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**LIMB POSITION DRIFT AND ITS IMPLICATIONS
FOR MOVEMENT AND POSITION CONTROL**

A Thesis in

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by

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ABSTRACT

Perception of limb position is dependent on visual, proprioceptive, and haptic information. Limb position information is important for movement planning and production, therefore changes in limb position can illuminate how vision and proprioception are used to control movement. Psychophysical research suggests that, without vision, perception of limb position drifts over time. Is this position drift due to a decay of proprioceptive information? If so, this decay should have consequences for movement performance. The experiments reported here address this hypothesis. Limb position cumulative drift was observed in repetitive shape-drawing and reaching tasks. After visual feedback was removed, drift accumulated over time in a systematic pattern. Drift increased quickly early in the series of movements, but then plateaued. The direction of drift accumulation varied widely between participants, but did not vary with the initial position of the limb in the workspace. Instantaneous drift distance, a measure of the movement-to-movement changes in limb position did not change over a series of movements. Instantaneous drift direction, however, was fairly consistent early in the series but then became less consistent, allowing drift to plateau. Both shape form and reaching trajectory were preserved as position drifted. An analysis of movement kinetics at the shoulder and elbow showed that movement distance and direction were preserved because shoulder torque was modified. A forward rigid-body simulation showed that if these torque modifications had not been made, movement direction would not have been preserved. We hypothesized a posture controller that allowed small position errors to accumulate to a fixed threshold.

Experimental manipulations of movement speed led to predictable changes in error that affected drift accumulation rates but not drift plateau level, confirming our hypothesis. Together, the results suggested that proprioception remains a reliable source of limb position information, but that it is used differently by separate movement and position controllers. This hypothesis was favored over explanations for drift in terms of a spatial attractor, a growing state estimation error, and differential salience of static and dynamic limb position information.

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CHAPTER 1

INTRODUCTION

Reach planning and control is conceived as a multi-step process that transforms visual target information into the set of time-varying muscle activations that bring the hand to the target. This process involves at least three steps: (1) a visuomotor transformation step that converts target information coded in visual coordinates (e.g., polar or Cartesian coordinates) to target information coded in posture coordinates (e.g., shoulder and elbow angles), (2) a trajectory planning step that defines movement distance and direction in either visual or joint coordinates, and (3) a dynamic transformation step that converts the trajectory plan into the muscle forces necessary to execute the plan (e.g., Kawato, 1996). As will be shown below, both neurophysiological and behavioral evidence suggests that trajectory planning and dynamic transformations depend on knowledge about the position of the limb prior to movement initiation. Initial limb position information is important because to produce the same hand trajectory from different start locations, different patterns of shoulder and elbow rotation, and different patterns of muscle activation, may be required.

Perception of limb position is dependent on visual, proprioceptive, and haptic information. Given that limb position information is important for movement planning and production, both manipulations of and naturally occurring changes in limb position prior to planned movement can illuminate how vision and proprioception are used to control limb movement and posture. Psychophysical

research suggests that, without vision, perception of limb position drifts over time. This drift has been attributed to a decay of proprioceptive information, however, little evidence supports this interpretation. If position drift is due to a decay of proprioceptive information, then this decay should have consequences for movement production. The series of experiments presented here directly address how movement production is affected by position drift.

This document is divided into chapters. This chapter first reviews two major conceptions of movement planning. Second, it reviews studies examining the relationship between perception of initial limb position and movement performance. Finally, it describes studies showing that, in the absence of vision, perception of limb position drifts. If movement planning and production are dependent on accurate perception of limb position, then drift should have consequences for movement production. In chapters 2 and 3, experiments that address this hypothesis and describe position drift in greater detail are presented. The findings of these experiments indicate that drift is not due to a loss or decay of proprioception over time. Instead, they suggest that drift reflects a separation between how proprioceptive information is used for movement control and how proprioceptive information is used for position control. In chapter 4, an experiment that tests this proposed separation is presented. The final chapter summarizes the project, evaluates several explanations for the results, and discusses the implications of separate posture control and movement control.

MOVEMENT PLANNING: WHAT IS PLANNED?

Movement planning is the process of formulating a movement goal, and movement control is the process of enacting that plan (Hollerbach, 1990). Theories of movement planning have been divided along many lines, two of which will be presented here. One line proposes that movement planning depends on the selection of a final posture. The second line proposes that movement planning involves the determination of a vector (movement distance and direction) that will bring the hand from the start location to the target location. These two views will be reviewed in turn.

Movement planning involves the selection of a final posture

Movement planning may be centered on the selection of a final posture without regard for the starting position of the limb. The equilibrium-point hypotheses of Feldman (the λ model; 1986) and Bizzi (the α model; Bizzi, Hogan, Mussa-Ivaldi, & Giszter, 1992) exemplify this approach. The λ model postulates that the limb is moved to the target position by central commands that act to shift the tonic stretch reflex threshold (λ) via alpha and gamma motorneuron input. Once λ has been modified, the spring-like properties of the muscle bring the limb to the new equilibrium point, the point at which the static load on the limb and the elastic properties of both agonist and antagonist muscles are balanced (Feldman, 1986). In the α model, the equilibrium position is defined by selecting positions along the length-tension curve for each muscle that balance agonist and antagonist muscle torque. According to this hypothesis, the limb is moved by selecting a series of

equilibrium positions that together form a virtual equilibrium trajectory. The limb moves as the muscle lengths change (via α motorneuron input) to reach successive equilibrium positions along this trajectory (Bizzi et al., 1992). These models make two predictions that may be addressed by the experiments presented here. First, the equilibrium point hypothesis predicts that goal postures can be achieved without regard for initial posture. Second, the equilibrium point hypothesis implies that posture and movement are controlled by a single central mechanism (Feldman, 1986).

Other models that tout the importance of the selection of a final limb configuration do not deny the importance of the initial limb configuration. The posture-based model of movement planning (Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001) proposes that end postures are chosen so that the resulting movement will satisfy multiple, rank-ordered constraints, defined in a constraint hierarchy. Constraints can be defined such that a wide variety of goals may be achieved. While the number and order of constraints may vary, this model always involves an evaluation of spatial accuracy and an evaluation of movement effort. The model first evaluates a set of n stored postures (postures that have been adopted recently) to find the stored posture that best suits the current constraint hierarchy. The model then searches in cycles for alternative postures that are generated around the best stored posture. The number and spatial distribution of generated postures depends upon the resolution of posture space (grain size) and the criterion number of generation cycles. At the end of each cycle, generated postures are evaluated with respect to the constraint hierarchy. Once the least-costly goal posture has been identified, the model plans a movement that reduces the angular distance between the current (initial)

posture and the selected goal posture in joint space. In contrast to the equilibrium point hypothesis, this model suggests that both initial and final postures contribute to the movement plan. It also suggests that the process of posture selection is different from the process of movement production.

Soechting and Flanders (1989a, 1989b) proposed a similar mechanism for movement control, although their proposal for how final postures are determined is quite different. According to them, the target is first represented as a visual location in spherical, shoulder-centered coordinates, and then this location is transformed into the set of arm and forearm segment orientations that would bring the hand to the target location. Like Rosenbaum et al., Soechting and Flanders suggest that the movement is then produced by interpolating between the current limb position and the final limb position in joint space.

End-posture planning is supported by both psychophysical and neuro-physiological data. Polit and Bizzi (1979) showed with a single-joint aiming task that the hand stopped at trained target positions even when a mechanical perturbation was applied prior to movement. This result also held after afferent feedback was eliminated, indicating that the endpoint was not achieved through the use of feedback-based corrections. End posture planning is also supported by experiments showing that spatial variability increases during movement but then decreases again near terminal positions (Darling & Cooke, 1987; Harris & Wolpert, 1998; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001; Roy, Brown, & Hardie, 1993), and that both practice moving to a specified endpoint and practice producing a specified movement distance reduced movement endpoint variability more than

movement distance variability (Jaric, Corcos, Gottlieb, Ilic, & Latash, 1994). Given that end postures are more stable in terms of spatial variability than are movements, it is perhaps not surprising that memory for final positions is more accurate and more durable than memory for movement (Marteniuk & Roy, 1972). Finally, Graziano, Taylor, and Moore (2002) recently showed that prolonged microstimulation over the precentral gyrus (including primary motor cortex and pre-motor cortex) induced movements that brought the hand to a common final posture regardless of the starting position of the hand. Together, this evidence supports the notion that movements are planned, at least in part, in terms of final postures.

Movement planning involves the determination of a hand-path vector

Goal-directed movements require that the target's visual representation be transformed from retina-centered coordinates to effector-centered coordinates (Caminiti et al, 1998; Rizzolatti et al., 1994). This effector-centered visual representation must be combined subsequently with spatial representations provided by other sensory modalities, and then transformed into an appropriate hand path, set of joint torques, and set of muscle commands (Kawato, 1996). There is both psychophysical and neurophysiological evidence suggesting that the movement plan begins with a representation of the movement path in terms of hand motion in extrinsic space. This vector represents an ideal, straight path that can bring the hand from the start location to the target location.

Theoretically, this hand-path plan may be useful to the system in two ways. First, it can be used to produce, in a feedforward manner, the neural commands

needed to transport the hand to the target. That is, once this plan has been determined, inverse internal models – models that store learned relationships between hand motion and joint rotations, between joint rotations and muscle activation patterns, and between muscle activation patterns and central neural commands – may be employed to transform the movement plan into the set of neural commands needed to move the hand to the target (Kawato, 1996; 1999; Wolpert & Kawato, 1998). Second, the hand-path plan can be used to produce, in a feedback manner, the neural commands needed to correct differences between the planned hand path and the executed hand path. For example, forward internal models – models that store learned relationships between motor neural commands and their sensory consequences – can be used to predict expected sensory outcomes from neural commands. Thus, expected sensory consequences can be compared with actual sensory consequences, and then deviations from expectations can be corrected in a feedback manner (Wolpert, Miall, & Kawato, 1998; Wolpert & Kawato, 1998).

The existence of hand-path vector coding has been supported by studies showing that the performed movement path can be reasonably approximated by a straight line (Flash & Hogan, 1985; Morasso, 1981) and by studies showing that distance and direction can be specified independently. Using a reaction time paradigm, Rosenbaum (1980) found that providing participants with advance information about the distance, direction, or hand of the upcoming response reduced movement preparation time, indicating that precue information could be used to specify parts of the upcoming response in advance. Moreover, he found that usefulness of one cue did not depend on the presentation of any other cue and that the

order of cue presentation did not matter, indicating that the different types of information (distance, direction, or hand) could be specified independently. In a complimentary study, in which the stimulus-response (S-R) interval was controlled and response accuracy was measured, Favilla, Hening and Ghez (1989) found that distance could be correctly specified in the wrong direction at short S-R intervals and that both distance and direction specification gradually improved as S-R interval increased, but over different time courses. This result indicated that distance and direction were specified in a predictable order but in parallel. In a pointing study, Gordon, Ghilardi, and Ghez (1994) demonstrated the independence of distance and direction specification by showing that endpoint distance variability varied reliably with movement distance but not movement direction, whereas endpoint direction variability was independent of movement distance. Furthermore, the reliable alignment of endpoint variability ellipses with movement direction indicate that movement distance and direction are specified, on some level, with respect to initial hand location and hand movement direction. Taken as a whole, results from reaction time, accuracy, and pointing studies converge to support the vector coding hypothesis.

Neurophysiological experiments also support vector coding. First, studies of single-cell selectivity in the posterior parietal cortex (PPC) have shown that target locations are coded by cells that have multimodal, effector-centered receptive fields, indicating that these cells integrate information from different sensory modalities, and code target location with respect to the movement system (eye or hand) to be employed (Buneo, Jarvis, Batista, & Andersen, 2002; Caminiti et al., 1998; Graziano

& Gross, 1996). For example, Buneo et al. (2002) recently showed that cells in the parietal reach region code both target location and hand location in eye-centered coordinates, meaning that PPC cells could compute the hand path vector simply by subtracting these two eye-centered representations.

Second, studies of single-cell movement direction selectivity have revealed that the preferred directions of cells both in the macaque primary motor (M1) and premotor cortex (PMC) reflect movement direction in the workspace, and that these preferred directions were modified as the hand adopted new start locations, such that the preferred direction rotated as the initial shoulder angle rotated (Caminiti, Johnson, & Urbano, 1990; 1991). Moreover, the M1 and PMC population vector reflects movement direction from hand location (Georgopoulos, Schwartz, & Kettner, 1982). These neurophysiological results indicate that the cortical areas responsible for issuing the neural commands for target-oriented movements are sensitive to the direction of the upcoming hand path.

The vector coding hypothesis is important to the current study because it explicitly emphasizes the importance of initial limb position for movement planning and control. In the next section, empirical studies testing the effects of altered initial limb position information on movement production are presented.

MOVEMENT PLANNING AND CONTROL IS DEPENDENT ON PERCEPTION OF STARTING LIMB POSITION

Both behavioural and neurophysiological evidence suggests that perception of initial limb position is important for multi-joint movement planning. Both deafferented patients (Ghez, Gordon, and Ghilardi, 1995) and healthy control

participants (Desmurget, Rossetti, Jordan, Meckler, & Prablanc, 1997; Ghilardi, Gordon, & Ghez, 1995; Prablanc, Echallier, Komilis, and Jeannerod, 1979; Vindras, Desmurget, Prablanc, & Viviani, 1998) reached more accurately or more precisely (Desmurget, Rossetti, Prablanc, Stelmach, & Jeannerod, 1995) to visible targets when vision of initial limb position was provided prior to a movement trial than when this information was not provided. Moreover, manipulations of initial limb position in the workspace caused systematic reaching direction errors (Ghilardi et al., 1995). Reaches made from left-of-midline start locations were characterized by counter clockwise direction errors, whereas reaches made from right-of-midline start locations were characterized by clockwise direction errors. The magnitude of the direction error varied directly with start location eccentricity. Ghilardi et al. speculated that because the direction errors were eliminated when participants viewed initial limb position between trials, proprioception alone may not provide accurate information about initial limb configuration. Vindras et al. (1998) tested this hypothesis by correlating reaching endpoint errors with errors made when participants explicitly reported the location of their unseen hand with a laser pointer. They found that movement errors were correlated significantly with explicit hand localization errors within participants, providing support for the claims that (1) movement planning and execution depends on perception of initial hand position, and (2) that proprioception alone provides a biased percept of the initial position of the hand and arm.

The dependence of reaching accuracy on accurate initial limb position information has also been shown by studies in which perception of initial limb

position has been perturbed. When visual information about initial limb position was shifted by displacing prisms, participants produced endpoint errors that were shifted in the opposite direction, indicating that they planned the movement from the shifted percept of hand position (Rossetti, Desmurget, & Prablanc, 1995). The magnitude of this error revealed that the perceived location of the hand had moved to a location between the shifted visual location of the hand and the unshifted felt location of the hand. In a complimentary study, visual information was preserved but proprioceptive information about initial limb position was shifted during “catch” trials in which arm position was covertly displaced with respect to a practiced start location (Sainburg, Lateiner, Latash & Bagesteiro, in press). In this case, participants produced movement trajectories that were parallel to the practiced trajectory. Because preserving hand direction required different elbow and shoulder torques to be planned and produced from the perturbed initial limb position, this result could have happened only if the new proprioceptive information about initial limb position was incorporated into the movement plan.

The dependence of movement performance on initial limb position information implies that limb position perception must play an important role in movement planning. The following section will review psychophysical studies of limb position perception showing that, in some cases, our sense of limb position may not be particularly reliable.

LIMB POSITION DRIFT: A FAILURE OF PROPRIOCEPTION?

Normally, humans use visual, proprioceptive, and tactile afferent information about limb position and efference copy – copies of central movement production commands – to keep track of limb and hand location with respect to both the body and the external world (Graziano, 1999; Lackner & DiZio, 2000; Mon-Williams, Tresilian, & Wann, 1999; Van Beers, Sittig, & Denier van der Gon, 1996, 1998). Van Beers et al. (1998) have shown that the hand's azimuthal position is perceived with greater precision by vision than by proprioception, whereas the hand's radial distance from the body is perceived with greater precision by proprioception than by vision. The integration of both visual and proprioceptive information is efficient, and is weighted by the direction-dependent precision of each of these information sources (van Beers, Sittig, & Denier van der Gon, 1996).

Although efficient, these vision-proprioreception integration processes are not perfect, and the relationship that is established by these integration processes appears to be unstable when vision is unavailable. Using perceptual matching tasks in which the participant explicitly reports the location of a hidden hand by matching its location with the other hand, a number of studies have shown that without vision, reports of limb position drift over time (Paillard & Brouchon, 1968; van Beers et al., 1999; Wann & Ibrahim, 1993; Wolpert, Goodbody, & Husain, 1998). For example, Paillard and Brouchon (1968) asked participants to point to the location of their occluded dominant fingertip and found that the reported location of the static, hidden hand drifted toward the body. Using a similar methodology, Wann and Ibrahim

(1992) showed that although participants' reports of occluded limb position drifted 28-30 mm over the course of repeated measurements, this distance was reduced to 22 mm, on average, when measurements were interspersed with periodic visual glimpses or brief isometric contractions (proprioceptive "glimpses") of the occluded limb. While both of the above studies showed systematic drift toward the body, other studies using similar methods have shown that overall drift direction is idiosyncratic (Desmurget et al., 2000; Helms-Tillery, Flanders, & Soechting, 1994; Vindras et al., 1998).

Drift has also been measured in repetitive movement tasks. These tasks have typically involved measuring participants' ability to maintain a particular spatial location while performing repetitive, straight-line, multi-joint movement tasks (Brown, Rosenbaum, and Sainburg, 2002; Rantanen, 2000), repetitive single-joint movement tasks (Miall, Haggard, & Cole, 1995), or repetitive shape-drawing tasks (Brown & Rosenbaum, 2001; Verschueren et al 1999; Zelaznik & Lantero, 1996) both with and without visual feedback. When haptic information was allowed, drift distance values measured during repetitive movement tasks agreed closely with drift distance values measured during perceptual matching tasks. Together, the results of these perceptual matching and repetitive movement experiments suggest that proprioception must be updated or recalibrated by vision to remain an accurate source of limb position information (Wann & Ibrahim, 1992).

The process of integrating proprioception with vision may involve both an updating procedure that aligns the current visual state of the limb with the current proprioceptive state of the limb (Redding & Wallace, 1996), and a storage mechanism

that stores the current state estimate (Wolpert, Goodbody, & Husain, 1998). Wolpert et al. proposed that estimates of the current state are based not only on presently available information, but also on the integrity of the stored state estimate. Therefore, any error introduced into the current estimate due to faulty or absent sensory information would be incorporated into the subsequent state estimates, and allowed to accumulate. They based this proposal on the performance of patient PJ, who suffers from a tumour that has gradually invaded her superior parietal lobe (SPL). With vision occluded, PJ reports a gradually fading perception of limb position over the course of approximately 20 seconds. This fading limb position perception has affected her ability to sustain isometric grip force over time and her ability to perform very slow movements (mean MT = 18.6 ± 1.0 s) accurately. Wolpert et al. suggested that failure to store the current state estimate adequately leads to symptoms of drift and proprioceptive fading, and linked this storage failure to PJ's SPL damage. This link is supported by a transcranial magnetic stimulation study showing that position errors incurred during a double-step task are not corrected when magnetic stimulation is applied over the posterior parietal cortex (Desmurget, Epstein, Turner, et al., 1999).

The drift-attenuating conditions reported by Wann and Ibrahim (1992) and the storage mechanism failure suggested by Wolpert et al. both suggest that drift arises because proprioceptive information about limb position is altered during prolonged periods without vision or without movement. However, there are several reasons to question the notion that proprioceptive fading lies at the root of limb position drift in healthy people. First, drift extent appears to be related to the movements of the reporting arm. 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 result suggests that past experiments seeking to measure drift may not have been measuring the accuracy of position sense per se, as much as they may have captured the growth of some bias that resulted from repeated position estimates. Second, drawing experiments have shown that that when participants drew shapes (circles and squares) continuously in the absence of vision, shape location drifted, whereas shape form and orientation were well-preserved (Brown & Rosenbaum, 2001; Verschueren, Swinnen, Cordo, & Dounskaia, 1999a&b; Zelaznik & Lantero, 1995). The preservation of shape form in the face of position drift suggests that proprioception did provide accurate information about the arm's current position, and that this information was used to maintain shape form at new locations. The shape-drawing experiments and the relationship between position drift and shape drawing movements will be presented in more detail in the following chapter.

PURPOSE OF THE PRESENT STUDY

Taken as a whole, the findings in this area of study leave open questions both about the source of position drift and about the effect that it may have on movement performance. The experiments presented here address these questions. The general approach was to employ repetitive shape drawing and straight-line movement tasks and to vary the availability of visual feedback, either by removing vision altogether or by removing visual feedback about limb position, to encourage the growth of drift. Thus, position drift and movement performance were assessed in the same task.

The approach used here represents an improvement on previously-reported methods for measuring limb position drift. First, this approach allowed direct assessment of the effects of position drift on movement production. Whereas other groups have attempted to link limb position matching errors to movement end-point errors (e.g., Vindras et al., 1998), they measured these two sources of error using two very different tasks. Second, the nature of the repetitive, straight-line movement tasks used in Experiments 2 and 3 are such that the drift observed (close to 10 cm on average) was considerably larger than that reported in other studies. This is likely because the task was performed on a frictionless surface and because, in addition to the removal of visual feedback, participants received little, if any, haptic position information. These large position changes increased the power to detect the effects of drift on the movement trajectory. Finally, the methods employed here allowed an analysis of the effects of limb position drift on both movement kinematics and movement kinetics. No other study has examined these details.

CHAPTER 2

POSITION DRIFT AND SHAPE DRAWING¹

The shape drawing studies were motivated by our interest in documenting drift, and by our interest in determining how drift was related to shape and the postural configurations and/or spatial locations adopted during drawing. Bernstein (1967) distinguished between the form and metrical properties of movement, and hypothesized that movement form, the qualitative properties of the spatial configuration, is more important to the perceptual-motor system than metrics, the quantitative properties of the spatial configuration (like size and orientation). As described in the previous chapter, the nature of the movement commands underlying the production of movement form depends on the initial position of the hand. Therefore, the maintenance of shape must depend critically on knowledge of current limb position. In the following experiments, we studied the relationship between spatial drift and drawing shape, size, and orientation.

To study this problem, we asked participants to draw shapes (squares and circles) at seven locations on a slightly pitched surface (see Figure 2.1). The seven locations were chosen to test a variety of locations in reach space under the stipulation that none of the positions be so extreme as to limit drift distance or direction. A shape template was provided at each drawing location. Each participant

¹ Brown, L. E. & Rosenbaum, D. A. (2001). Coordinate systems for movement planning: Evidence from positional drift. Poster presented at the annual meeting of the Psychonomics Society, Orlando, FL.

was instructed to trace the template provided as accurately as possible, at a comfortable pace, continuously for 20 seconds. On half the trials, the participant closed his/her eyes prior to initiating the movement trial. At the end of the trial, the participant was instructed to lift his/her hand up from the table surface before opening the eyes. Therefore, participants received no feedback about how far they drifted on any vision-absent trial. Drawing movements were recorded with an OPTOTRAK 3200 motion analysis system (Northern Digital, Waterloo, Ontario); infrared light emitting diodes were placed on the drawing finger, wrist, elbow, shoulder, and sternum.

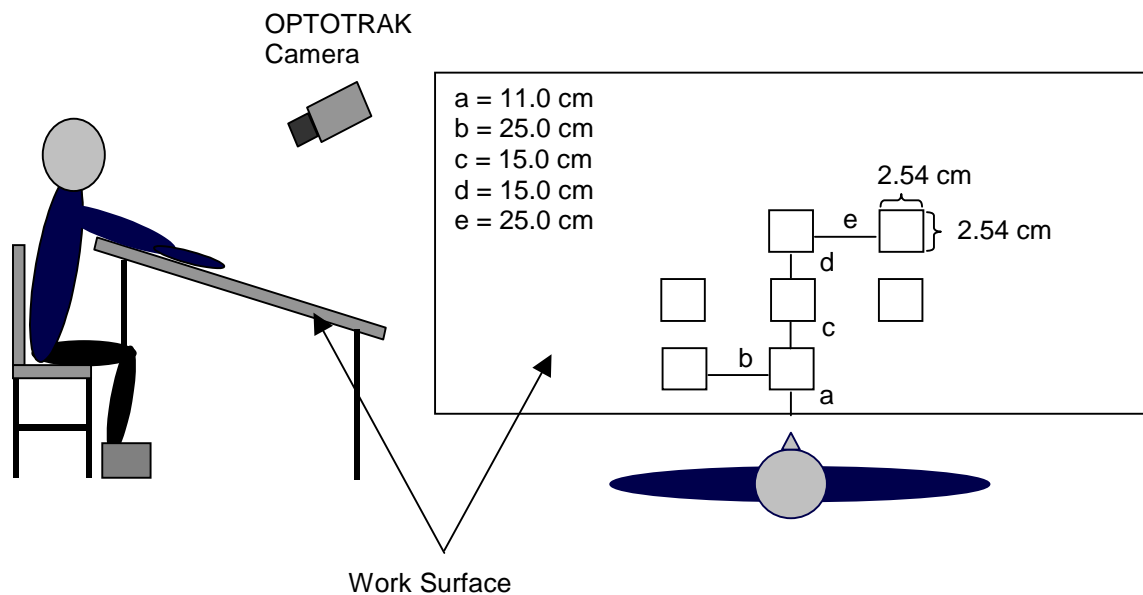
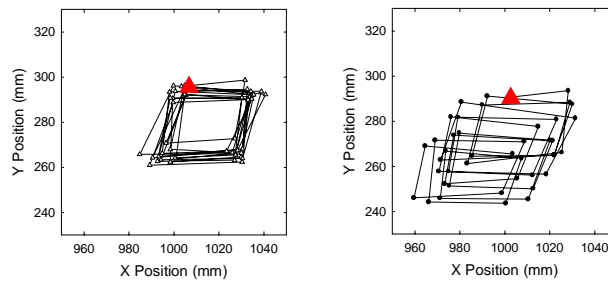


Figure 2.1: Set-up for the drawing experiments.

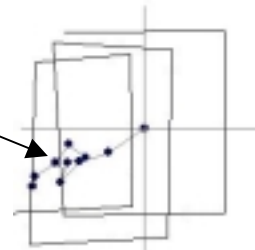
We estimated the location of the shape's center in terms of both spatial Cartesian (x, y) coordinates and joint (shoulder, elbow) coordinates using a moving average procedure (see Figure 2.2). Each subsequent corner position coordinate was

averaged with the previous three coordinates to produce a new estimate of shape center at each additional corner. Spatial drift was calculated as the Euclidean distance between the first spatial center estimate and each subsequent center estimate over the course of the trial. Similarly, joint drift was calculated as the Euclidean distance between the first joint center estimate and each subsequent joint center estimate over the course of a block of trials. In the square-drawing experiments, shape integrity was measured by calculating the aspect ratio [side width (mm)/side height (mm)], the

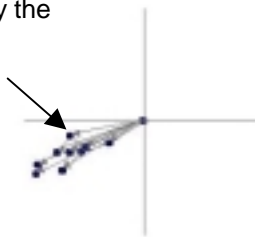
Figure 2.2: Example squares drawn by a single participant with vision (top left panel) and without vision (top right panel). Square centers were estimated using a moving average of 4 consecutive corner positions, then the drift was calculated as a difference from the first calculated center estimate.



An estimate of each shape's center was calculated.



The path followed by the shape centers was analyzed over time.



internal angle at each corner (degrees), and square orientation with respect to the horizontal (degrees). In the circle-drawing experiment, circle width was measured as the horizontal distance between the maximum and minimum positions achieved along the horizontal axis, and circle height was measured as the distance between the maximum and minimum positions achieved along the vertical axis. These distances were used to calculate circle aspect ratio and orientation with respect to the horizontal.

In the initial experiment, the objective was to document the pattern of drift and determine how this drift affected production of one-inch squares, drawn both with and without vision. Spatial and joint drift are presented in Figure 2.3A. The accumulation of spatial drift over time depended on vision, such that there was an interaction between vision condition and percent trial time, $F(4, 24) = 26.39$, $p < .001$. Joint drift accumulated regardless of the availability of vision, as shown by the significant main effect for percent trial time $F(4, 24) = 73.77$, $p < .001$, and the lack of interaction between vision and percent trial time, $F(4, 24) = 0.06$, n.s. This dissociation of spatial drift from joint drift is problematic to some extent, because it suggests that the drift may have occurred at joints other than those of interest. Shape integrity measures are presented in Figure 2.3B. Importantly, none of the measures of shape integrity changed significantly as the trial progressed, indicating that shape was preserved as the hand drifted (all $ps > .3$). In contrast, shape side lengths were significantly smaller when vision was removed, $F(1, 10413) = 1657.46$, $p < .01$. Thus, in the absence of vision, hand spatial position drifted and shape size diminished, but

shape integrity was preserved. For shape to be preserved, the motor system must have accounted for these new start postures.

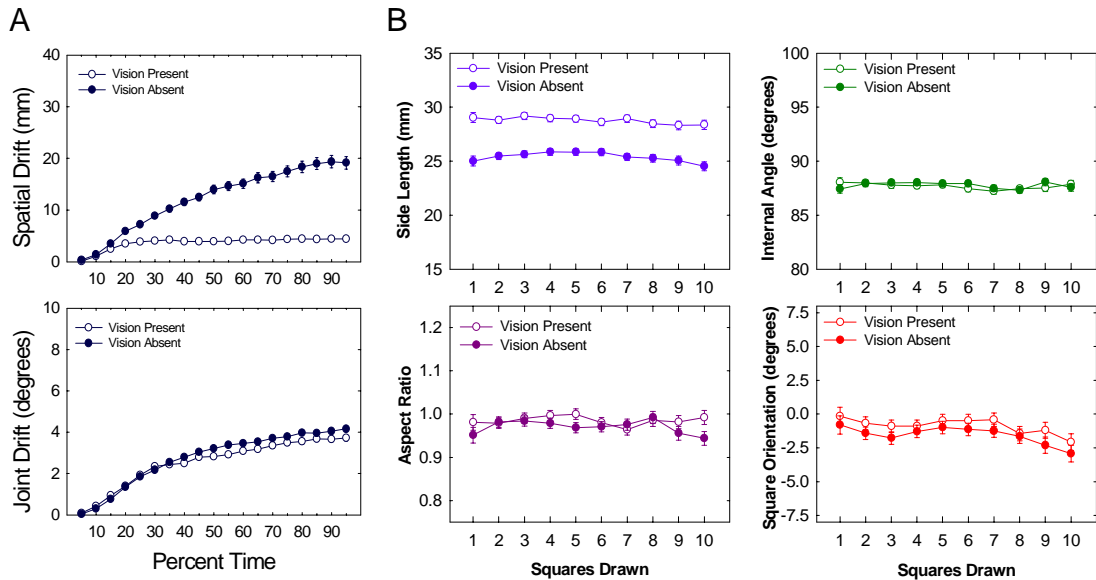


Figure 2.3: A. Top, spatial drift as a function of percent trial time. When vision was present, drift quickly reached a plateau. When vision was absent, drift continued to accumulate over the entire trial. Bottom, joint drift increased over time regardless of the availability of vision. B. Measures of square shape as a function of the number of squares drawn. Top left, side length was reduced during vision absent trials, but was well maintained over time. Top right, internal corner angle did not change when vision was removed, and it did not change over time. Bottom left, aspect ratio did not change when vision was removed, and it did not change over time. Bottom right, square orientation with respect to the horizontal, did not change when vision was removed, and it did not change significantly over time.

In the second experiment, the objective was to determine if and how drift depended on the size of the shape drawn (or the distance of the movements made). Participants drew squares of three different sizes (one-, two-, and three-inches), either with or without vision, continuously for 20 seconds. Spatial and joint drift are presented in the left panel of Figure 2.4. Once again, we found that spatial drift accumulation as a function of percent trial time depended on the availability of vision, $F(4, 6) = 33.99$, $p < .001$, but that joint drift did not, $F(4, 6) = 2.33$, n.s. The effects of

square size were only apparent under vision absent conditions: without vision, spatial drift was greater when large squares were drawn than when small squares were drawn, $F(2, 12) = 9.37$, $p < .01$. Again, despite this drift, square aspect ratio, internal corner angle, and orientation were preserved over number of squares drawn at all sizes (all p s $> .1$; see Figure 2.4B).

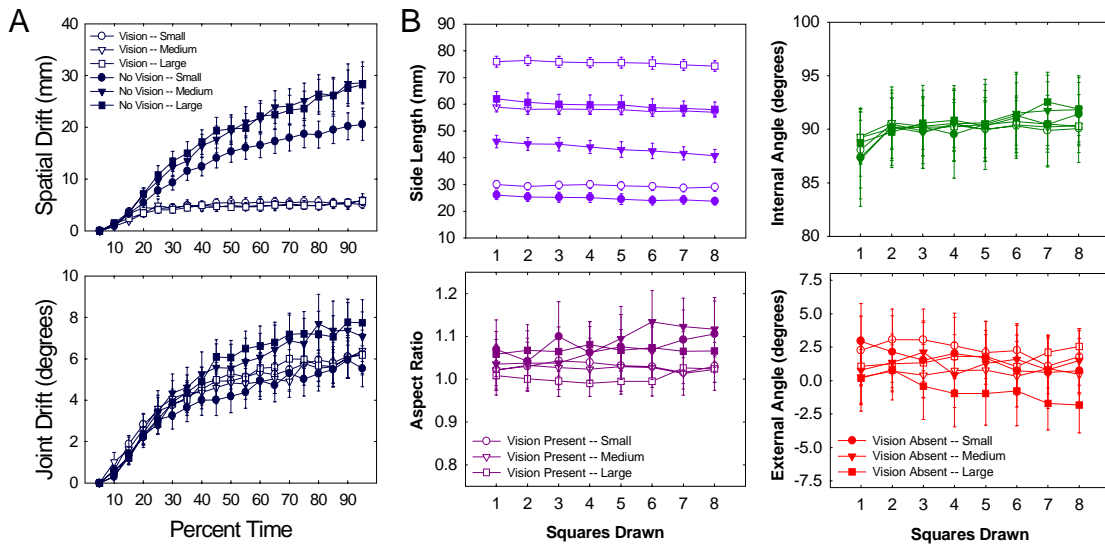


Figure 2.4: Top, spatial drift as a function of percent trial time. When vision was present, drift quickly reached a plateau and did not differ as a function of square size. When vision was absent, drift continued to accumulate over the entire trial, and this drift was greater for large squares than for small squares. Bottom, joint drift increased over time regardless of the availability of vision, and was greater for large squares than for small squares. B. Measures of square shape as a function of the number of squares drawn. Top left, side length was reduced during vision absent trials, and varied with square size, but was well maintained over time. Top right, internal corner angle did not change when vision was removed, did not depend on square size, and it did not change over time. Bottom left, aspect ratio did not change when vision was removed, was not dependent on square size, and it did not change over time. Bottom right, square orientation with respect to the horizontal did not change when vision was removed, did not vary with square size, and did not change significantly over time.

In the third experiment, we addressed the possibility that our results were unique to square-drawing. It is possible that producing corners (producing a 90°

direction change) may have allowed participants to encode the task as a sequence of short, straight movements, helping them to preserve shape. Indeed, Bock & Arnold (1993) suggested that abrupt direction changes invoke an error-correction mechanism that may aid in this process. To remove this possibility, we asked participants to draw one-inch diameter circles, either with or without vision, continuously for 20 seconds. Spatial and joint drift are presented in Figure 2.5A. The pattern of spatial and joint drift observed is remarkably similar to that observed during our initial square-drawing experiment: the accumulation of spatial drift over time depended on vision, $F(4, 24) = 31.61$, $p < .01$, whereas joint drift accumulated regardless of the availability of vision, such that the interaction of vision and percent trial time was no longer significant, $F(4, 24) = 1.22$, $p < .01$. Most importantly, however, circle aspect ratio and orientation were preserved with number of circles drawn ($ps > .2$) despite the fact that participants did not have the opportunity to anchor shape-drawing with abrupt direction changes. Therefore, the observations of position and posture drift coupled with shape preservation reported here are not specific to square-drawing.

To summarize, shape form (topology) was preserved over time, regardless of shape size, shape type, or the availability of vision during drawing. Without vision, spatial location and shape size (metrics) were not preserved: the hand drifted away from its initial spatial location and shape size decreased. In addition, joint position drifted away from the initial joint configuration. In all, participants maintained shape form better than they maintained spatial position or shape size. Indeed, form was preserved *despite* drift. Therefore, despite that participants could not use current hand

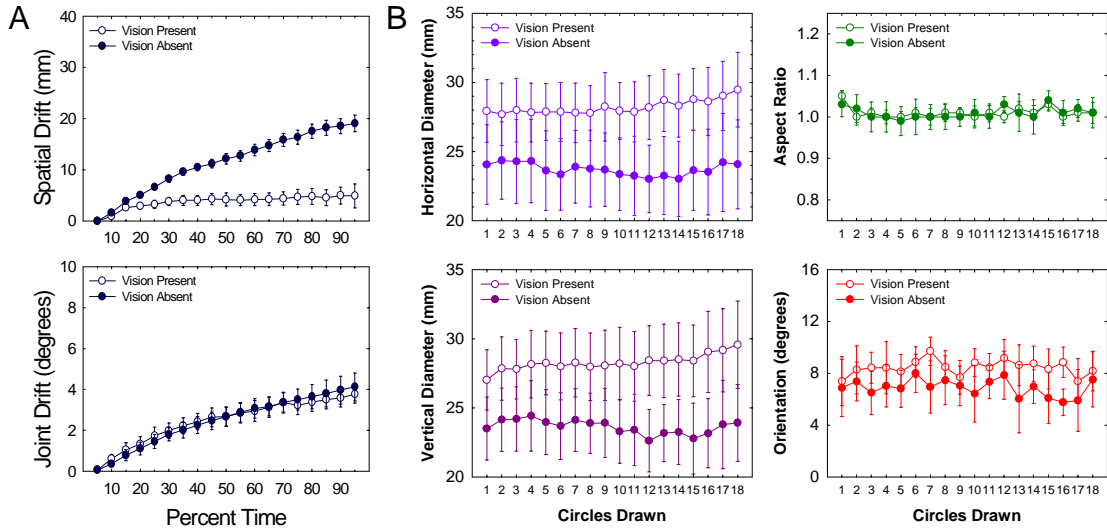


Figure 2.5: Top, spatial drift as a function of percent trial time. When vision was present, drift quickly reached a plateau. When vision was absent, drift continued to accumulate over the entire trial. Bottom, joint drift increased over time regardless of the availability of vision. B. Measures of circle shape as a function of the number of circles drawn. Top left, horizontal diameter was reduced during vision absent trials, but was well maintained over time. Top right, aspect ratio did not change when vision was removed, and it did not change over time. Bottom left, vertical diameter was reduced during vision absent trials, but was well maintained over time. Bottom right, circle orientation with respect to the horizontal, did not change when vision was removed, and it did not change significantly over time.

and arm position information to maintain the hand's spatial position, at some level the system must have been able to gather and use current limb position information to plan and execute movements consistent with the current drawing goal. This is because as the hand drifted, new joint configuration patterns were necessary to produce the movements that maintained shape. This current limb position information may have been provided by proprioception. Limb position information may have been provided by haptics, as crude haptic information was available to the participant during these experiments. DiZio and Lackner (1999; Lackner & DiZio, 2000) have shown that the magnitude and direction of shear forces generated during the first 30

ms of finger contact at the end of pointing movements can specify the position of the hand with respect to the body.

These experiments provided promising new information about how limb position information is monitored and used to maintain spatial form and position during continuous movement. There were several problems with these experiments, however. First, the fingers, wrist, and trunk were not immobilized. Instead, we tried to minimize wrist movements by asking participants to keep their wrist straight and we tried to minimize trunk movements by asking participants to rest their trunk against the edge of the table. To the extent that we were not able to control contributions from the wrist and trunk through instruction, the drift results reported above may reflect movements at those joints. Second, drawing was unpaced. Participants were instructed to draw at a comfortable pace, therefore some participants drew shapes quickly whereas others drew quite slowly. Because drawing time was held constant, some participants produced more shapes but drew less accurately, whereas other participants produced fewer shapes, but drew more accurately. This situation is problematic because it is difficult to tease apart whether drift accumulation was more dependent on number of shapes drawn or on time spent drawing.

The experiment reported in the next chapter was designed to address these concerns. First, movements were limited to rotations about the shoulder and elbow by restricting movements of the trunk, and by immobilizing the wrist and fingers with a splint. Second, limb position information was restricted to proprioceptive information as both visual and haptic information about limb position were removed. Third, the

movements were reduced to repetitive out and back movements between visible start and target positions. These movements were performed on a frictionless surface. Finally, the movements were paced to a metronome to ensure that the speed of movement and number of movements performed were controlled. These restrictions made it possible to estimate the flexor and extensor torques produced at each joint during movement (Sainburg et al., 1995), allowing for a more thorough analysis of the potential sources of drift. Details of the rationale, methods, and results of this new experiment are presented in the next chapter.

CHAPTER 3

LIMB POSITION DRIFT: IMPLICATIONS FOR CONTROL OF MOVEMENT AND POSTURE²

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, Sittig, and Denier van der Gon 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, hand location reports become increasingly inaccurate 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. Second, several researchers have

² Brown, L. E., Rosenbaum, D. A., & Sainburg, R. L. (revisions in progress). Limb position drift: Implications for control of movement and posture. Journal of Neurophysiology.

demonstrated that when shapes are drawn continuously without vision, shape position drifts but shape form is preserved (Brown and Rosenbaum 2001; Verschueren et al 1999; Zelaznik and Lantero 1996).

Shape form preservation coupled with shape position drift appears inconsistent with decay in the efficacy of proprioception for signalling limb position because movement production depends on knowledge of current limb position. Previous studies have shown that initial limb position information influences 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 hand position and somatosensory feedback about limb position (Rossetti et al. 1995; Sainburg et al. in press). Moreover, single-unit recording studies have shown that limb position information influences the neural coding of movement parameters. Population vectors, the weighted averages of single-cell movement direction selectivity, in the macaque primary motor and premotor cortex reflect movement direction in relation to the start position of the hand in extrinsic space (Georgopoulos et al. 1986). In single-unit activity, preferred directions are modified as the hand adopts new starting postures (Caminiti et al. 1990; Caminiti et al. 1991) even when initial hand location, movement trajectory, and end position were held constant (Scott and Kalaska 1996; Scott et al. 1997). This implies coding of movement in relation to both intrinsic and extrinsic representations of hand position.

The experiment reported here was designed to investigate the source of limb position drift and to determine if and how drift affects movement production. Bock (Bock and Eckmiller 1986; Bock and Arnold 1993) has shown that pointing errors accumulate over the course of a movement sequence while movement amplitude is preserved such that end position errors mirror earlier start position errors. The possibility that drift is movement-dependent was tested in the current study by asking participants to perform continuous 30° and 120° movements in the absence of visual feedback. These two directions require different relative amounts of shoulder and elbow motion. This results in movement-dependent differences in both the dynamic interactions between the segments, and the inertia that must be overcome to initiate and produce movement (Gordon et al. 1994b; Sainburg et al. 1995; Gribble and Ostry 1998). If position drift is dependent on such dynamic factors, then the drift associated with the 120° movements should be different from the drift associated with 30° movements. We also tested the possibility that drift is position-dependent by varying start location. If drift is position-dependent such that the limb drifts toward a specific spatial location or posture, then both drift distance and direction should vary with start location. Finally, we examined if and how drift affects movement production by analyzing hand movement distance and direction over time. We reasoned that if drift is the result of decay in the efficacy of proprioceptive information about start position in the absence of vision, then movement distance and direction should vary as the hand drifts away from its initial position.

Participants performed blocks of 75 repetitive movements in one of two directions (30° and 120° with respect to the right horizontal) from three start locations,

in time with a metronome. Hand location information was shown during the first five movements, but then 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.

METHOD

Participants

Five healthy students (3 female, 2 male), aged 21 – 25, 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 just below shoulder height. 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 surface of the table without friction. Movements of the arm and forearm were monitored with a Flock of Birds® (Ascension-Technology) magnetic motion recording system that was 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 written in REALbasic (REAL Software, Inc.) 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 as depicted in Figure 3.1. A back-projection screen was suspended 21 cm above a mirror that was in turn suspended 21 cm above the table surface. This arrangement provided the impression that the visual display was in the same horizontal plane as the table surface.

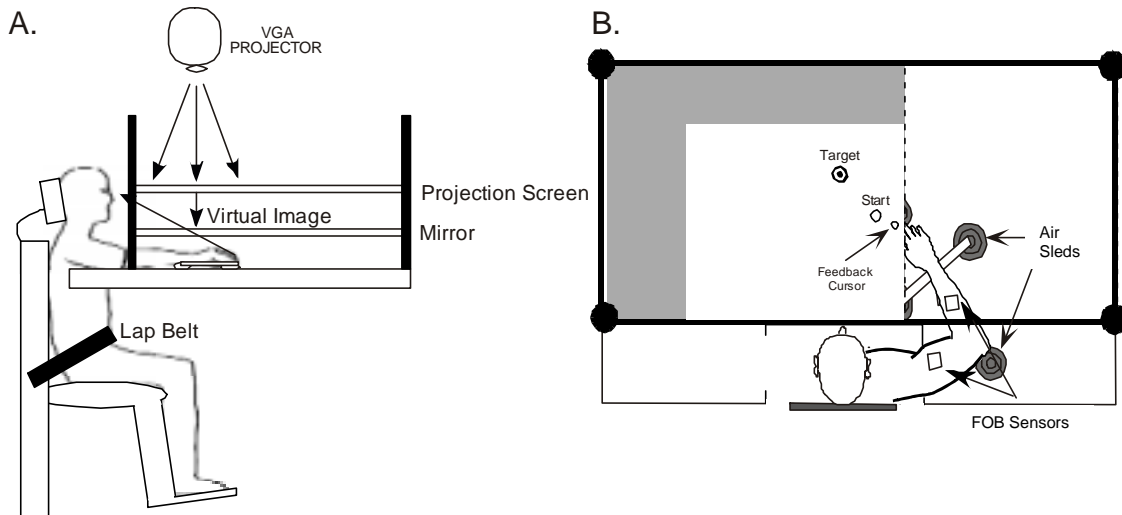


Figure 3.1: The experimental setup. A. A back projection screen was suspended above a one-way mirror suspended above a glass-covered table surface. This arrangement provided the impression that the display was in the same depth plane as the table surface. B. The forearm was secured to a custom-made air-jet sled. Flock of Bird [®] sensors (shown as open squares) were fixed to the sled and the upper arm.

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 parent 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 2.3 cm and 4 cm in diameter, respectively, and were separated by 15 centimeters.

Start and target circles were presented on a white rectangular display (90.7 x 67.0 cm) which was projected onto the framed, rectangular (87 x 153.5 cm) back projection screen. The mirror through which the participant viewed the display (also 87 x 153.5 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 frame reduced the likelihood that hand drift arose from visual drift (Adams, 1912).

Experimental Design

We used a 3 start locations x 2 movement directions x 75 movement trials within-participants design. Each participant performed 2 practice blocks of 25 trials prior to performing six blocks of 75 repetitive movement trials. Each of the 6 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 120s. During the first 5 trials of each block, the participant viewed a 1-cm diameter cursor that reflected the continuous location of the index fingertip. The participant initiated the trial by aligning the cursor with the

start circle. At that time, a 50-ms tone was presented. This tone recurred at 1.6 s intervals for the remainder of the block and did not depend on hand location. The participant was instructed that upon hearing each tone, s/he should move quickly and accurately to the target and back to the start location before hearing the next tone. The participant was further instructed that s/he 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 and s/he 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, Inc.) and Matlab™ (Mathworks, Inc.). Prior to data collection, the 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 3rd 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 last velocity minimum that preceded peak velocity and 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 ($\text{location}_i - \text{location}_1$, $i = 1$ through 70), whereas instantaneous drift was defined as the Euclidean distance between each start location and the previously adopted start location ($\text{location}_i - \text{location}_{i-1}$, $i = 2$ through 71). These distances are shown in Figure 3.2. Shoulder and elbow angular cumulative and instantaneous drift were similarly calculated. 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.

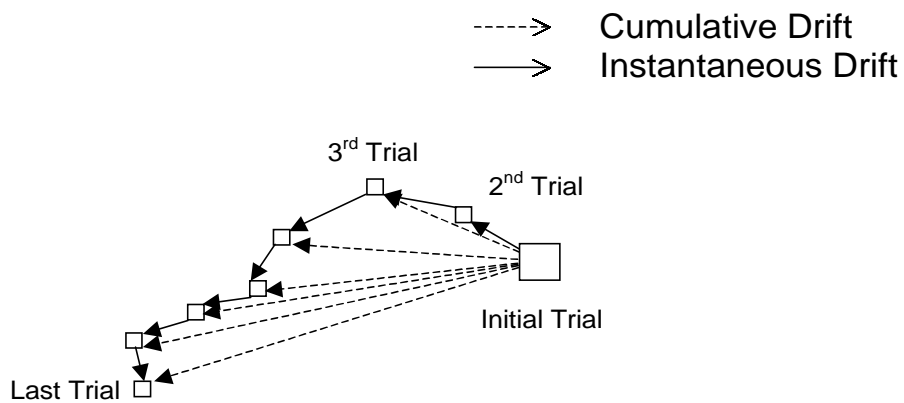


Figure 3.2: Calculation of cumulative (dashed lines) and instantaneous drift (solid lines). Cumulative drift was defined as the Euclidean distance between the start location adopted on the initial trial and each successive start location. Instantaneous drift was defined as the Euclidean distance between each start location and the previously-adopted start location.

Hand movement distance and direction were measured for the movement from the start location to the target, and for the return movement from the target to the start location. Hand distance out was defined as the Euclidean distance between the hand location at movement start and the hand location at movement end, and hand distance in was defined as the Euclidean distance between the hand location at the previously identified movement end and the subsequently adopted start location. 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 shoulder (T_s) and elbow (T_e) using the equations detailed below (from Bagesteiro & Sainburg, 2002). For the purpose of this study, 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. The inertia and mass of the forearm support were 0.0247kgm^2 and 0.58kg , 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).

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

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

where:

$$\alpha = m_s r_s^2 + I_s + m_e [l_s^2 + r_e^2 + 2l_s r_e \cos(\theta_e)] + I_e$$

$$\beta = m_e l_s r_e \cos(\theta_e) + m_e r_e^2 + I_e$$

$$\gamma = m_e l_s r_e \sin(\theta_e)$$

$$\delta = [m_s r_s \cos(\theta_s) + m_e (r_e \cos(\theta_s + \theta_e) + l_s \cos(\theta_s))] \ddot{y} \dots$$

$$\dots - [m_s r_s \sin(\theta_s) + m_e (r_e \sin(\theta_s + \theta_e) + l_s \sin(\theta_s))] \ddot{x}$$

$$\varepsilon = m_e r_e^2 + I_e$$

$$\varphi = [m_e r_e \cos(\theta_s + \theta_e)] \ddot{y} - [m_e r_e \sin(\theta_s + \theta_e)] \ddot{x}$$

m_s and m_e = masses of upper arm and forearm.

r_s and r_e = distances from the proximal joint to center of mass of upper arm and forearm.

l_s and l_e = lengths of upper arm and forearm.

I_s and I_e = moments of inertia at center of mass of upper arm and forearm.

θ_s and θ_e = orientation angles at proximal end of segment for upper arm and forearm.

x = x position of the shoulder.

y = y position of the shoulder.

It is important to note that computed joint muscle torque (T_s and T_e at the shoulder and elbow, respectively) 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 from movement initiation to peak tangential hand velocity to obtain measures of initial shoulder and elbow torque impulse. Torque impulse provides 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 applied 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, 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 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) x movement direction (30°; 120°) x trial number (1-70) repeated-measures analysis of variance ($\alpha = .05$). We removed the final 5 movement trials from the analysis to eliminate artefacts 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 analyzed further using planned comparisons (t-tests) 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 statistical methods (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 analysis of variance.

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 3.3 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 grey shade of the movement paths. In all of the plots, although hand position drift is evident, movement extent and direction appears relatively preserved over time. To quantify the drift, we computed both cumulative and instantaneous drift over trials. The results are presented in Figure 3.4.

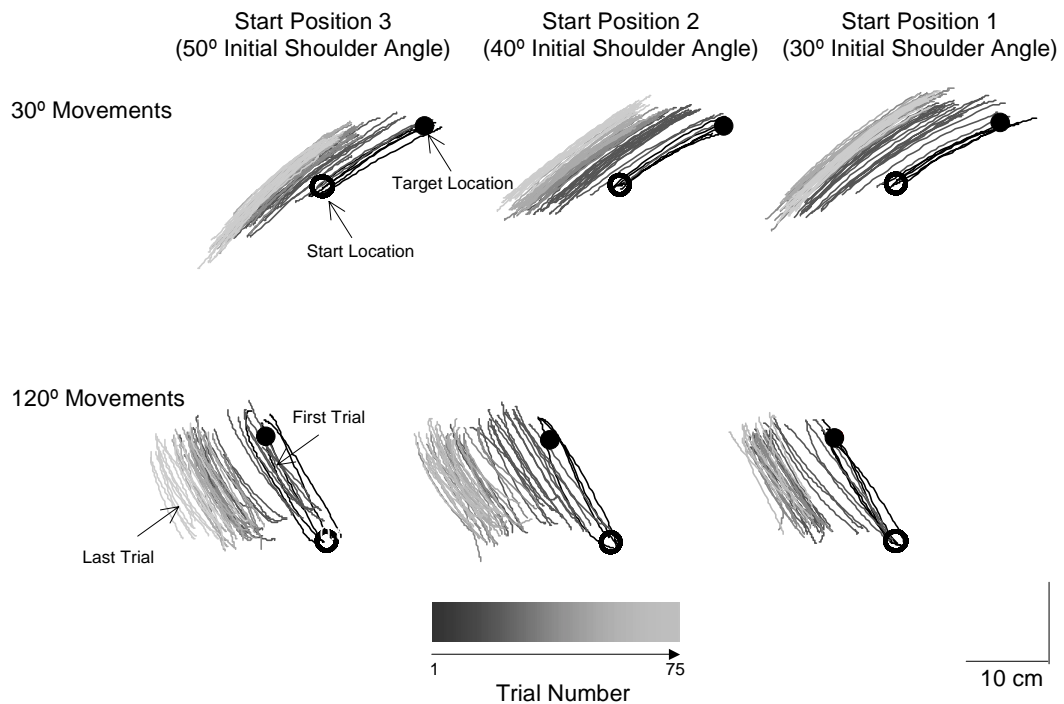


Figure 3.3: A series of 70 hand paths produced by one participant (P5) in each start location and movement direction. Start locations and targets are indicated by open and closed circles, respectively. Progression of trials over time is represented by the grey shade of the path, where early trials are darker than late trials. Trials with fingertip position feedback are drawn in black.

Without Hand Position Feedback, Drift Accumulates Over Time

Figure 3.4A 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 shown, instantaneous hand drift (1.37 ± 0.1 cm) remained constant across successive trials, $F(69, 276) = 1.19$, *n.s.* Instantaneous drift did vary reliably with movement direction, $F(1, 4) = 96.63$, $p = .001$, 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 Figure 3.4B). There was also a main effect for start location, $F(2, 8) = 8.21$, $p = .012$, 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 start location 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 Figure 3.4C. Hand position drift increased early in the trial block, reaching an apparent plateau near trial 40. The presence of an increase was confirmed by a main effect for trial number, $F(69, 276) = 12.69$, $p < .001$. Cumulative drift increased abruptly when vision was removed (vision-present vs. early vision-absent, $p < .001$), and continued to accumulate to mid-block (early vision-absent vs. mid-block vision-absent, $p = .005$). However, drift did not accumulate appreciably beyond mid-block (mid-block vision-absent vs. late vision-absent, $p = .424$). On average, hand position drifted 7.9 ± 0.2 cm from the initial start

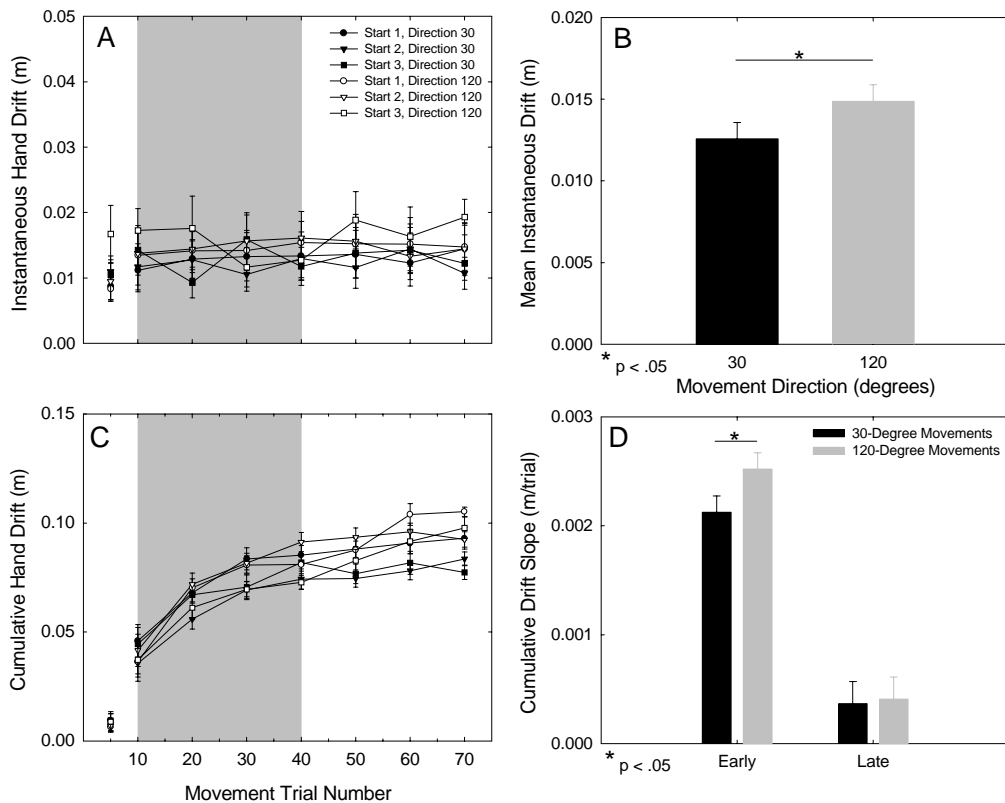


Figure 3.4: Mean instantaneous and cumulative hand position drift. A. Mean instantaneous drift (m) as a function of trial number, start location, and movement direction. Error bars represent the standard error of the mean. The shaded area represents the portion of the block during which drift accumulated rapidly (see panel C). 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 the standard error of the mean. Drift accumulated rapidly over the first 40 trials and then reached a plateau. The shaded area in both panel 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.

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 3.4D 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, $F(69, 276) = 1.42$, $p = .027$, showed that drift accumulated more quickly for 120° movements than for 30° movements early in the block, but that there was no effect of movement direction on drift accumulation rate late in the block. Furthermore, total distance drifted was not different for the two movement directions ($p = .269$). Finally, there were no significant main effects or interactions involving start location.

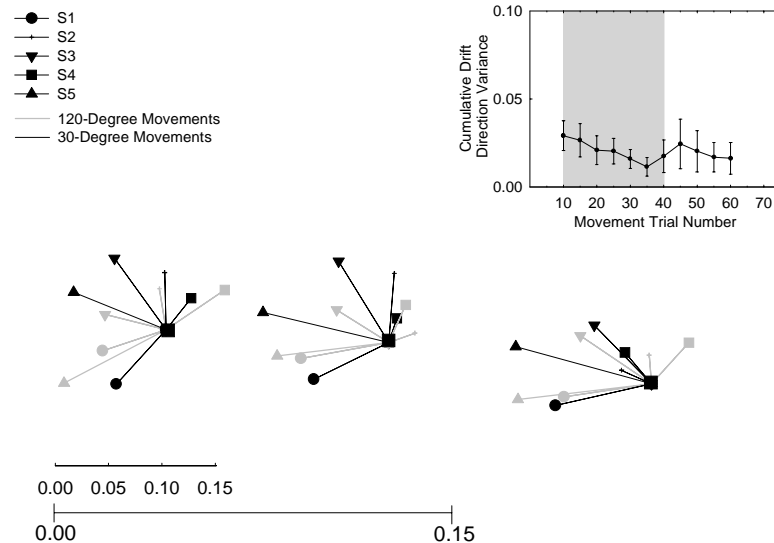


Figure 3.5: Vectors representing mean drift distance and direction for each participant. The outer scale shows the relative positions of the three start locations. The inner scale reflects the distances of the drift vectors. These drift vectors show that although participants did not drift toward their body, there was no one direction toward which drift was directed. In the upper right corner, mean deviations from mean within-trial drift direction, as a function of trial number, start location, and movement direction. This plot indicates that participants drifted consistently after vision was removed.

Figure 3.5 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, in both the 30° and 120° targets (black and grey, respectively). Cumulative drift direction did not vary as a function of movement direction ($p = .60$). 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 ($p < .001$) and start location 3 ($p < .05$). Start location 1, however, did not differ significantly from start location 3 ($p = .86$), 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 variance over time by computing variance in moving windows of 10 points from trial 6 (the first vision-absent trial) through trial 70. Analysis of cumulative drift direction variance, shown in the inset of Figure 3.5, indicated that cumulative drift direction variance decreased significantly as a function of movement number, $F(54, 216) = 1.88, p = .001$.

We analysed 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 Figure 3.6. Panel A 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 and 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 crosshairs), instantaneous (movement-to-movement) drift

vectors were more likely to fall along a particular direction, allowing drift to accumulate, than later in the trial. 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 variance over time by computing instantaneous drift direction variance 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 Figure 3.6B, reflect the single participant data shown in Figure 3.6A: instantaneous drift direction variance was relatively low early in the series, but then increased later in the series, $F(54, 216) = 5.02$, $p < .001$. This increase halted drift accumulation.

To summarize, participants' hand position drifted as they performed 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 a decay in the efficacy of proprioception in the absence of vision, then movement distance and direction should vary considerably as the hand drifted away from its initial position. In contrast, if proprioception remains a reliable source of limb configuration information, then movement distance and direction should be preserved as the hand drifts.

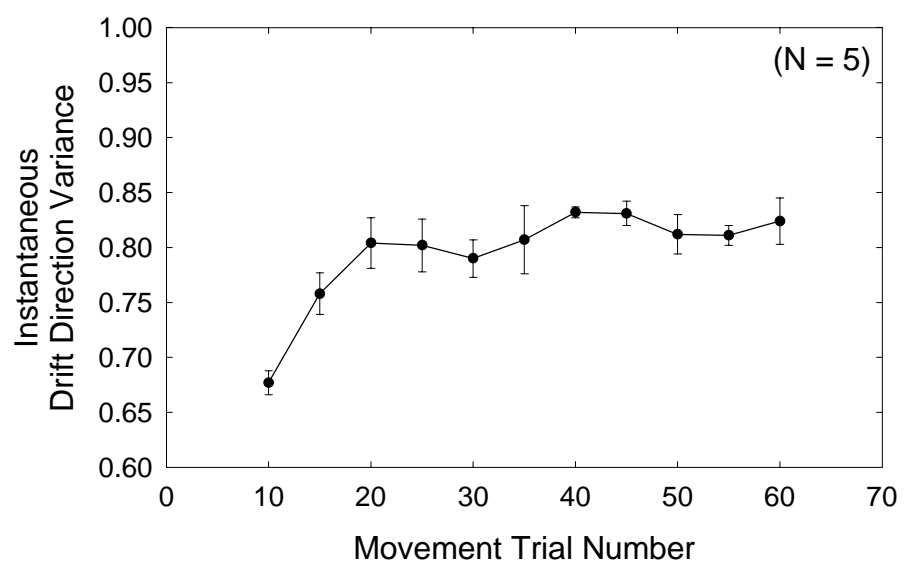
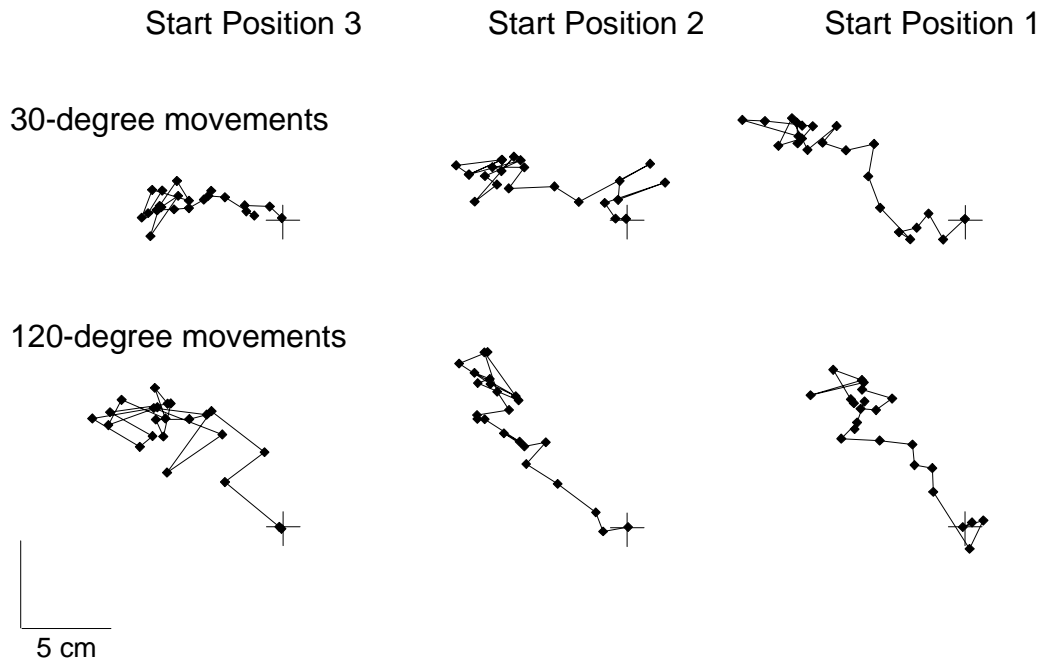


Figure 3.6: A. Paths produced by plotting the series of movement start positions adopted by one participant (P4) in each condition. For clarity, we plotted start positions from vision-absent trials only and only every third start location is plotted. The initial starting position is represented by crosshairs (+). B. Instantaneous drift direction variance as a function of movement number. Only vision absent trials were included in this analysis.

Data bearing on these predictions – hand movement distance and direction from the start location to the target – are presented in Figures 3.7A and 3.7B, respectively. For this figure, every 10 trials were averaged for graphical clarity. Statistical analyses were conducted using individual trials. Because hand position drift reached a plateau by trial 40, we looked for changes to 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.

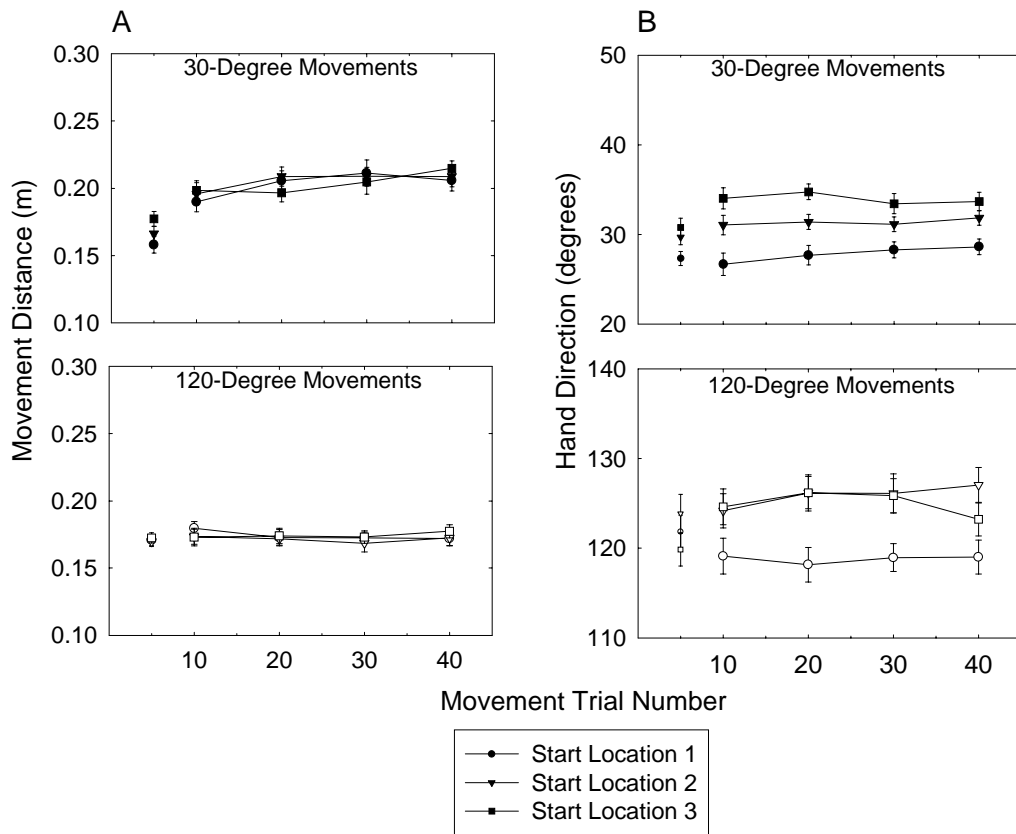


Figure 3.7: Hand movement distance (A) and direction (B) as a function of trial number, start location, and movement direction. Results are shown for the trials over which drift accumulated most rapidly.

Movement distance increased significantly as a function of movement direction and trial number, $F(39, 156) = 3.63$, $p < .001$. This interaction, however, could be attributed more to the removal of visual feedback than to hand position drift. Figure 3.7A shows that for 30° movements, movement distance increased abruptly when visual feedback was removed, but movement distance did not change significantly thereafter ($M_{\text{early}} = 0.189 \pm 0.014$ m vs. $M_{\text{mid-block}} = 0.207 \pm 0.018$ m, n.s.). In contrast, for 120° movements, movement distance was not affected by the removal of visual feedback and did not change significantly thereafter ($M_{\text{early}} = 0.175 \pm 0.007$ m vs. $M_{\text{mid-block}} = 0.170 \pm 0.015$ m, n.s.). On the whole, the results show that movement distance was preserved as hand position drifted.

Even though participants were presented with a target circle that was located 15 cm from the start location circle, movement distance was generally greater than 15 cm, even when vision was available. This hypermetria was greater for movements in the 30° direction ($0.199 \pm .001$ m) than for movements in the 120° direction ($0.173 \pm .001$ m), $F(1, 4) = 8.19$, $p = .046$. Similar accounts of direction-dependent hypermetria have been described in previous studies of horizontal reaching (Gordon et al. 1994a, 1994b; Sainburg et al. 1995).

Mean movement direction produced over time is summarized in Figure 3.7B. Most importantly, movement direction did not vary significantly with trial number, $F(39, 156) = .953$, n.s., indicating that movement direction was preserved relative to the initial trial over the portion of the block when hand position drifted most rapidly. Not surprisingly, observed movement direction varied significantly with prescribed movement direction, $F(1, 4) = 674.96$, $p < .0001$. Observed movement direction also

varied significantly with manipulated start location, $F(2, 8) = 10.29$, $p = .006$.

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 next calculated the muscle torques generated at the elbow and shoulder by each participant. Results for a representative participant (P3) are shown in Figure 3.8. In this example, movements were performed in the 120° direction from start location 3. In Figure 3.8A, the movement path for a trial generated early in the block, immediately after vision was removed (left), is juxtaposed with a movement path generated late in the block, after the participant reached the cumulative drift plateau (right). Although this participant drifted 9.1 cm to the left and toward the body as the block progressed, the late

movement path is very similar to the early movement path in both distance and direction. To test whether these trends were representative of the participant's early- and late-block movements, we compared the mean of the first five post-vision trials with the mean of five consecutive post-plateau trials with an independent-samples t-test. Figure 3.8B demonstrates that while early-block hand position was significantly different from late-block hand position ($p < .001$), movement distance ($p = .241$), movement direction ($p = .206$), and peak velocity ($p = .774$) were preserved.

Figure 3.8C 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 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 quantify the differences in muscle torque between trials, the shoulder and elbow muscle torque profiles were integrated from movement initiation to peak velocity to obtain measures of initial shoulder and elbow torque impulse. Mean shoulder and elbow torque impulse are presented in Figure 3.8D. Positive impulse values represent flexor muscle torque impulse, and 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 ($p = .070$), early-block shoulder muscle torque impulse was consistently different from late-block shoulder torque impulse ($p = .019$).

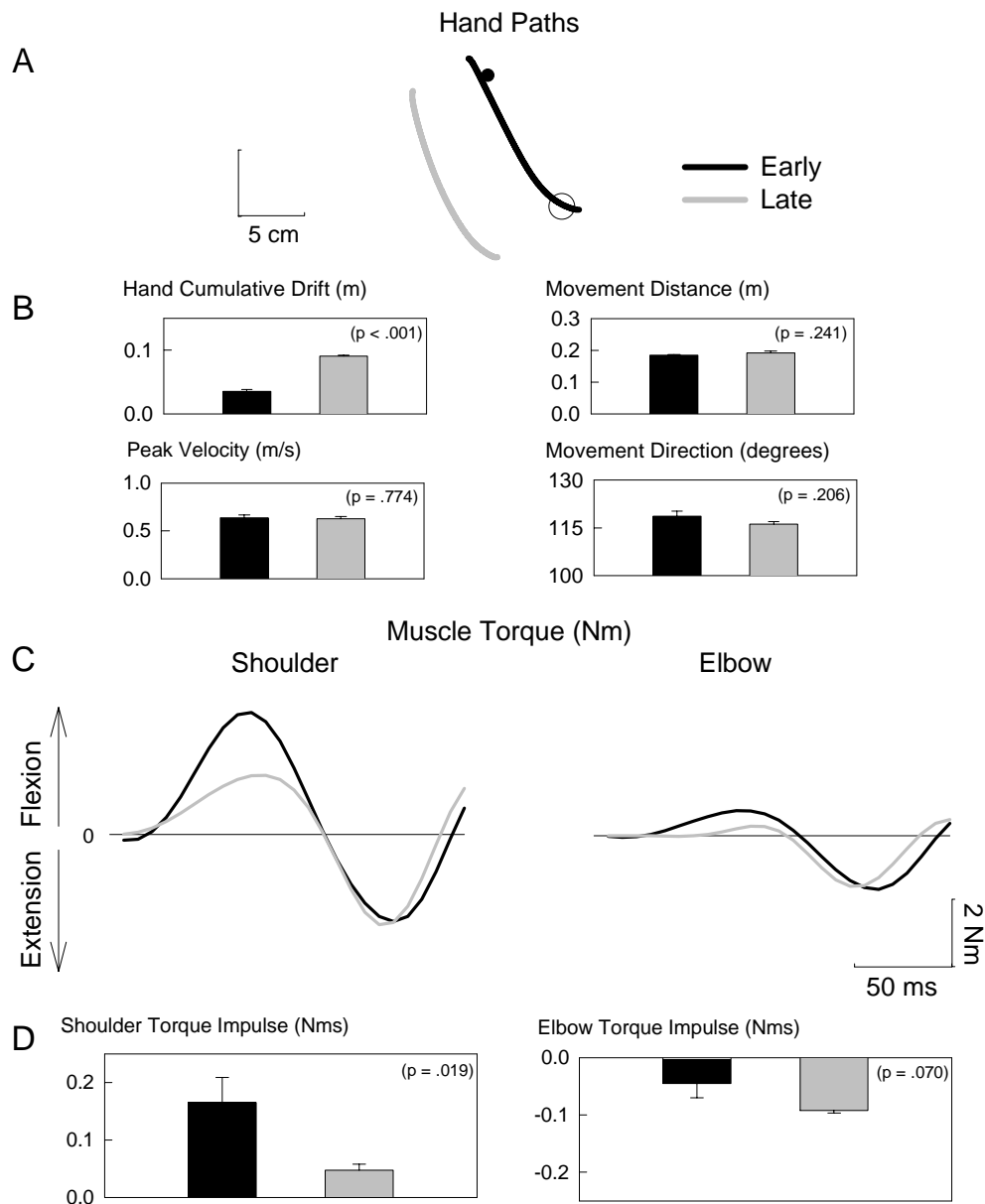


Figure 8

Figure 3.8: A. Representative hand paths from a single participant (P3). The start location and target are indicated by an open and closed circle, respectively. The early-block hand path is the first 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 movement direction. The hand drifted significantly but maintained movement distance and direction. C. Shoulder (left panel) and elbow (right panel) muscle torque profiles during the first 250 ms of the same early- and late-block movements. Values greater and less than zero reflect flexor and extensor muscle torque, respectively. D. Comparisons of early- and late-block shoulder (left) and elbow (right) muscle torque impulse.

This analysis was repeated for each participant individually. Because drift varied in extent and direction across participants, we expected that drift-dependent modifications of torque would also be different 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, all of the participants modified their muscle torque strategy as hand position drifted.

Table 3.1. Comparisons of early- and late-block torque impulse at the shoulder and elbow.

Participant	Shoulder Torque Impulse (Nms)			Elbow Torque Impulse (Nms)		
	Early	Late	p	Early	Late	p
1	.079 ± .324	.662 ± .031	.021	-.010 ± .013	.028 ± .008	.035
2	.303 ± .059	.653 ± .030	.002	-.023 ± .022	.037 ± .014	.074
3	.165 ± .044	.047 ± .011	.019	-.045 ± .025	-.092 ± .004	.070
4	.138 ± .124	.397 ± .014	.048	-.033 ± .019	.032 ± .006	.006
5	.304 ± .065	.139 ± .014	.000	-.045 ± .008	-.055 ± .003	.283

If Movement Dynamics Had Not Changed, Movement Direction Would 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 rigid body simulation to better understand how movement distance and direction were maintained in the face of substantial limb position drift.

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 post drift plateau trials in the trial block. In effect, the simulation predicted what would have happened if the participant had continued to use the same torque profile for the displaced hand positions as was used for non-displaced hand positions.

Figure 3.9A shows the results for typical trials to the 120° and 30° targets. On the left are shown the 120° movement hand paths from an observed early trial, an observed late trial, and a simulated trial. Notice that the direction and lengths of the early and late trial are similar, even though the late trial was initiated some 9 cm medial and posterior to the early trial. In contrast, the simulated trial predicted a 33° counter clockwise shift in movement direction when compared with the actual late-block trial. Thus, our simulation demonstrates that using the same torque profiles to drive the limb from the drifted position would result in a notably different movement direction. As can be seen from the torque profiles shown in Figure 3.9B, shoulder flexor muscle torque for the later movement was reduced nearly 50% relative to the early movement. In the simulation, this reduction in torque did not occur, which resulted in greater shoulder flexion, producing the large counter clockwise direction error in the simulated trial.

The right panel of Figure 3.9A 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 a 8.4° counter clockwise error. As reflected by

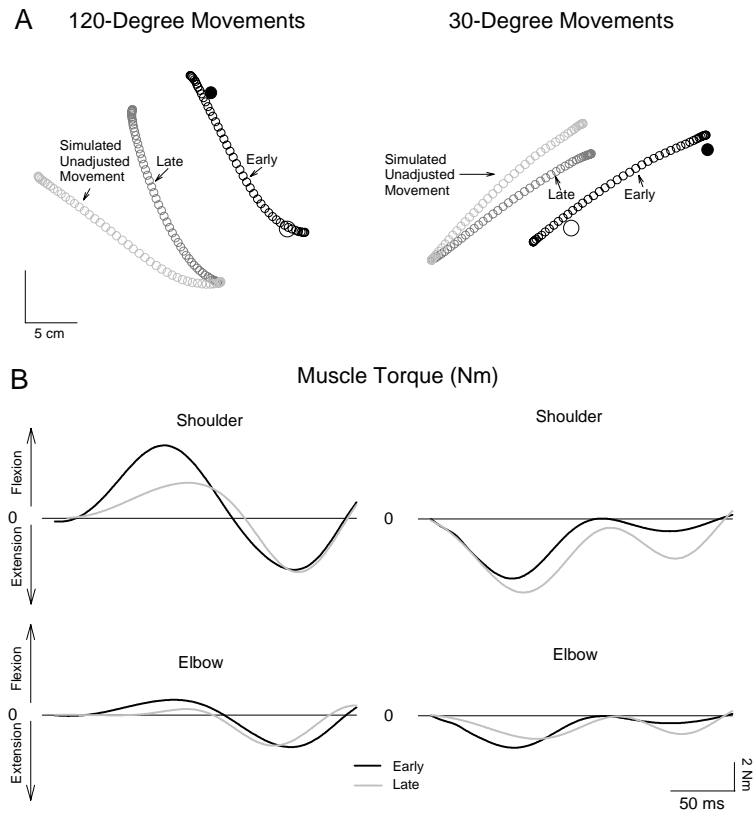


Figure 3.9: Top: Simulation results for representative 120° (left) and 30° (right) movement paths. Observed early (black) and late (grey) paths are shown next to paths predicted by the simulation (light grey). Predicted paths represent the movement path that would have been performed had participants not modified muscle torque profiles as the hand drifted. Bottom: Observed early (black) and late (grey) 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.

the torques shown in Figure 3.9B (right panel), the late block trial was associated with a near 20% increase in shoulder extensor torque. In the simulation, this extensor torque increase did not occur, resulting in less shoulder extension and a clear counter clockwise direction error.

It should be noted that this simulation is based on a simple rigid body model that does not include muscle, tendons, and soft tissue. However, the simulation effectively illustrates, for a two-segment, rigid body system, how application of the same torque to a “drifted” limb configuration will 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 dynamic control strategies in accord with drift-induced changes in initial limb configuration.

Joint Angular Cumulative Drift Depends On Role In 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 Figure 3.10, respectively. Figure 3.10A shows that for 120° movements, the elbow and shoulder contributed both to movement production and posture maintenance, and Figure 3.10C shows that there was significant drift

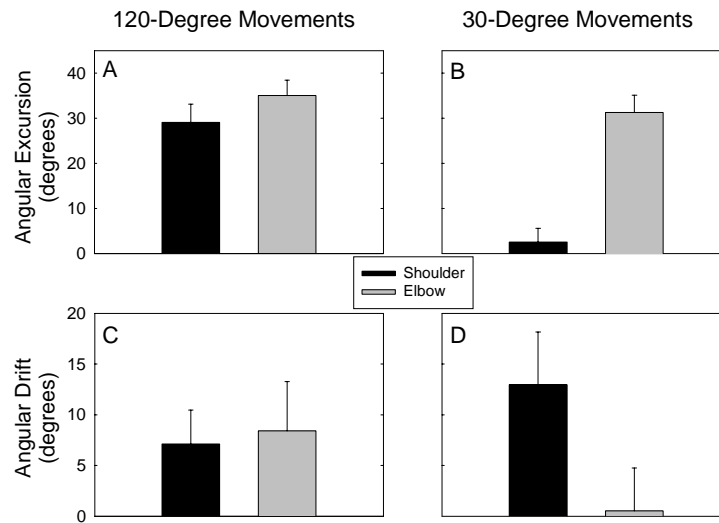


Figure 3.10: A. Mean angular excursion at each joint for 120-degree movements. B. Mean angular excursion at each joint for 30-degree movements. C. Mean angular drift at each joint for 120-degree movements. D. Mean angular drift at each joint for 30-degree movements.

accumulation both at the elbow ($p = .019$) and the shoulder ($p = .022$). Figure 3.10B shows that for 30° movements, there was a well-defined division of labour between the shoulder and elbow joints: movement occurred primarily through elbow motion (the focal joint) while the shoulder served to stabilize limb position (the non-focal joint). Figure 3.10D shows that for 30° movements, there was significant angular drift accumulation at the shoulder (the non-focal joint; $p=.045$) but not at the elbow (the focal joint; $p=.367$). This pattern described here, which for 30° movements links the majority of drift to the non-focal joint, 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 this experiment was to determine the source of naturally occurring limb position drift and to determine how this drift affected movement performance. Participants performed blocks of 75 repetitive movements in one of two directions (30° and 120°), from one of three start locations, in time with a metronome. Fingertip location feedback was provided during the first five movements and 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 was related to movement error. Although hand position drifted on average 8 cm from its original location, hand movement distance and direction were preserved over repeated trials. Inverse dynamic analysis showed that muscle torque profiles 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. 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 by separate position and movement controllers.

On one hand, the preservation of movement distance and direction as limb position drifted, and the reliable and appropriate modification of muscle torques

produced at the shoulder and elbow as the limb drifted, indicates that accurate limb position information must have been available to the movement control system. Because both haptic and visual information about limb position were removed, this information must have been provided by proprioception. On the other hand, limb position drift appears to indicate that limb position information was not reliable for maintaining limb position in space. This suggests an apparent paradox in which proprioceptive limb position information was used to update and produce appropriate movement trajectories but was not used to maintain the limb's spatial position. We considered four possible explanations for this pattern of results.

Is Drift Driven by an Attractor?

First, by manipulating start location, we tested the hypothesis that drift results from attraction to or repulsion from specific postures or positions in space. Theoretically, attractive postures may be distinguished by high levels of comfort, or high sensory or perceptual resolution, characteristics usually associated with the center of joint range of motion. In addition, attractive postures or locations may support preservation of movement trajectory because the attractor may promote the emergence of stable movement production. The spatial attractor hypothesis predicted that cumulative drift distance and direction would vary with manipulated start location, and that drift would converge upon a common spatial or postural region near the center of joint range of motion. These predictions were not supported. Drift distance was not affected by start location manipulations, drift did not converge upon any one position in space, and drift was often directed away from the center of joint

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

Does Drift Reflect A Growing State Estimation Error?

Wolpert et al. (1998) proposed an account of limb position error accumulation which may provide a second 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 storage mechanism that stores past limb position estimates (Wolpert et al. 1998). Estimates of the current state are based both on the currently 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 would accumulate. This account may explain how drift accumulates with respect to the visually-presented initial start position. It does not account, however, for how participants were able to adequately update limb position information for maintaining movement trajectory accuracy.

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 provided in this task. Type 1a (large-fiber) muscle spindle afferents respond both to changes in static muscle length and rate of change of muscle length, indicating that 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), indicating that 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 limb position as it moved at imperceptively slow speeds. Under these conditions, participants have been able to detect excursions at the elbow and shoulder that produce fingertip position changes of under five mm with 70% accuracy in the rate of rotation ranges employed in the current study (Hall and McCloskey, 1983). In our task, however, participants were required to monitor both position and movement trajectory simultaneously. This dual-task situation may have raised the threshold for position change detection, allowing position errors not only to go undetected but 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 the instantaneous position changes observed in this experiment are well above the position change detection thresholds reported by McCloskey (Hall and McCloskey, 1983; Taylor and McCloskey, 1990) and Clark et al. (1985), it is possible that limb position drift accompanied by the relative preservation of movement may be attributable to differences between position information salience and movement information salience.

Although we cannot rule out this possibility with the present data set, we recently tested this hypothesis in an experiment designed to manipulate the magnitude of instantaneous drift (Brown, Rosenbaum, & Sainburg, 2002). This information salience hypothesis predicts that position changes should be harder to detect and correct when they are small than when they are large. Therefore, this information salience hypothesis predicted that drift should accumulate more quickly when movement-to-movement position changes are small than when they are large and that the final plateau level should vary with the amount of instantaneous drift. In this study we manipulated the amount instantaneous drift by varying movement speed and found that drift accumulated more quickly under fast movement conditions (when errors were large) than under slow movement conditions (when errors were small) but that plateau level did not vary with movement speed. Thus, the results of this experiment did not agree with the predictions of the information salience hypothesis, casting doubt on this possible explanation for drift.

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, whereas 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, categorical changes in limb position are sensed.

At the present time, we cannot provide a satisfactory explanation for the mechanism underlying the drift plateau. We are fascinated by the fact that changes in instantaneous drift direction variability seem to be linked to the cumulative drift plateau, which presumably reflects some active regulatory process (see Figure 3.6). Currently, we cannot explain why cumulative drift is characterized by systematic instantaneous drift direction but that the plateau, which reflects the stabilization of overall position, is characterized by randomness in instantaneous drift direction. On the surface, this state of affairs – higher movement-to-movement position variability leading to high overall movement and position stability – appears to be inconsistent with a planning model based on the minimization of variability (Harris & Wolpert, 1998). These issues will help guide our future investigations.

The suggestion that movement and position are controlled separately contrasts with the conclusions of Vindras et al. (1998) who 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., however, did not directly assess the interplay of position drift and movement production as we have done. In fact, the experimenters tried to prevent drift during their movement task both 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.

Other findings, however, support our suggestion that limb position and movement trajectory are represented and controlled separately. In one of the clearest demonstrations of this separation, participants were asked 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. Nonetheless, when they were asked to stop tracking and point to the target location, they did so accurately (Sittig et al. 1985).

Several motor learning experiments have shown independent acquisition and transfer of limb position and movement information. DiZio and Lackner (1995) showed that exposure training with Coriolis forces produced different movement and 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 represented separately. This conclusion is strengthened by observations that, during exposure to Coriolis force perturbations, training improved the movement path more than endpoint accuracy when endpoint finger contact was either absent (Lackner and DiZio 1994) or abnormal (DiZio and Lackner 2001).

Further supporting the hypothesis that position and movement are controlled independently, Sainburg and Wang (2002) recently showed that these features of movement showed different patterns of interlimb transfer following adaptation to novel visuomotor rotations. When participants first adapted to a 30° rotation of the visual projection of hand position with their non-dominant 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 non-dominant arm performance. These findings were consistent with earlier reports that the dominant arm controls intersegmental dynamics more efficiently than the non-dominant arm, whereas the non-dominant arm controls final position accuracy better than the dominant arm (Sainburg and Kalakanis 2000). Separate representations of position and movement is also supported by studies demonstrating that memory for position is better than memory for movement (Marteniuk and Roy 1972; Smyth 1984). Rosenbaum et al. (1999) showed that that memory for posture is dissociable from memory for spatial location. Rosenbaum et al. (2001) also showed that computational simulation of motor planning and control works well when one assumes distinct representations for postures and movements.

On the whole, our current findings show that position drifts with movement repetition while the distance and direction of movement remain relatively preserved. These observations are consistent with other studies suggesting that limb position is controlled separately from movement. The next experiment tests this separate controllers hypothesis.

CHAPTER 4

MOVEMENT SPEED EFFECTS ON LIMB POSITION DRIFT³

Vision, touch, and proprioception all contribute to our ability to locate our limbs with respect to the body and the external world (Graziano 1999; van Beers, Sittig, and Denier van der Gon 1998, 1999). Hand position matching experiments, in which participants indicate the location of an occluded (target) hand by matching its location with the other (reporting) hand, show that without vision, the accuracy with which finger location is reported decays over time such that perception of limb position appears to drift, even though the actual location of the occluded hand remains fixed (Desmurget et al. 2000; Paillard and Brouchon 1968; Wann and Ibrahim 1993; Wolpert et al. 1998). Drift can be attenuated when passive or active movements are performed with the target limb between reports (Paillard and Brouchon 1968) or when brief isometric contractions are performed with the target limb between reports (Wann and Ibrahim 1993). These drift-attenuating conditions suggest that drift arises because proprioceptive information about limb position is altered during prolonged periods without vision or without movement.

This explanation is challenged, however, by findings that drift growth is related more to the number of reports made by the matching hand than to the duration of target limb occlusion (Desmurget et al., 2000). The proprioception explanation is also

³ Brown, L. E., Rosenbaum, D. A., & Sainburg, R. L. (submitted). Movement speed effects on limb position drift. Experimental Brain Research.

challenged by experiments showing that when shapes are drawn continuously without vision, shape position drifts but shape form is preserved (Brown and Rosenbaum 2001; Verschueren et al 1999; Zelaznik and Lantero 1996). These results suggest that drift is not just a perceptual effect ascribable to the target limb, but that it is an effect related to the movements of the reporting limb. Taken as a whole, however, the findings in this area of study leave open questions both about the source of position drift and about the effect that position drift may have on movement performance.

Recently, we attempted to address these questions with an experiment designed to measure in considerable detail how limb position drift unfolds over a series of movements and to determine how position drift affects movement trajectory performance (Brown, Rosenbaum, and Sainburg 2002). Our participants performed blocks of 75 repetitive movements in one of two directions (30° and 120°), from one of three start locations in time with a metronome. Feedback about visual fingertip location was provided during the first five movements and then was removed for the remainder of the block. We measured how hand position at the beginning of each outward movement changed over the course of the block. Although hand position drifted on average 8 cm from its initial location, hand movement distance and direction were preserved. Inverse dynamic analysis showed that muscle torque profiles changed substantially so as to preserve movement distance and direction. An examination of limb position changes showed that although instantaneous drift (movement-to-movement position error) remained small and constant over time, cumulative drift (distance from initial hand location) increased rapidly during the early portion of the block before reaching an apparent plateau at mid-block.

Instantaneous drift was greater for 120° movements than for 30° movements and drift accumulation was faster for 120° movements than for 30° movements. These observations suggested that drift was related to movement error because 120° movements are associated with greater movement error than are 30° movements (Gordon et al. 1994a, 1994b; Sainburg et al., 1995). 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, whereas 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, categorical changes in limb position are sensed.

An alternative possibility is that limb position and movement are controlled using different qualities of proprioceptive information. Type Ia (large-fiber) muscle spindle afferents respond both to changes in static muscle length and rate of change of muscle length, indicating that 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), indicating 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. First, limb excursions performed at imperceptibly slow movement speeds give rise to

an accurate sense of change in static position, and this position sense is significantly impaired when the muscles around the tested joints are anaesthetized (Clark et al. 1985; Taylor and McCloskey 1990), suggesting an independent position sense served by muscle spindle afferents. Second, when participants track a moving target with their finger while also being exposed to elbow flexor vibration, they consistently lag behind the target in a way consistent with the vibration illusion. The participants, unaware of the discrepancy between target and finger position, report performing accurately. Nonetheless, when they are asked to stop tracking and point to the target location, they do so accurately (Sittig et al. 1985). This finding suggests not only that position can be perceived separately from movement, but that this independence is served mainly by type II afferents because muscle vibration is thought to selectively influence type Ia afferents (Goodwin, McCloskey, and Matthews, 1972).

In the studies described above, evidence for independent perception of position and movement was been acquired under conditions in which the participant's task was to monitor position. Under these conditions, participants have been able to detect excursions at the elbow and shoulder that produce fingertip position changes of under five mm with 70% accuracy in the rate of rotation ranges employed in our previous study (Hall and McCloskey, 1983). In our task, however, participants were required to monitor both position and movement trajectory simultaneously. This dual-task situation may have raised the threshold for position change detection, allowing position errors not only to go undetected but 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 the position errors measured in our previous experiment were well above the position change detection thresholds reported by McCloskey (Hall and McCloskey, 1983; Taylor and McCloskey, 1990) and Clark et al. (1985), it is possible that the limb position drift accompanied by the relative preservation of movement observed in our previous experiment may be attributable to differences between position information salience and movement information salience. We call this latter hypothesis the information salience hypothesis.

Our goal in the present study was to distinguish between the two hypotheses outlined above. Both the separate controllers hypothesis and the information salience hypothesis suggest that limb position drift should be sensitive to the magnitude of position errors, but in different ways. We manipulated the magnitude of position error by having participants perform our repetitive movement task at different speeds. The information salience hypothesis says that error magnitude and direction should be harder to detect and subsequently correct when movement speed is low (when errors are small) than when movement speed is high (when errors are large). This hypothesis predicts, then, that drift should accumulate more quickly at low movement speeds than at high speeds and that the final plateau level should be higher when movement speed is low than when movement speed is high.

The separate controller hypothesis, by contrast, says that the movement controller can monitor small changes in position for the sake of maintaining movement trajectory but the limb position controller is insensitive to these errors below some critical value. The separate controller hypothesis predicts, then, that drift should accumulate more quickly at high movement speeds (when errors are large)

than at low movement speeds (when errors are low) but that movement speed should have no effect on final plateau level.

METHOD

Participants

Nine Pennsylvania State University students (6 female, 3 male), aged 20 - 25, participated in this experiment. 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

The apparatus was identical to that described in Chapter 3 (see Figure 3.1).

Experimental Design And Task

The experiment used a movement speed (slow, medium, fast) x movement direction (30°, 120°) x movement trial (1-75) within-participants design. A single start location, defined by initial shoulder and elbow angles of 50° and 90°, respectively, was customized for each individual. Joint angles were defined with respect to the extension of the parent (more proximal) limb. Target locations were defined such that movement direction was 30° or 120° counter clockwise with respect to the horizontal. The start and target circles were 2.3 cm and 4 cm in diameter, respectively, and were separated by 15 centimeters.

Each block consisted of 75 back-and-forth movements between the start location and target. Movement speed was conveyed with a metronome. Movements to the target and back were performed within 1.6 s (slow), 1.3 s (medium), or 1.0 s (fast). Participants were instructed to begin each back-and-forth movement in time with each metronome tone. Varying movement speed while controlling the number of movements performed in each block meant that block duration also varied with movement speed. This procedure was used because a perceptual matching task showed that drift varies more with the number of matching movements performed than with the time between matching movements (Desmurget et al. 2000).

Each block was self-initiated. During the first 5 movements, the participant viewed a 1-cm diameter cross-hair cursor that reflected the continuous location of the index fingertip. The participant initiated the block by place the cursor within the start circle. At that time, a tone sounded for 50 ms. This tone recurred at regular intervals for the remainder of the block and did not depend on hand location. The participant was instructed that upon hearing each tone, s/he should move quickly and accurately to the target and back to the start location before hearing the next tone. The participant was further instructed that s/he 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 told that cursor feedback would be removed after the fifth movement and s/he was instructed to continue to perform the task on-pace and as accurately as possible for the remainder of the block. To gain familiarity with the task, each participant performed 2 practice blocks of 25 movements at the fastest pace

prior to performing six blocks of 75 continuous movement trials. Each of the 6 combinations of movement speed and movement direction was presented randomly.

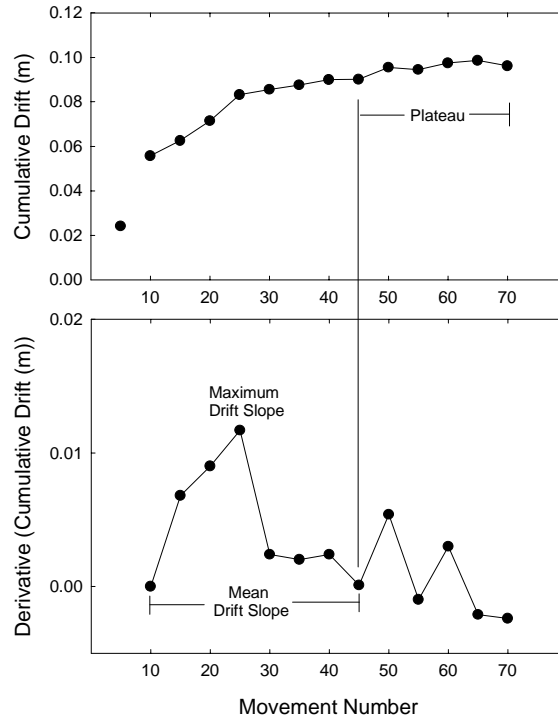
Kinematic Analysis

Initial data analysis and calculation of cumulative and instantaneous drift were identical to the method described in Chapter 3 (see Figure 3.2). Because we predicted differential effects of movement speed on drift accumulation slope and drift plateau, we developed separate measures of these two features of the cumulative drift profile. The following procedure was used (see Figure 4.1). Only no-visual-feedback trials were included. For each participant, within each condition, the cumulative drift profile was averaged within bins of 5 movements. The binned profile was differentiated to produce a drift change profile. The maximum point of this change profile was identified and recorded as the maximum slope. The first zero-crossing following the maximum slope was then identified. Mean slope was calculated as the mean of all points on the differentiated curve between the first bin of no-visual-feedback trials and the first zero-crossing. For cases in which there was no zero-crossing, minimum change was identified instead. Finally, drift plateau was defined as the average level of cumulative drift after the zero-crossing.

We also assessed the effects of movement speed on the slope of drift accumulation by fitting the average slow and fast curvilinear cumulative drift profiles with a power function whose possible slope exponents lay between 0 and 1 in steps of .001. The plateau level was fixed at the mean value of the last cumulative drift bin, and the y-intercept was fixed at 0. The fit was evaluated by calculating R^2 values for

each iteration and the best fit was chosen by selecting the slope values that produced the highest R^2 .

Figure 4.1: Calculation of maximum and mean drift slope, and plateau level.



We were interested in how drift was related to movement distance and direction error. To measure these effects, we calculated instantaneous and cumulative drift both parallel to and perpendicular to the main movement axis. These measures were obtained using the following two-step method. First, we rotated the movement vectors an amount equal to the target vector. Therefore, movements performed in the 30° direction were rotated -30° and movements performed in the 120° direction were rotated -120° so that the target vector laid parallel to the positive x-axis. On the basis of these transformations, we defined parallel instantaneous drift and parallel

cumulative drift as occurring on the x-axis, and perpendicular instantaneous drift and perpendicular cumulative drift as occurring on the y-axis.

Statistical Analysis

Measures of instantaneous drift and movement speed, time, distance, and direction were submitted to a speed (slow, medium, fast) x movement direction (30°; 120°) x movement number (1-70) repeated-measures analysis of variance. Derived cumulative drift slope and plateau values were submitted to an analysis of variance that had the same design except for the omission of time, that is, speed (slow, medium, fast) x movement direction (30°, 120°). We removed the final 5 movement trials from the first analysis to eliminate artefacts associated with the end of the block. Significant interactions were decomposed by computing simple main effects. Significant main effects of speed were analyzed further using Bonferroni-corrected pairwise comparisons.

RESULTS

Figure 4.2 shows a series of 70 movement paths produced by one participant in each speed and direction condition. In each plot, the start location is shown as a black ring, and the target location is shown as a closed circle. Progression of the block is represented by the grey shade of the movement paths. In all of the plots, although there is hand position drift, there is no apparent effect of either required speed or direction on observed distance or direction. In our previous study we demonstrated that movement distance and direction were preserved as the hand drifted, and we observed the same general effect here as well. Although movement

distance increased after visual feedback was removed ($p = .016$), it then stabilized for the remainder of the block. Similarly, movement direction showed only a 3.5° change that occurred gradually over the entire block. Neither movement distance nor movement direction were influenced by the speed manipulation.

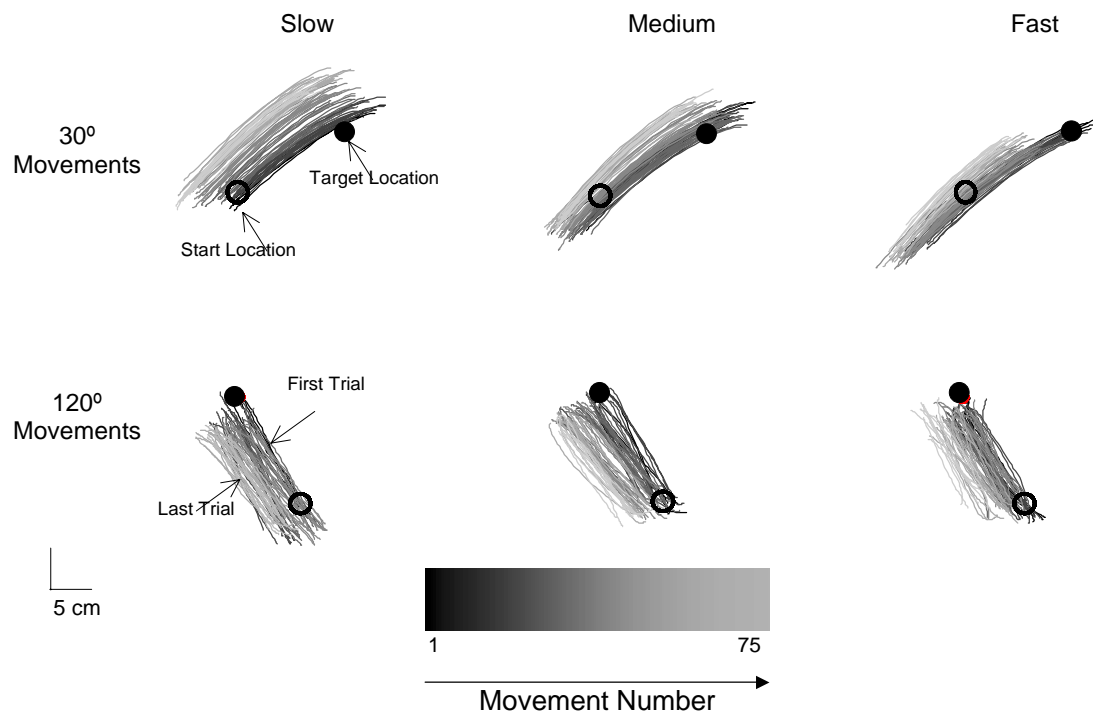


Figure 4.2: A series of 70 hand paths produced by one participant in each speed condition and movement direction. The start position and target are indicated by open and closed circles, respectively. Progression of trials over time is represented by the gray shade of the path, where early trials are darker than late trials. Trials with fingertip position feedback are drawn in black.

We next evaluated how speed influenced hand position drift. We evaluated the effectiveness of our speed manipulation first by assessing its effect on movement time, peak movement velocity, and mean movement velocity. The results for mean movement velocity are presented in Figure 4.3A. We found significant main effects of speed for movement time, $F(2, 16) = 17.61, p < .001$, peak velocity, $F(2, 16) = 17.29, p < .001$, and mean velocity, $F(2, 16) = 16.70, p < .001$, such that movement

time significantly decreased, and peak and mean velocity significantly increased, with each decrease in metronome interval. We also found significant interactions of speed and direction for all three measures. Simple main effects showed that although there was a direction effect at the two fastest speed levels, such that 30° movements were performed more quickly than 120° movements, this direction effect was not present at the slowest speed. From this analysis we concluded that movement speed was successfully manipulated by varying the metronome period.

Instantaneous Drift

Figure 4.3B shows mean instantaneous hand drift, a measure of the change in hand start location between each successive outward movement, as a function of speed condition. There was a marginal main effect for speed, $F(2, 16) = 3.43$, $p = .058$, such that average instantaneous drift was greater under the fast condition (1.64 ± 0.1 cm) than under the slow condition (1.38 ± 0.1 cm). Hierarchical linear regression analysis with movement number, movement direction, and mean velocity as predictors showed that instantaneous drift varied significantly with mean movement velocity ($p < .001$). Instantaneous drift was also influenced by movement number, such that it increased significantly when visual feedback was removed ($p = .001$). There were no changes in instantaneous drift during visual-feedback-absent trials ($p = .505$). Instantaneous drift also varied reliably with movement direction, $F(1, 8) = 43.28$, $p < .001$, such that it was consistently greater for movements to the 120° target (1.74 ± 0.1 cm) than for movements to the 30° target (1.27 ± 0.1 cm). There were no other significant main effects or interactions for these measures.

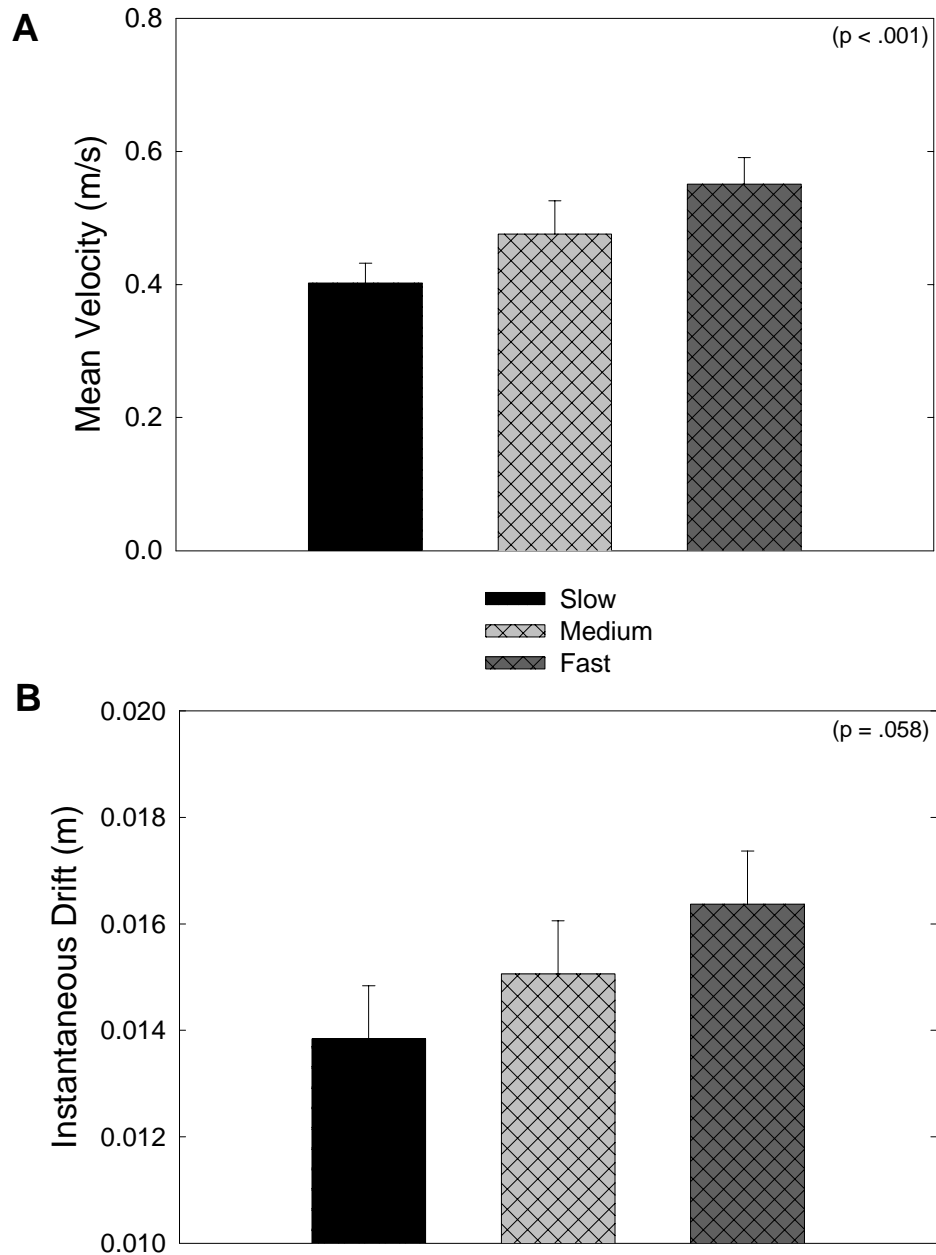


Figure 4.3: Mean fingertip velocity (m/s) and instantaneous hand position drift (m). A. Mean velocity (m/s) as a function of speed condition. Error bars represent the standard error of the mean. B. Mean instantaneous drift (m) as a function of speed condition. Error bars represent the standard error of the mean. Instantaneous drift was greater for the high speed condition than for the low speed condition.

Cumulative Drift

The information salience hypothesis predicted that drift should accumulate less rapidly and reach a smaller plateau level when participants experienced larger position errors (at high movement speeds) than smaller position errors (at low movement speeds). Alternatively, the separate controllers hypothesis predicted that drift should accumulate more rapidly when participants experienced larger position errors (at high movement speeds) than smaller position errors (at low movement speeds), but that plateau level should not vary with movement speed.

The effects of movement speed on cumulative drift are summarized in Figure 4.4. Figure 4.4A shows that in both fast and slow speed conditions, drift accumulation increased relatively quickly during the first portion of the block before levelling off during the latter portion. This pattern was confirmed by a main effect for movement number, $F(69, 522) = 17.21, p < .001$. Cumulative drift increased abruptly when vision was removed ($p < .001$), and continued to accumulate over the next 35 trials ($p = .002$). However, hand position drift did not accumulate appreciably beyond this point ($p = .106$). On average, hand position drifted 5.84 ± 0.41 cm from the initial start location.

Figure 4.4A also shows that, during the first portion of the block, drift accumulated more quickly in the fast condition than in the slow condition. We evaluated this observation by calculating maximum rate of accumulation (maximum drift slope), the mean rate of accumulation (mean drift slope), and the drift plateau level within each condition for each participant as described in the Method section.

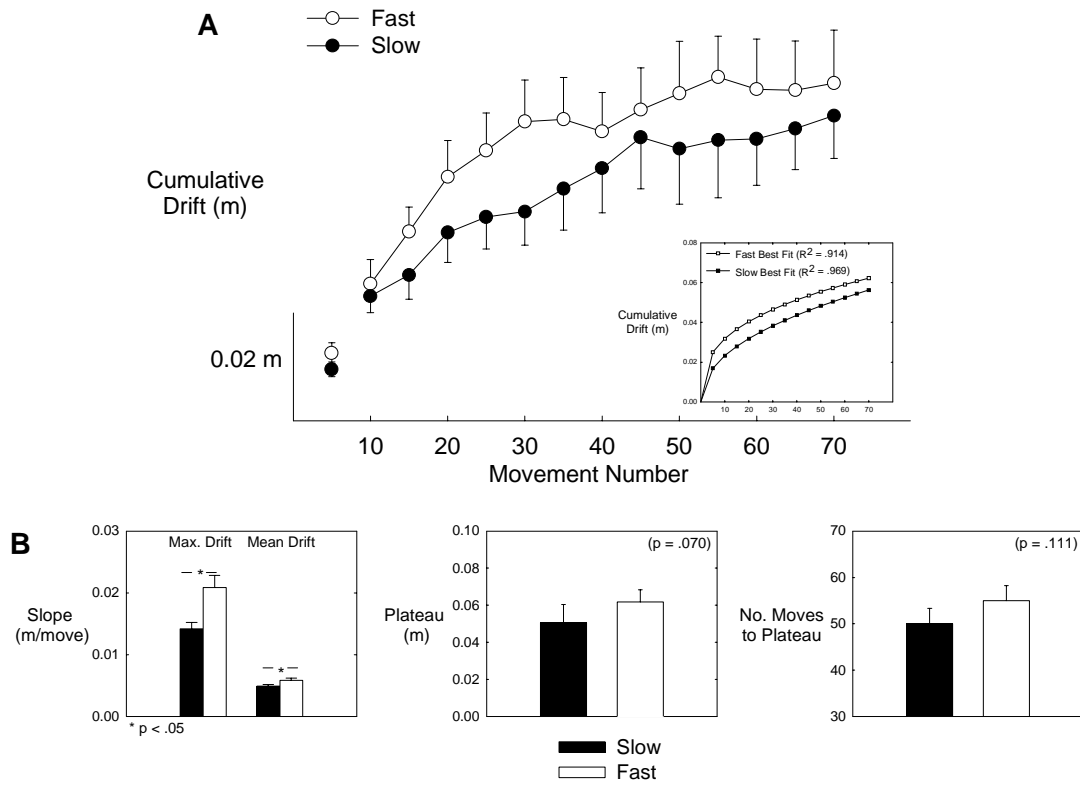


Figure 4.4: A. Mean cumulative hand drift (m) as a function of speed and movement number. This plot shows that movement speed accumulated more quickly in the fast condition than in the slow condition. Inset: Power function best fit curves for the fast and slow conditions as a function of movement number. B. Left panel: Maximum and mean cumulative drift slope (m/movement) as a function of speed condition. In both cases, drift slope was greater in the fast condition than in the slow condition. Middle panel: Mean plateau (m) as a function of speed condition. There was no significant difference between speed conditions. Right panel: Mean number of movements to reach the drift plateau in both the fast and slow speed conditions.

These measures were submitted to a repeated-measures analysis of variance with speed and direction as factors. The results of this analysis are summarized in Figure 4.4B. Maximum slope was significantly greater for fast movements than for slow movements, $F(2, 16) = 12.92$, $p < .001$, but did not vary with movement direction. The mean slope was also significantly greater for fast movements than for slow movements, $F(2, 16) = 3.80$, $p = .045$, but did not vary with movement direction.

Drift plateau, on the other hand, did not vary with movement speed, $F(2, 16) = 3.14$, n.s. Consistent with relationship between movement speed and accumulation slope, a greater number of movements was required to reach the plateau in the slow condition than in the fast condition.

In addition to obtaining the above measures of slope, we fit a power function to the average cumulative drift profiles for the fast and slow conditions. The possible exponents ranged from 0 to 1, the plateau was fixed at the mean cumulative drift during late-block trials, and the y-intercept was fixed at 0. If drift accumulated more slowly during the slow-movement trials than during the fast-movement trials, the best fit exponent should be greater (closer to 1) for the slow condition than for the fast condition.

Table 4.1: Best fit exponents and their respective R^2 values.

	Best Exponent	Best R^2	Total R^2
Intercept = 0			
Fast	.303	.8767	.9174
Slow	.476	.9716	
Intercept not = 0			
Fast	.277	.8830	.9241
Slow	.500	.9757	
Plateau fixed but differs by speed			
Fast	.345	.9135	.9371
Slow	.455	.9685	

The best fit curves and their respective exponents and R^2 values are presented in the inset of Figure 4.4A. In Table 4.1, we also present the results for the fit when the y-intercept equalled vision-present cumulative drift, and when the plateau levels were fixed to late-block cumulative drift for each speed level. The best-fit exponent was

greater for the slow condition than for the fast condition in every case, supporting the separate controller hypothesis.

Summarizing the foregoing results concerning instantaneous and cumulative drift, these results show that drift was sensitive to manipulations of movement speed. Drift accumulated more quickly for fast-paced movements than for slow-paced movements, but drift plateau was not significantly different. This pattern of results supports the separate controller hypothesis but not the information salience hypothesis.

Drift Parallel To And Perpendicular To The Axis Of Movement

We next investigated two potential sources of movement error and how they contributed to speed-related drift. One potential error source is movement direction error; the other is movement distance error (Gordon et al., 1994a).

To capture position changes due to movement direction error, we calculated movement-to-movement changes in hand position along the axis perpendicular to movement direction, calling this measure perpendicular instantaneous drift. Similarly, to capture position changes due to movement distance error, we calculated movement-to-movement position changes in hand position along the axis of movement, calling this measure parallel instantaneous drift. The results, shown in Figure 4.5, indicate that distance-dependent position errors were both larger and more variable than direction-dependent position errors. This distribution has been observed previously (Gordon et al., 1994a). Analysis of perpendicular instantaneous drift showed that it was significantly greater for fast movements than for slow movements, $F(2, 18) = 7.25, p = .006$ (see left panel of Figure 4.5). Analysis of parallel

instantaneous drift revealed no significant effect of speed, $F(2, 18) = 1.41, p = .273$ (see right panel of Figure 4.5). Summarizing these results, they indicate that direction errors were affected by the speed manipulation but distance errors were not.

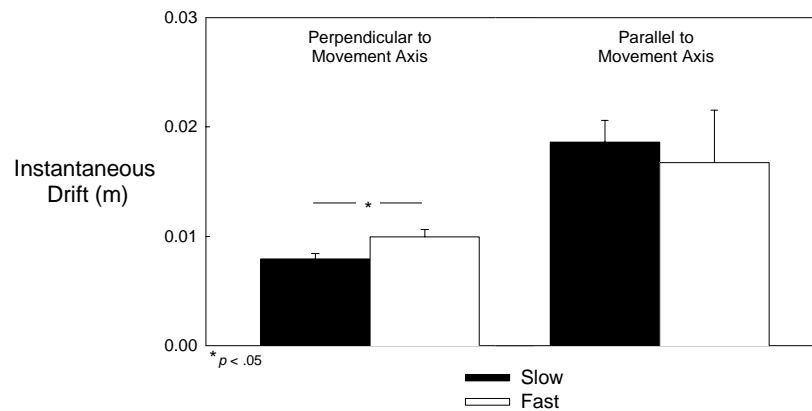


Figure 4.5: Mean instantaneous drift perpendicular and parallel to the axis of movement (m) as a function of speed condition. Perpendicular drift was greater in the fast condition than in the slow condition. For parallel drift, there was no significant difference between speed conditions.

Direction errors, measured as perpendicular instantaneous drift, varied directly with movement speed. The separate controllers hypothesis predicted, then, that accumulation rates for perpendicular drift should also depend on movement speed. Figure 4.6A shows perpendicular drift accumulation as a function of both movement number and movement speed. The figure shows that perpendicular drift accumulates

more quickly for fast movements than for slow movements but that the same plateau is reached regardless of movement speed. This impression was confirmed by an analysis of mean drift slope and drift plateau level, presented in the inset of Figure 4.6A. Whereas mean drift slope was significantly greater for fast movements than for slow movements ($p = .045$), drift plateau did not vary with speed ($p = .591$). Therefore, the movement direction errors that produce perpendicular drift are both significantly affected by movement speed and contribute strongly to the accumulation of position drift.

Distance errors, measured as parallel instantaneous drift, did not vary with movement speed. The separate controllers hypothesis predicted, then, that accumulation rates for parallel drift should not depend on movement speed. Figure 4.6B shows parallel drift accumulation as a function of both movement number and movement speed. The figure shows that parallel drift accumulates at the same rate for both fast and slow movements and that drift plateau did not vary with speed. This was confirmed by an analysis of parallel mean drift slope and drift plateau level, presented in the inset of Figure 4.6B. Both mean drift slope and drift plateau did not vary with speed (both $ps > .70$).

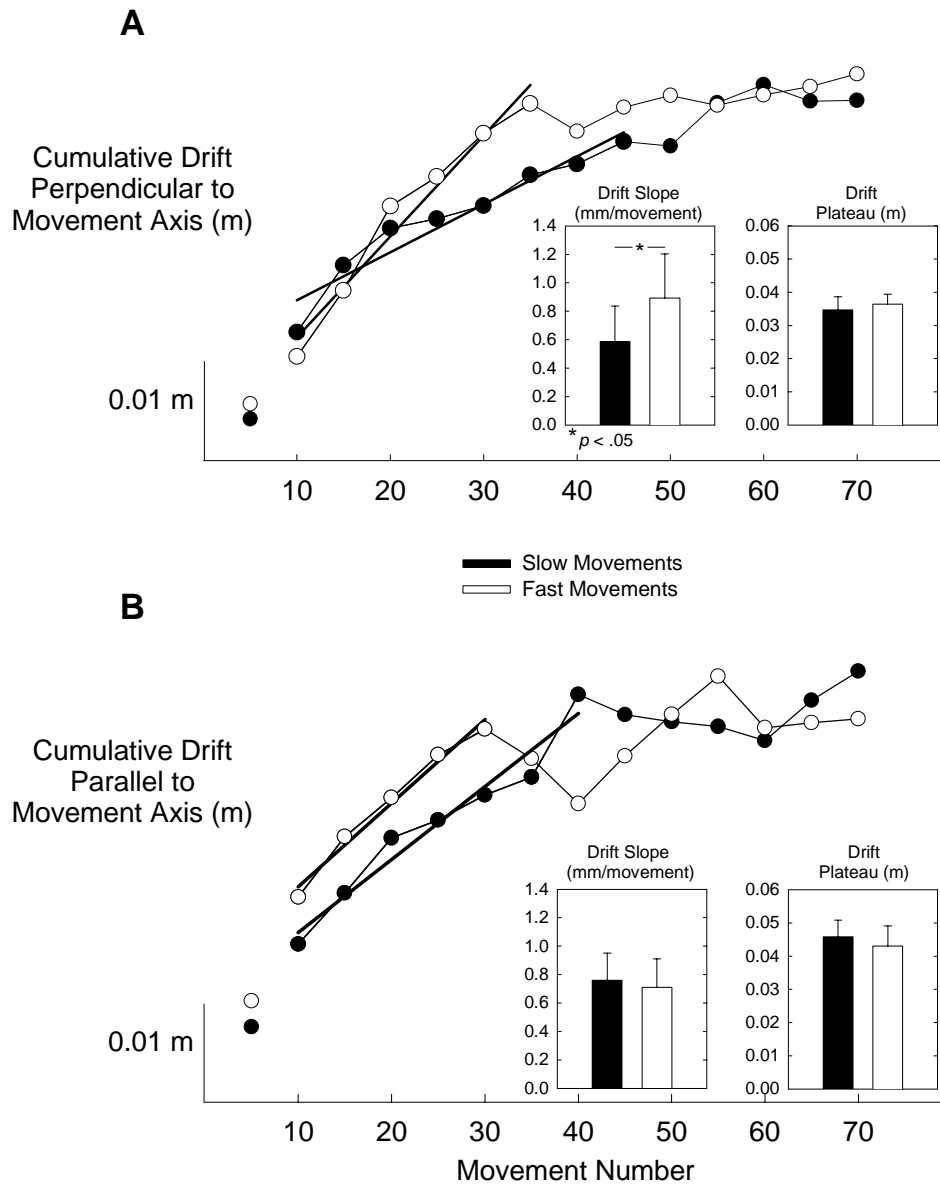


Figure 4.6: A. Mean cumulative drift perpendicular to the axis of movement (m) as a function of speed condition and movement number. Perpendicular drift accumulated more quickly under the fast movement condition than under the slow movement condition. Left inset: Mean drift slope (m/movement) is greater in the fast condition than in the slow condition. Right inset: Drift plateau (m) does not vary with speed condition. B. Mean cumulative drift parallel to the axis of movement (m) as a function of speed condition and movement number. Parallel drift accumulation did not vary with speed condition. Neither mean drift slope (left inset) nor drift plateau (right inset) varied with speed condition.

DISCUSSION

The purpose of this experiment was to study how limb position drift varied with magnitude of movement error. We manipulated movement error by varying movement speed. Participants performed six blocks of 75 repetitive movements in each of two directions (30° and 120° with respect to the horizontal) and at each of three speeds (slow, medium, and fast), defined by metronome period. Fingertip location feedback was provided during the first five movements and then removed for the remainder of the block. As in our previous study, although hand position drifted on average 6 cm from its original location, hand movement distance and direction were preserved over repeated trials. The results showed that instantaneous (movement-to-movement) hand position drift varied with speed, such that instantaneous drift was larger under fast conditions than under slow conditions. Cumulative drift increased rapidly during the early portion of the block before reaching an apparent plateau at mid-block. The rate of drift accumulation varied with movement speed such that position drift grew more quickly under high speed conditions than under low speed conditions, but speed did not significantly affect the plateau level. When we parsed position drift due to movement distance error from drift due to movement direction error, we found that distance errors did not vary with speed and that the accumulation of distance error did not vary with speed. In contrast, drift due to direction error was greater under high speed conditions than under low speed conditions and drift accumulation rate was also greater under fast conditions than under slow conditions. These contrasting effects of speed on accumulation of

movement direction and distance errors establishes a causal relationship between movement error and drift accumulation.

In our previous experiment (Brown et al. 2002), we used a task similar to the one employed here to study how limb position drift varied with spatial position and to determine how drift affected movement trajectory outcome. Participants performed blocks of repetitive movements in one of two directions (30° and 120°), from one of three start locations, in time with a metronome. Fingertip location feedback was provided during the first five movements and then removed for the remainder of the block. As in the current study, instantaneous drift remained small and constant over time, whereas cumulative drift increased rapidly during the early portion of the block before reaching a plateau at mid-block. Drift did not vary consistently with start location, suggesting that it was not driven by a spatial attractor. Although hand position drifted on average 8 cm from its initial location, hand movement distance and direction were preserved over repeated trials. Inverse dynamic analysis showed that muscle torque profiles changed substantially to preserve movement distance and direction. Forward simulations predicted large changes in movement direction without such modifications in joint torque. Because accurate performance of movement distance and direction requires that initial limb position information be known (Desmurget et al. 2000; Ghez et al. 1995; Ghilardi et al. 1995; Prablanc et al. 1979; Vindras et al. 1998), these results suggested that proprioception continues to be a reliable source of limb position information after prolonged time without vision.

To resolve the paradox of how movement trajectories could be preserved as limb position drifts, we proposed that movement and position are controlled by

independent neural modules that use proprioceptive information differently. This separate controllers hypothesis predicted that drift would accumulate more quickly when position errors were larger (at high movement speeds) than when position errors were smaller (at low movement speeds) but that final levels of instantaneous drift would be the same in the high- and low-speed conditions. This prediction was confirmed. The predictions of an alternative hypothesis – the information salience hypothesis – were not confirmed.

Our results are similar to error accumulation reported by Bock and colleagues (Bock and Arnold 1993; Bock and Eckmiller 1986) who likewise proposed different systems for distance and position control. The proposal that limb position and movement trajectory and controlled separately is also supported by DiZio and Lackner (1995), who reported that adaptation to Coriolis force perturbations selectively affected reach trajectory curvature and endpoint error. The adaptation produced different aftereffect patterns in the trained and untrained arm, such that the trained arm showed curvature and endpoint aftereffects but the untrained arm showed only endpoint aftereffects, suggesting that learned end position and trajectory information are represented separately. DiZio and Lackner also observed that during exposure to Coriolis force perturbations, training improved the movement path more than it improved the endpoint accuracy when endpoint finger contact – which, like vision, can provide explicit information about limb spatial position with respect to the body – was either absent (Lackner and DiZio 1994) or abnormal (DiZio and Lackner 2001).

Recently, Sainburg and Wang (2002) demonstrated that learned endpoint and trajectory information showed different patterns of interlimb transfer following adaptation to novel visuomotor rotations. When their participants adapted to a 30° rotation of hand position feedback with their non-dominant arm, the first movements made with the dominant arm revealed transfer of trajectory direction information. By contrast, when participants adapted to the visuomotor rotation using the dominant arm, non-dominant arm performance revealed transfer of information used to specify final position accuracy. These findings were consistent with earlier reports that the dominant arm controls intersegmental dynamics more efficiently than the non-dominant arm, whereas the non-dominant arm controls final position accuracy better than the dominant arm (Sainburg and Kalakanis 2000). Once again, this outcome fits with the idea of separate position and movement controllers.

The proposal that there are separate representations of position and movement is also supported by studies demonstrating that 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.

A final source of support for the dissociation of position and movement comes from computational modelling work. Rosenbaum et al. (2001) showed that computational simulation of motor planning and control works well when one assumes distinct representations for goal postures and movements. If one assumes that goal postures are represented at a different level than movements, many findings in the field of motor control are easily explained, and many basic competencies are

also easily accounted for (e.g., the capacity for immediate compensation for changes in joint mobility). The data reported here lend support to the division between movements and goal positions adopted in the computational model of Rosenbaum et al. At the same time, the computational advantage conferred by assigning different levels of control to positions and movements provides a way of understanding why the data of the present study turned out as they did.

CHAPTER 5

GENERAL DISCUSSION AND CONCLUSIONS

The purpose of this project was to determine the source of limb position drift and to study the effect of drift on movement performance. The general approach was to measure limb position drift and movement performance in a single task. Both repetitive shape drawing and straight aiming movement tasks were employed, and the availability of visual feedback was manipulated, either by removing vision altogether or by removing visual feedback about limb position. These conditions produced substantial drift that changed over time in a relatively stereotypical manner.

The approach taken here has several advantages over past studies of limb position drift. First, by measuring drift and movement production in a single task, the effects of drift on movement could be assessed directly. Second, the drift observed in the studies presented here was considerably larger than that reported in previous studies, and these large position changes afforded more confidence in the conclusions reached with these analyses. Finally, the methods employed here allowed an analysis of the effects of limb position drift on both movement kinematics and movement kinetics. No other study has examined these details.

MOVEMENT FORM WAS PRESERVED AS LIMB POSITION DRIFTED

The results of the first square-drawing study showed that shape form was preserved over time, regardless of the availability of vision. Without vision, spatial location and square size were not preserved: the hand drifted away from its initial

spatial location and square size decreased. These results were also found in an experiment in which the square size was varied, and in an experiment in which circles were drawn instead of squares. In all, participants maintained shape form better than they maintained spatial position or shape size. Indeed, form was preserved despite position drift. Therefore, despite the fact that participants could not use current hand and arm position information to maintain the hand's spatial position, at some level the system must have been able to gather and use current limb position information to plan and execute movements consistent with the current drawing goal. This limb position information may have been provided by proprioception or haptics.

The purpose of the second experiment was to study how naturally occurring limb position drift unfolded over a series of repetitive, straight aiming movements and to determine how this drift affected movement performance. Movement direction was varied to test the hypothesis that drift was movement-dependent. The two directions tested require different relative amounts of shoulder and elbow motion. These differences result in movement-dependent differences in both the dynamic interactions between the segments, and the inertia that must be overcome to initiate and produce movement (Gordon et al. 1994b; Sainburg et al. 1995; Gribble and Ostry 1998). If drift is dependent on such dynamic factors, then drift should have varied with movement direction. Movement start position was varied to test the hypothesis that drift was position-dependent. If drift is position-dependent such that the limb drifts toward a specific spatial location or posture, then both drift distance and direction should have varied with start location.

Participants performed blocks of 75 repetitive movements in one of two directions (30° and 120°), from one of three start locations, in time with a metronome. Fingertip location feedback was provided during the first five movements and then removed for the remainder of the block. The results showed that instantaneous drift remained constant over time, and that cumulative drift increased rapidly early in the block before reaching an apparent plateau at mid-block. Both instantaneous and cumulative drift varied consistently with movement direction, suggesting that drift was related to movement error. Neither instantaneous nor cumulative drift varied systematically with movement start position. As in the shape-drawing experiments, 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 profiles changed substantially, so as to preserve movement distance and direction. Forward simulations predicted large changes in movement direction without such modifications in joint torque. Therefore, the results of both the shape-drawing experiments and this repetitive aiming task experiment suggested that proprioception continued to be a reliable source of limb position information after prolonged time without visual feedback.

On one hand, the preservation of movement distance and direction as limb position drifted, and the reliable and appropriate modification of muscle torques produced at the shoulder and elbow as the limb drifted, indicate that accurate limb position information must have been available to the movement control system. Because in the second experiment both haptic and visual information about limb position were removed, limb position must have been signalled by proprioception. On

the other hand, drift appears to indicate that proprioception was not available for maintaining limb position in space. This suggests an apparent paradox in which proprioceptive limb position information was used to produce and update appropriate movement trajectories but was not used to maintain the limb's spatial position. Four possible explanations for this pattern of results were presented in Chapter 3, but in the end, an explanation based on separate movement and position controllers was favored. However, before this explanation can be described more fully, several concerns about the task need to be considered.

WERE PARTICIPANTS BIASED BY TASK CONDITIONS?

The task requirements were to perform movements established with feedback as well as possible without feedback, while keeping pace with the metronome. Presumably, if participants could not control both position and movement at the same time, but could choose to maintain either position or movement at the expense of the other, then we would have found some evidence for that choice. That is, we would have seen that some participants preserved position at the expense of trajectory, while others preserved trajectory at the expense of position. Instead, participants always preserved trajectory. Similarly, if participants had been able to maintain both spatial position and movement trajectory simultaneously, then we would have found some evidence for that ability. To the extent that some participants drifted less or more than others, some participants may have been better or poorer at preserving both position and trajectory simultaneously than others. Nonetheless, participants always preserved trajectory.

Is it possible that the task instructions biased participants toward preserving trajectory? Once again, the initial instructions to the participant were to perform the reciprocal aiming task as accurately as possible while maintaining pace with the metronome. When visual feedback was available, “as accurately as possible” emphasized spatial position and trajectory accuracy equally. When visual feedback was removed, the instruction to the participant was to continue to perform “the task” as well as possible while maintaining pace with the metronome. Thus, this instruction emphasized preservation of trajectory and spatial position equally. Moreover, removing visual feedback eliminated extrinsic feedback about both position and movement equally, and so it seems unlikely that this step biased participants toward preserving movement over position.

Finally, the start location and target circles remained on-screen throughout each block of trials. Is it possible that this information biased participants toward preserving trajectory over position? This possibility seems unlikely for the following reasons. First, vision of the start and target locations should have provided visual information about both the required position and the required trajectory equally. Second, in the shape-drawing experiments, participants closed their eyes, meaning that the opportunity to glean position or trajectory information from the visual template was completely removed in those experiments. Despite this fact, preservation of movement form over position was observed in those experiments as well. This means that it is unlikely that participants were using visual information offered by the template to preserve trajectory over position. Together, these points

appear to rule out the notion that participants were biased toward preserving trajectory at the expense of spatial position.

LIMB MOVEMENT AND POSITION ARE CONTROLLED SEPARATELY

The data suggest that there is a dissociation between participants' ability to use proprioceptive information about current limb position to correctly plan and execute movement and their ability to use the same information to maintain limb position in space with respect to a visible anchor, in this case the visible start and target locations. Whereas participants used proprioceptive information to effectively change movement production as the hand drifted, it appears that they were willing to allow a much larger discrepancy to grow between the proprioceptively felt position and visible goal workspace position. We propose that limb position drifts while movement integrity is maintained because (1) movement and position are controlled independently, and (2) these two control systems may be differentially sensitive to proprioceptive information about limb position.

The Movement Controller

Movement production was remarkably robust in all of the experiments reported. It appears as though the processes responsible for planning and controlling the movement trajectory can keep track of small changes in limb position, and make adjustments to control signals to maintain trajectory as limb position drifts. One could envision the movement controller as an inverse internal model that used both visible trajectory information provided by the display and current limb position information provided by both proprioception and vision (when it was available) to transform

trajectory information into the set of movement commands necessary to produce that trajectory (e.g., Wolpert & Kawato, 1998). Although this process produced both movement and endpoint position errors, it appears as though these errors were accounted for when subsequent estimates of limb position information were made. This may be because forward internal models were used to estimate endpoint position errors in advance and that these estimations could be integrated with current proprioceptive information to keep track of current position for movement. This position information, however, was not available to the position controller.

The Position Controller

In contrast to movement trajectory, limb position was not well-maintained after visual feedback about limb position and movement was removed. Limb position drift was characterized by rapid early growth which eventually reached a plateau level. This pattern suggests a position controller that allowed small position errors to accumulate until some, more categorical threshold position change was perceived.

The position controller appears to be particularly sensitive to the removal of extrinsic limb position information. This information can be provided directly by both vision and haptics (DiZio & Lackner, 1999). This sensitivity suggests that the position controller may be concerned with the calibration and alignment of intrinsic limb position information with respect to extrinsic visual locations. Evidence from both prism experiments (e.g., Harris, 1965; Held, 1965) and vibration-illusion experiments (e.g., DiZio & Lackner, 1993) suggests that the correspondence between visual space and proprioception is highly malleable, and that it needs to be continually updated to remain accurate. Although normally this malleability is seen as

an asset to the system, as it allows for flexible and fast adaptation to new workspaces, when one source of information is absent, this updating procedure may be one-sided. This means that when visual and haptic information is removed, as it was in the present experiments, current proprioception may be relinked to a salient, but incorrect, visual location. This resetting process may allow small errors to accumulate undetected until some threshold difference is detected.

This threshold represents a limit to error accumulation in the neurologically normal individuals tested here. This threshold may be defined with respect to the task, such that it reflects the range of movement distances covered in the task. In the shape-drawing experiments, in which participants made movements of only 2.5 cm in length, there was only 2 cm drift on average. When shape size was varied, final drift extent (it is questionable whether a plateau was reached in these experiments) varied with size and reached extents of 3 cm on average. Finally, in the straight-line movement experiments, in which participants made movement of 15 cm, the drift accumulated up to 8 cm on average. Although these differences between experiments in terms of final drift extents or plateau levels were most certainly influenced by other factors, it is interesting to speculate that the drift plateau level may be related to the movement distance prescribed by the task.

At the present time, we cannot provide a satisfactory explanation for what happens when this drift threshold is reached. Presumably, the threshold reflects some active regulatory process, and that this process is linked to the increases in instantaneous drift direction variability observed in Figure 3.6. Currently, we cannot explain why cumulative drift is characterized by low instantaneous drift direction

variability and that the plateau, which reflects the stabilization of overall position, is characterized by high instantaneous drift direction variability. On the surface, this state of affairs – higher movement-to-movement position variability leading to higher overall movement and position stability – appears to be inconsistent with a movement planning model based on the minimization of variability (Harris & Wolpert, 1998). The issues surrounding the plateau level and how it is activated will help guide future investigations.

Despite the questions remaining about the position controller, its proposed characteristics motivated the final experiment. If the position controller is unaware of small changes in position and allows them to accumulate until some threshold position change has been reached, then manipulations of the size of small position errors should affect the rate of drift accumulation, but should not affect the plateau level. Furthermore, if these position changes are being monitored by an independent movement controller, then the size of the small position errors should have no effect on movement trajectory performance. Thus, the purpose of the last experiment in this series was to study how limb position drift varied with magnitude of position error.

Position error was manipulated by varying movement speed. Participants performed six blocks of 75 repetitive movements in each of two directions (30° and 120° with respect to the horizontal) and at each of three speeds (slow, medium, and fast), defined by metronome period. Fingertip location feedback was provided during the first five movements and then removed for the remainder of the block. As in the initial repetitive aiming study, although hand position drifted on average 6 cm from its original location, hand movement distance and direction were preserved over

repeated trials. The results showed that instantaneous (movement-to-movement) hand position drift varied with speed, such that it was larger under fast conditions than under slow conditions. Cumulative drift increased rapidly during the early portion of the block before reaching an apparent plateau at mid-block. The rate of drift accumulation varied with movement speed such that position drift grew more quickly under high speed conditions than under low speed conditions. Drift plateau, however, was not significantly affected by speed. When we parsed position drift due to movement distance error from drift due to movement direction error, we found that distance errors did not vary with speed and that the accumulation of distance error did not vary with speed. In contrast, drift due to direction error was greater under high speed conditions than under low speed conditions and drift accumulation rate was also greater under fast conditions than under slow conditions. These contrasting effects of speed on accumulation of movement direction and distance errors established a causal relationship between movement error and drift accumulation rate. Thus, the results of this final experiment fit well with the predictions of the separate controllers hypothesis.

CONCLUSIONS

1. Limb position cumulative drift was observed in repetitive shape-drawing and repetitive aiming tasks. After visual feedback was removed, cumulative drift unfolded over time in a fairly stereotypical pattern as drawing movements or aiming movements were repeated. It increased quickly early in the series of movements, but then plateaued. Cumulative drift direction varied widely between participants, and did not vary with the limb's initial spatial position.

2. Instantaneous drift distance, a measure of the movement-to-movement changes in limb position did not change over a series of movements. Instantaneous drift direction, however, was fairly consistent early in the series but then became less consistent. This increase in instantaneous drift direction variability appears to be related to the cumulative drift plateau.
3. Movement distance and direction were preserved as position drifted. An analysis of movement kinetics at the shoulder and elbow showed that movement distance and direction were preserved because shoulder torque was modified. A forward simulation showed that if these torque modifications had not been made, movement distance and direction would not have been preserved.
4. Manipulations of position error produced by varying movement speed affected drift accumulation rates but did not affect drift plateau level.
5. Together these results suggested that proprioception remains a reliable source of limb position information, but that it is used differently by separate movement and position controllers. This hypothesis was favored over explanations for drift in terms of a spatial attractor, a growing state estimation error, and differential salience of static and dynamic limb position information.
6. Support for separate position and movement controllers is evidence against the equilibrium-point hypothesis (Feldman, 1986; Bizzi et al., 1992), as the equilibrium-point hypothesis implies that posture and movement are controlled by a single central mechanism.

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