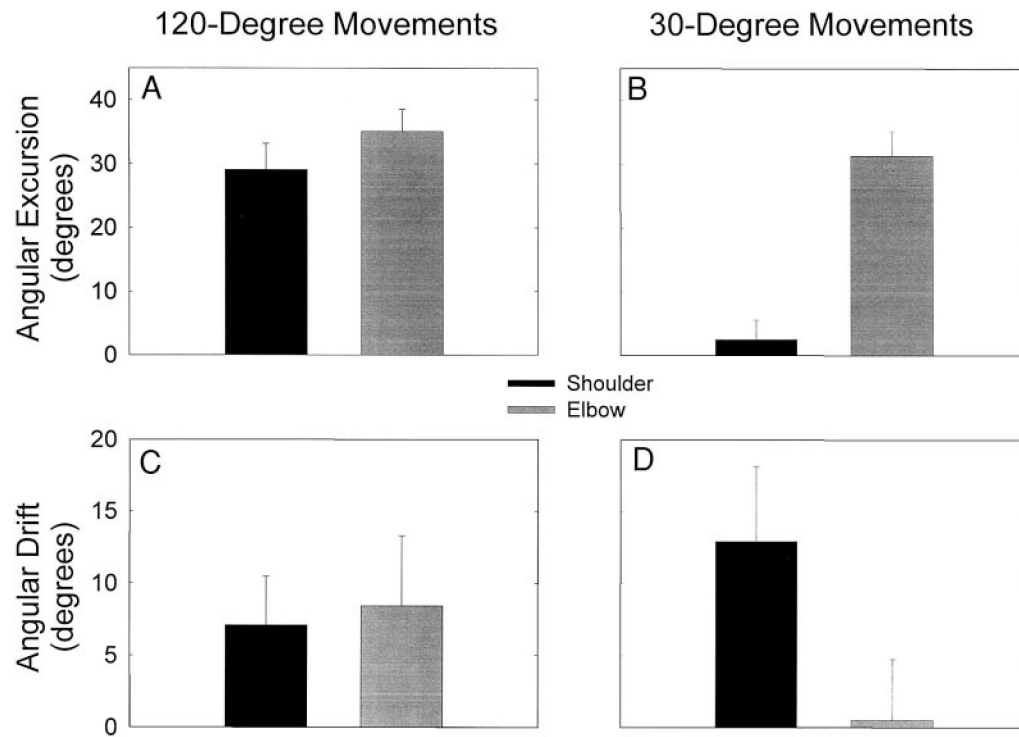


FIG. 10. *A*: mean angular excursion at each joint for 120° movements. *B*: mean angular excursion at each joint for 30° movements. *C*: mean angular drift at each joint for 120° movements. *D*: mean angular drift at each joint for 30° movements. In all panels, error bars represent inter-subject SE.

Comparisons of early- and late-block torque impulse at the shoulder and elbow for 120° movements performed at start location 3

Table 1.

Participant	Shoulder Torque Impulse (Nms)		Elbow Torque Impulse (Nms)		P	
	Early	Late	Early	Late		
1	0.079 ± .324	0.662 ± .031	0.021	-0.010 ± .013	0.028 ± .008	0.035
2	0.303 ± .059	0.653 ± .030	0.002	-0.023 ± .022	0.037 ± .014	0.074
3	0.165 ± .044	0.047 ± .011	0.019	-0.045 ± .025	-0.092 ± .004	0.070
4	0.138 ± .124	0.397 ± .014	0.048	-0.033 ± .019	0.032 ± .006	0.006
5	0.304 ± .065	0.139 ± .014	0.000	-0.045 ± .008	-0.055 ± .003	0.283

Values are mean ± SD.