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LIMB POSITION DRIFT INDICATES INDEPENDENT MODULES FOR SPECIFYING
MOVEMENT DISTANCE AND DIRECTION

JACQUELINE ROSE PATTERSON
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Reviewed and approved* by the following:

Robert Sainburg, Ph.D.
Professor of Kinesiology and Neurology
Thesis Supervisor

Jaime Shultz
Associate Professor of Kinesiology
Honors Adviser

* Signatures are on file in the Schreyer Honors College.

ABSTRACT

Previous work (Brown et al., 2003) has shown that limb position drifts when individuals make repetitive movements in the absence of visual feedback. Regardless of the extent of drift, distance and direction of the repetitive movements are maintained. Currently, we examine how individuals program new movements following drift based on visual and proprioceptive maps. We hypothesize that limb drift reflects a misalignment of intact visual and proprioceptive maps. In a VR environment, participants made continuous movements with their dominant right hand between two targets positioned 15 cm apart, paced by a two Hertz metronome. After five cycles, cursor feedback of hand was removed for the next 44 cycles, which induced an average drift in hand position of roughly five centimeters. Kinematic analysis indicates differential programming, with movement direction specified by the visual input of the initial, last-seen position and movement distance specified by proprioceptive input of the current, drifted hand position. We conclude that limb position drift arises from a progressive misalignment of intact visual and proprioceptive maps. Integration of these maps is attained differently for perception versus action: uncertainty in positional sense results in drift while movements maintain accuracy.

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Chapter 1

Introduction

Most common everyday activities, like picking up a glass of water, are smoothly performed by most people without much thought or apparent effort. However, even simple movements require complex perceptual motor processing, integrating multiple sensory modalities to inform accurate motor control. In reaching for a glass of water, vision and proprioception (sense of position and movement of body parts) inform of the position of the hand, both in relation to the body and to the environment, and of the position of the glass and the environment as a whole (Graziano 1999; van Beers et al., 1998; 1999). The complexity of these apparently simple daily activities is revealed with damage to the central nervous system, which often makes even the most mundane tasks, difficult or impossible to carry out. Loss of vision or proprioception can each produce deficits in movement, with proprioceptive loss producing the most profound deficits in movement and motor coordination (Ghez et al., 1995; Sainburg et al., 1993). However, damage to visuomotor integration processes in the absence of damage to either modality, in itself, can also cause substantial deficits in motor control and adaptation (Mutha et al., 2011). The question of how these two modalities are integrated to perform visual-motor tasks has been addressed by studies that examine damage to visual motor integration centers, such as posterior parietal cortical areas (Mutha et al., 2011; Andersen and Zipser 1988; Andersen and Buneo 2002; Kertzman et al., 1997), dorsal visual stream networks (Culham et al., 2003; Tanne et al. 1995; Fridman et al., 2006), and studies that produce discrepancies in visual and proprioceptive feedback using either vibration to distort proprioceptive information, or visual feedback distortions through prism glasses or computer mediated displays (Gilhodes et al., 1986; Sittig et al., 1985; Harris 1965; Welch and Warren 1980; Lateiner and Sainburg 2003). In the absence of central nervous system damage or distorted feedback, another example of visual motor discrepancy occurs when individuals are instructed to maintain postures or repetitive

movements in the absence of visual feedback (Rothwell et al., 1982; Brown et al., 2003) In these cases, the position of the limb tends to drift over time, while the participant is unaware of this drift.

Position drift during posture or movement indicates that simultaneous visual and proprioceptive information about body position is required to accurately stabilize posture and maintain consistent limb orientation, whether the limb is stable or moving. In addition, it is very unlikely that limb drift reflects a degradation of either visual or proprioceptive acuity, as individual modalities. Instead, it likely reflects a drift of the alignment of intact visual and proprioceptive maps, an alignment that seems to be mediated largely by regions of posterior parietal cortex (Mutha et al., 2011; Ghilardi et al., 2000). However, there is also a hypothesis that this alignment involves a weighted fusion of proprioceptive and visual modality information, rather than a simple alignment of the two coordinate systems (Rossetti et al., 1995). This study is designed to differentiate between these two alternative explanations for limb drift, and more generally for visual-motor integration. We exploit the phenomenon of limb-drift during cyclic repetitive movements in the absence of vision, to examine how participants plan new movements to visual targets from drifted limb positions, in the absence of updated visual information about limb position.

In a series of previous studies, Brown et al. (2003) examined how participants' limb position drifted when making cyclic out and back movements between two visual targets on a frictionless horizontal surface, in the absence of visual feedback about limb position. Whereas limb position drifted an average of about eight centimeters during the course of the sequence of repetitive cycles, the direction and the distance of the individual cycles was maintained. Inverse dynamic analysis, and forward dynamic simulations, confirmed that joint muscle torques varied as much as 100% in amplitude in order to maintain the direction and distance of motion from the drifted limb configurations. Thus, while the limb position drifted, the distance and the direction of motion continued to specified in accord with the visual displacement vector between the two displayed targets, while apparently accurate proprioceptive information about limb configuration was used to adapt motor commands to the progressively drifted limb positions. This brought up the question of why limb position drifted, if both visual and

proprioceptive and visual modalities remained largely intact and accurate. Given a great deal of research on how participants adapt to visual-motor discrepancies, such as rotated visual feedback (Mutha et al., 2011; Schaefer et al., 2009; Wang and Sainburg 2005; Ghahramani et al., 1996; Imamizu et al., 1995), we now propose that drift represents a progressive misalignment of two accurate maps of the visual environment and proprioceptively derived map of body configuration.

Alternatively, a very prominent line of research has suggested that proprioception and vision are integrated into a fused map that reflects a weighted combination of the two inputs, the weighting of each dependent upon each modality's reliability. This line of research has often depended on experimental paradigms in which visual feedback of limb position is distorted, and a participant is asked to identify the position in space of the occluded limb, given a discrepancy between visual information and proprioceptive information. A classical hypothesis called visual capture proposes that vision attracts proprioception when the senses are misaligned (Pick et al., 1969; Rock 1966; Welch 1986; Mon-William et al., 1997). However, more recent research has suggested that vision influences hand positional sense, not by realignment of the proprioceptive map, but by fusion with proprioception to form a visual-proprioceptive multimodal map more stable and accurate than either independent modality (Desmurget et al., 1995; Rossetti et al., 1995; van Beers et al., 1996). This might explain the limb position drift as a progressive reliance on a less-accurate uni-modal proprioceptive map alone (Desmurget 2000).

In a seminal series of studies, Van Beers et al. (1996, 1999, 2002) provided evidence that in the event of sensory discrepancy, the modality that has the highest reliability has the greatest weight in position judgments. In a series of position matching experiments, subjects had to mimic the position of their unseen, opposite hand using proprioceptive-only, visual-only, or proprioceptive and visual information. Conditions with both vision and proprioception had the least variance than that of other conditions, suggesting that the two modalities were integrated in an optimal way and that visual and proprioceptive information are not of wholly independent streams. Weighing of the two inputs may form based on the direction-dependent precision of the modality, a precision that may be learned from

experience or that may arise instantaneously. Prisms inducing a sensory mismatch along the azimuth showed adaptation towards the visual information, consistent with vision being a more accurate information source than proprioception in the azimuth direction. These results support the optimal integration model in which the CNS integrates the sensory modalities in a way that minimizes positional uncertainty. Multisensory areas in the CNS, such as the parietal lobes, may be the location of the integrative computations producing a multimodal sensory map (Clower et al., 1996; Graziano et al., 2000; Mutha et al., 2011).

However, whether these results can explain the phenomenon of limb position drift remains to be determined. When vision is occluded during repetitive cyclic motion, the average limb drifts, but the essential elements of the movements, remain consistent. For example, Zelaznik and Lantero (1996) showed that when subjects repetitively produce a circular motion with their dominant hand while wearing opaque goggles, the position of their hand systematically drifted while circularity of the movement was maintained. Similarly, Brown and Rosenbaum showed that in the absence of vision, drawing of squares in space drifted in location, but not in size or shape. As discussed above, Brown et al. demonstrated that as limb position drifted during cyclic out and back movements made in the horizontal plane, the direction and distance of the movements remained constant, which required substantial changes in joint torque to accommodate the progressive changes in limb position. They concluded that the accuracy of proprioception remained intact during the drift. Consistent with the studies of Brown et al. (2003), Lateiner et al. (2003) introduced a discrepancy between visual feedback and proprioceptive information about limb position by displacing a cursor representing finger position by about five centimeters, prior to placement of the finger in a start circle. No visual feedback of the cursor was available during movement, and the displacements only occurred in a small amount of perturbation trials. The result was that when initial limb position was displaced from visual feedback, participants produced movements that were parallel in direction to the baseline movements. Furthermore, they adjusted joint muscle torques in order to produce motions that were parallel in direction, even though actually starting from a new location than

baseline (veridical) movements. Thus, again, a dissociation between vision and proprioception appears to reflect intact, undistorted information from each modality, vision being used to specify movement direction and proprioception to adjust muscle actions to changes in real-limb configuration to achieve these specified directions. The use of these modalities for these two processes was also proposed by Sober and Sabes in a series of simulation studies (Sober and Sabes 2003; 2005). The apparent discrepancy between this set of findings and those of Van Beers et al., likely reflects the sensory integration processes addressed by the two different lines of research. While Van Beers assessed conscious reporting of limb location in space, the studies discussed above address how these modalities are utilized to specify and produce motion. The idea that two different pathways might exist for neural processing of conscious proprioception for declarative reporting of limb configuration, and unconscious use of proprioception in specifying and controlling movements is not a new idea (Brown et al., 2003; Sittig et al., 1985; DiZio and Lackner 1995; Sainburg and Wang 2002), neither is the idea of two visual pathways for processing declarative information about objects and for interacting with those objects (Goodale and Milner 1992; Schenk and McIntosh 2010; Goodale and Westwood 2004).

We now hypothesize that movement drift, in the absence of visual feedback during cyclic repetitive movements, reflects a misalignment between largely accurate visual and proprioceptive maps, rather than a weighted fusion of the misaligned modalities. We test this hypothesis by inducing limb drift during repetitive out and back movements, and then immediately requiring participants to make movements toward one of six different targets from the drifted limb position, in the absence of visual feedback. In a control session, subjects return to the laboratory another day, and they are provided start circles that match their previously drifted start positions, in order to provide baseline movements that reflect matched proprioceptive and visual information from those positions to the new targets. We are then able to compare the direction and distance of their movements made from the drifted positions in session 1 to movements made when they have accurate visual information and matched proprioceptive information about the initial position from 1) the initial visually displayed start position prior to drift and

2) the previously drifted positions. By comparing these conditions we can discriminate between the following hypotheses:

H1: New movements are specified according to visual information about start position, but adapted to limb configuration based on accurate proprioceptive information about drifted configuration: This predicts that movements from session 1 to the new targets from the drifted locations will match movements made from the original start location in session 2.

H2: New movements are specified according to accurate proprioceptive information about limb configuration: This predicts that movements from session 1 to the new targets from the drifted locations will match movements made from the drifted locations in session 2.

H3: New movements are specified according to a fusion between vision and proprioceptive information: This predicts that movements from session 1 to the new targets from the drifted locations will not match either movements made from the original start location in session 2, or movements made from the drifted positions in session 2.

Our results for movement direction unambiguously support hypothesis 1, indicating that participants specified the new movements based on the last seen visual information about original start location. This supports the idea that visual information predominates in specifying movement direction, while proprioceptive information is used to adjust movement commands to take account of precise variations in real-limb configuration. However, our results also reveal that movement distance is scaled with actual limb configuration, but not with the initial visual start position. These findings are consistent with previous studies indicating independent specification of direction and distance (Rosenbaum et al 1980; Gordon et al. 1994), and that proprioceptive information plays a particularly important role in controlling movement distance (Ghez et al., 1995; Lateiner and Sainburg 2003).

Chapter 2

Methods

Participants

Eleven volunteers, four males and seven females ages 20 – 23, participated in the experiment. According to the Edinburgh Handedness Questionnaire (Oldfield 1971), all participants were right-handed. Each had normal or corrected-to-normal vision and no history of neurological disorder. All volunteers gave informed consent before participating and were compensated at minimum wage. Procedures fully complied with the Institutional Review Board of Penn State University.

Apparatus

Each participant sat at a horizontal surface leveled just below shoulder height. The seat was secured with the participant's trunk touching the edge of the table to minimize the influence to drift that misalignment of the trunk in relation to the table's center might have caused if unsecured. Through a mirror suspended 21 cm above the horizontal table, a digital projector (Sanyo PLC/XP) and back-projection screen (87x153.5 cm) suspended an additional 21 cm above the mirror projected a visual display of targets against a white, rectangular background that in turn appeared to be in the same horizontal plane as the table surface. When the participants looked through the mirror (87x153.5 cm) framed by dark green fiberglass, a computer-generated display of targets appeared to be originating on the horizontal surface. The mirror blocked view of the participant's arm and hand, but a visual cursor could be programmed to track the hand's location on the projected screen.

The participant's dominant right forearm was placed on air-jet sleds that allowed movement atop the horizontal table with minimal friction, while their non-dominant arm rested on their lap. The fingers, hand, and wrist were immobilized by a splint within the air-jet sled to minimize any rotation or

displacement of the hand during movement of the arm. Arm movements were tracked by a Flock of Birds (Ascension-Technology) magnetic motion recording system connected to a Macintosh computer. A 6-DOF sensor was tightly secured to the center of the back of the hand with a wrap and medical tape. A second 6-DOF was also tightly secured with a wrap and tape to the side of the upper right arm. The sensors collected positional information, calibrated for each participant's dimensions, and digitized at 103 Hz. Customized software (REAL Software, In., Austin, TX, USA) synchronized the presentation of stimuli and data collection.
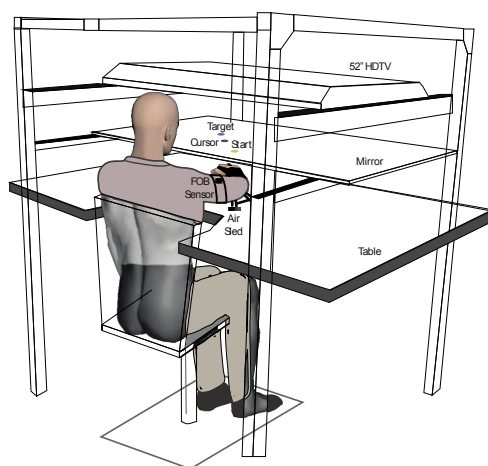
Figure 1 *Experimental Setup. Participants sat at a virtual reality system with their arms supported by air sleds. Vision of the hand was blocked as participants made repetitive movements between two targets and new movements towards varying targets.*

Experimental design and task

Session 1

Participants were tested across two sessions. In Session 1, a start location (two centimeter diameter) was customized to each participant, defined at a 50° shoulder angle and 90° elbow angle. An original target circle (four centimeter diameter) was located 15 cm and 120° counterclockwise from the 0° vector extending to the right of the start circle. A new set of six target circles were located five centimeters and either 60°, 80°, 100°, 140°, 160°, or 180° from the start circle.

After two practice blocks of 20 trials each to have participants gain familiarity with the set-up, participants performed a block of 40 repetitive movements between the original start circle and original target circle. For the first five movement trials of each block, the participant could track the location of their hand through a one centimeter diameter cursor that marked the position of the center of the back of their right hand, where one of the 6-DOF sensors was secured. After the fifth trial, vision of the hand disappeared so that when the participant looked through the mirror, they saw a white screen with the start circle and target circle.

The first movement of each block was initiated when the cursor marking the hand was placed within the start circle, triggering a 50 ms tone go-signal. For subsequent movements, an 800 Hz metronome tone maintained movement speed, sounding at regular intervals independent of hand location. The 50 ms tone marked one movement to either the target circle or the start circle: two tones, or 1.6 s for one complete cycle. Participants were given the instructions to move quickly and accurately and to arrive at the circle with enough time to treat the next metronome tone as the beginning of a new movement.

After 40 repetitive movement trials, both the original start circle and the original target circle disappeared and one of the six new targets was presented; all that could be viewed through the mirror was a white background with one new target. At the next metronome tone, participants were instructed to move quickly and accurately to the new target circle, and to return to their previous hand location upon the following metronome tone.

The new target then disappeared and the original start and original target reappeared to resume repetitive movements for nine trials, paced by the same metronome tone. Next, the original start circle and original target circle disappeared again, and one of the six new targets reappeared. Participants were given the same instructions to move quickly and accurately to the new target and to return to their previous hand location upon the next metronome tone. Across six blocks, each of the six new targets was presented twice, for a total of 12 new movement trials and 294 repetitive movement trials.

Session 2

Participants returned for a second session to record baseline movements in the absence of drift. In Session II, a within-subject design involved seven start locations and six target circles. The start locations included the original start circle, plus six new start circles calibrated to each participant's final position, or drifted position, for each of the six blocks of Session 1. The six target circles were consistent with the six new target circles of Session 1. Movements from the original start circle to the original target circle (15 cm, 120°) were also included, for a total of 43 movement combinations.

The session began with five practice trials moving between the original start circle and original target circle with vision of the cursor marking the center of the hand. Following the fifth trial, vision of the cursor disappeared and movements were made without vision of the hand. A new start circle and target circle appeared, replacing the previous circles.

Like Session 1, each trial of Session 2 was timed with an 800 Hz metronome tone, and participants were instructed to move quickly and accurately to the target circle. Because the location of the start circle was constantly changing between the seven possible circles for each trial, vision of the cursor was briefly restored between trials so that the participants could find the new start position. Upon placing the cursor within the new start circle, vision of the cursor disappeared and the 50 ms metronome tone sounded as a go-signal to begin moving towards the target circle. After 800 ms and a brief pause at the target circle, that trial's set of circles disappeared and a new trial's start circle and target circle appeared with vision of the cursor briefly restored. Each start-target location was presented in a pseudo-random fashion once per block for a total of 43 trials per block, and five blocks for a total of 220 trials.

Kinematic analysis

A custom-designed software developed with IgorPro (Wavemetrics, Inc., Lake Oswego, OR, USA) was used to analyze the data. Before beginning the experiment, the 3-D positions of each participant's fingertip, elbow, and shoulder were measured using a calibration stylus. Stylus position

relative to the 6-DOF sensors on the hand and upper arm was used to calculate joint position and orientation. A third-order dual-pass Butterworth filter with a cutoff frequency of eight Hertz was used to calculate linear velocity and acceleration of each joint. Movement initiation and termination were calculated with respect to a 12% peak velocity cutoff threshold; initiation as the last minimum that fell below the threshold before peak velocity and termination as the first minimum that fell below the threshold after peak velocity. These marker selections were visually confirmed.

Cumulative hand drift was measured over the 44 repetitive movement trials without vision of the hand. Cumulative drift is the Euclidean distance between the original start position (1) of the first trial without vision (sixth trial) and each subsequent start position (i): $position_i - position_1$ where $i = 1$ through 44. This was measured in both the parallel and perpendicular planes to the movement. As the repetitive movements were made in 120° direction, movement vectors were rotated -30°, to align the parallel vector to the y-axis and the perpendicular vector to the x-axis. In this way, movement distance and direction were calculated. Data was compared to the actual movement kinematics to calculate error.

Statistical analysis

Both repetitive movement trials and new movement trials without vision underwent statistical analysis for cumulative drift and movement velocity, acceleration, duration, distance, and direction. One Way Repeated Measures ANOVAs with movement vector (actual, original start, drifted start) x target as factors, along with post-hoc analysis (T-test), was used to determine significance.

Chapter 3

Results

Limb Position Drifts With Repetitive Movements

Participants performed repetitive movements between two targets with the dominant arm. After five trials with veridical visual feedback of the cursor, representing the position of the tip of the dominant index finger, visual feedback was removed, and participants continued to move another 44 cycles (out and back motions). Figure 1a shows a typical set of outward hand paths. The paths show substantial drift in start position, but remain parallel in direction and consistent with respect to distance. In this case, the movements show drift that is directed roughly perpendicular to the direction of movement. These trends are similar to that reported by Brown et al. 2003.

Figure 2b shows the average drift in initial cycle location, across the trials for all 11 participants. Whereas participant 11 drifted on average 8.54 cm, participants 1 and 2 drifted less than 2.5 cm. The average drift across all participants was 4.89 cm. The goal of this study was to determine how participants planned and executed new movements from drifted positions. Thus, the study depends on substantial drift in initial hand position. We therefore restricted our analysis to those subjects who drifted > 2.5 cm, the diameter of the initial start circle, removing participants 1 and 2 from analysis, for a total of 9 participants.
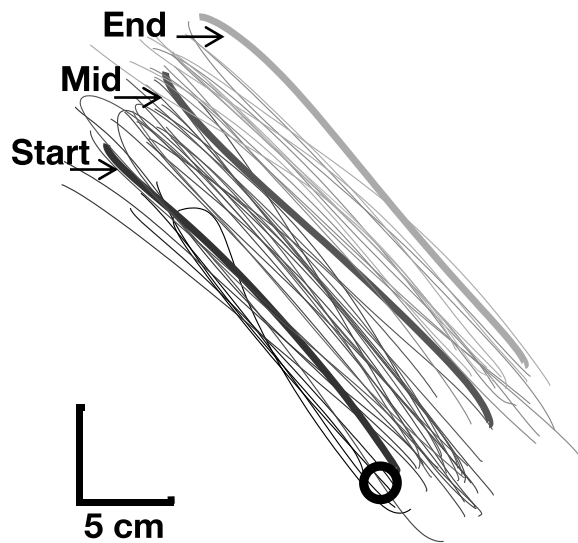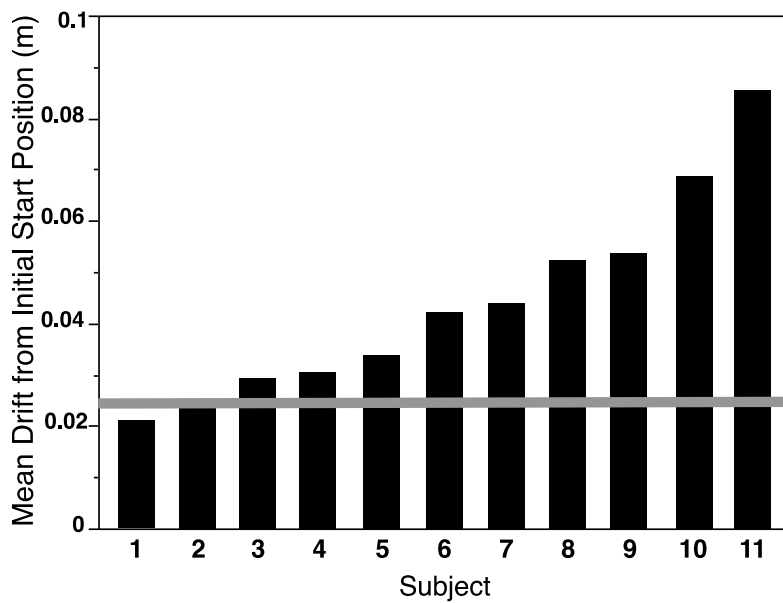
Figure 2. Limb Position Drift. (A) The first half of each cycle of repetitive movements towards a target. The lighter the color of the line, the higher the trial number. The first trial without vision (Start), the trial midway through (Mid), and the final trial for each block (End) are marked as bold lines. (B) Average limb position drift from the initial start position for each subject. The gray horizontal line marks 2.5 cm.

Drift Accumulation Averages 5 cm
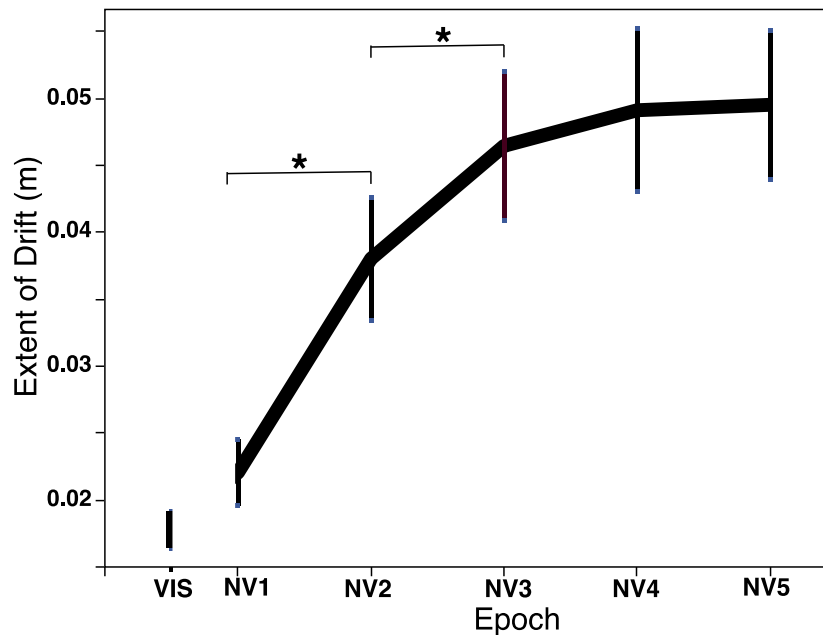
Figure 3*. Cumulative Drift. Positional difference from original start location to current hand position. The first five trials were with vision (VIS) and the next 45 trials without vision (NV). No vision trials are split up into 5 blocks (NV1, NV2, NV3, NV4, NV5). Standard error bars are shown.*

Figure 3 shows the time course of drift in initial cycle location across the whole trial block of 50 movements. The first five trials were performed with vision (VIS), followed by five epochs performed without vision (NV_{1-6}). The asymptotic profile in Figure 3 reflects the time course of drift, which was highest in the early phase (NV_1-NV_2). The rate of drift became lower between NV3 and NV4, and initial cycle position did not show drift between NV3, NV4, and NV5. This profile is consistent with the data of Brown et al., for a similar paradigm and is reflected in our one way repeated measures ANOVA, for drift extent across all six trial blocks. There is a main effect of trial block (NV_{1-6}) ([$F(5, 40) = 34.4887$, <0.0001]. Post-hoc analysis (T-test) showed significant drift between epochs NV1 and NV2 (T= 4.716, P= <0.0001), NV2 and NV3 (T= 2.493, P=0.0169), but not between NV3 and NV4 (T=0.787, P=0.4359) nor NV4 and NV5 (T=0.1188, P=0.906). Across subjects, hand position at the initiation of each cycle of

movement drifted, on average 4.89 cm ± 0.0236 cm (Mean ±SE). After about 35 cycles of repetitive movement, drift in hand position no longer accumulated.
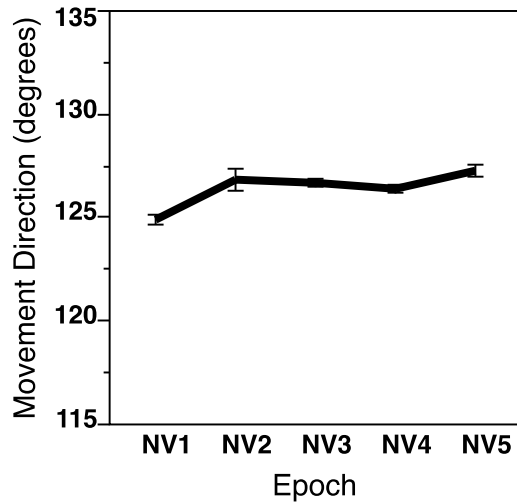
Movement Distance and Direction are Maintained

Regardless of substantial drift in hand position during the course of repetitive movements, the distance and direction of movements remained fairly constant throughout the session (see figure 2A). This is reflected in Figure 4A and 4B, which shows average direction (4A) and distance (4B) of each outward path of each cycle of movement. Repeated measures one way ANOVA for movement distance across cycle number, showed a main effect of cycle [$F(5, 40)=5.4446$, $P=0.0007$], once vision was removed. However, when vision was initially removed, there was a significant increase in movement distance ($T= 2.723$, $P = 0.0095$), consistent with the tendency to overshoot targets during planar reaching movements in the absence of vision (Gordon et al., 1994a,b; Sainburg et al., 1995). Additionally, movement direction showed no main effect of cycle number [$F(5,40)=0.2417$, $P=0.9415$]. Average movement direction for the first block of no vision trials was $124.082° ± 2.157°$ and for the final block of trials without vision it was $126.576° ± 2.157°$.

To summarize, when performing repetitive movements in the absence of visual feedback, subjects' hand position drifted approximately five centimeters from the initial starting position. The directions and distances of these repetitive movements, however, were maintained, suggesting that subjects were able to use accurate proprioceptive information to modify motor outputs so that movement direction and distance was maintained in the face of significant drift in limb configuration. These results demonstrate the replication of previous findings by Brown et al., 2003, and provide the means to analyze new movements following drift.
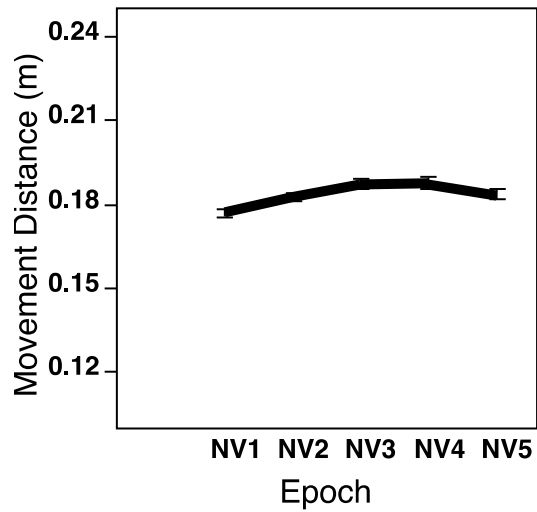
A.

B.

Figure 4. *Repetitive movement distance (A) and direction (B). Measurements from trials of cumulative drift with error bars representing inter-subject SE.*

Movement direction reflects initial hand position

The aim of this study was to examine how new movements are programmed following drift. As such, following 44 cycles of repetitive movements that resulted in the accumulation of hand position drift, the original start circle and target circle were removed and a new target, five centimeters from the original start, was introduced. Still without vision, participants made movements towards the new target.

To determine how the movement from the drifted position was influenced by visual and proprioceptive input, baseline movements from both the original start position and the post-drift hand start positions were measured. Figure 5 displays the new targets.
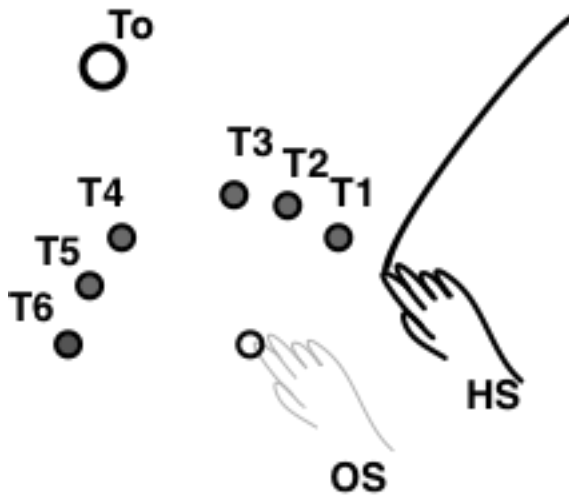
Figure 5. *Display of Targets. V = visual, or initial position. P = proprioceptive, or hand position. The repetitive movement axis is between V and To (Original Target). New targets that appear individually are T1 – T6. Drifted (D) movement is marked by a black line.*
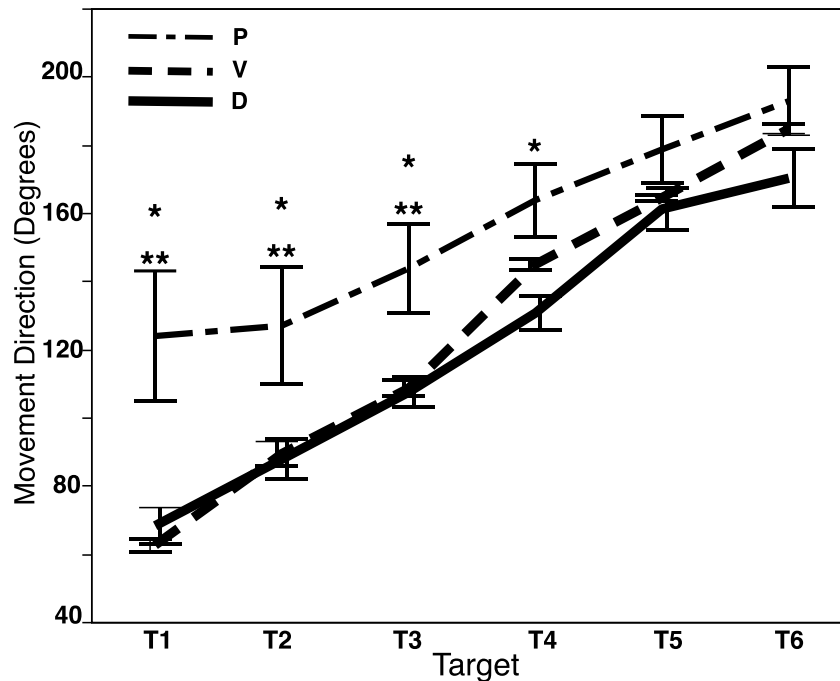
Figure 6. *Movement Direction Condition Separated by Target. Solid line marks subject's movements from an unknown drifted position towards a new target. Evenly dotted line marks subjects' baseline movements from the initial position (V) to the new target. Unevenly dotted line marks subjects' baseline movements from the hand position (P) to the new target. The solid black line marks movement from the drifted position (D) during session 1. (*) signifies a significant difference between P and D. (**) signifies a significant difference between P and V.*

We predicted that movement direction specification would be influenced by:

Hypothesis 1 (H1): vision, and thus movement direction would reflect the last seen visual

position (V) to target direction.

Hypothesis 2 (H2): proprioception, and thus movement direction would reflect the hand

position (P) to target direction.

Hypothesis 3 (H3): would be neither influenced by vision or proprioception, or would be

influenced by a combination of the two, and thus movement direction would reflect a

unique direction.

An example of one subject's movement towards T1 is displayed in Figure 5, showing that the

movement direction very clearly parallels that from V to T1. When looking across all movements,

separated by target, a repeated measures one way ANOVA for movement direction showed a main effect of movement condition [$F_{(2, 16)}$= 5.8593, 0.0123]. However, only T1, T2, and T3, and T4 displayed individual significance, as seen in Figure 6. For T5 and T6, there was not a significant difference in the direction to the target from the initial position versus from the hand position, so the preferential use of visual or proprioceptive input could not be detected for movement direction towards those targets.

Figure 5 demonstrates a movement cycle in which only T1 is presented. From the initial start, the target is 60°, which is confirmed in Figure 5 looking at the V line. From the hand position the direction to the target appears in Figure 5 to be around 125° which also coincides with that of the P line in Figure 6. The participant's movement, marked by the black line, which appears to parallel the V to T1 direction, is not significantly different from 60°, demonstrating the reliance of movement direction on positional information from the last-seen visual location.

Figure 6 displays the close correspondence of the initial start direction and the unknown drifted direction, demonstrating that visual input is paramount in specifying movement direction. Figure 7 further solidifies this relationship, collapsed across target.

Post-hoc analysis (T-test) showed a significant difference between the unknown drifted to target movement direction and the hand position to target direction (T= 3.046, P = 0.0077). No significance was found between the drifted position to target movement direction and the initial position to target direction (T= 0.0998, P= 0.9217).
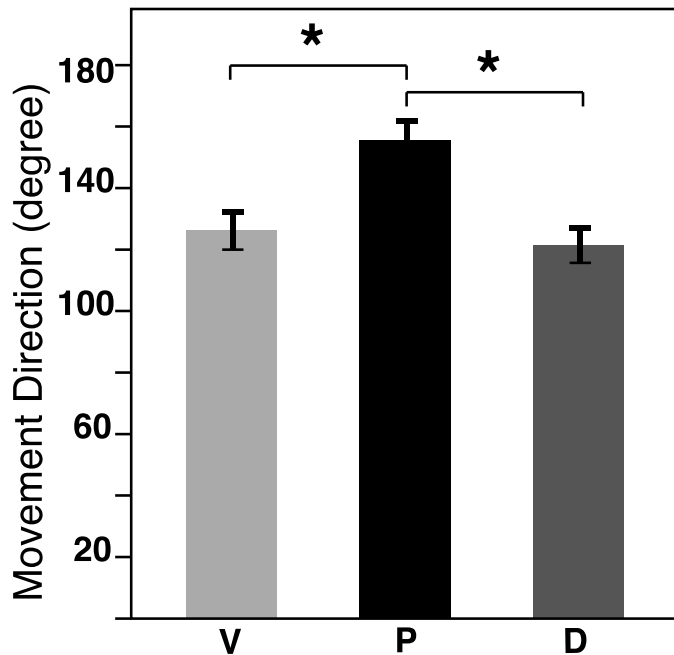
Figure 7. Movement Direction Conditions. Initial position (V) to target direction and hand position (P) to target direction are baseline measurements from session 2. Drifted position (D) to target direction was measured during session 1.

Movement direction (M= 121.081° ± 7.419°) reflected the initial start to target direction (M = 125.943° ± 7.419°) but was not associated with the hand position to target direction (M = 155.144° ± 7.419°). Therefore, movement direction appears to depend heavily on visual input.

Participants all have unique drift patterns, but the direction of their drift had no effect on movement direction [$F(1, 7) = 0.5009$, $P= 0.5020$]. Additionally, the extent of a subject's drift also had no significant effect on their movement direction to a new target ($T=0.10$, $P= 0.9199$), revealed by post-hoc analysis (T-test). We therefore could examine direction without separating out these factors.

Movement direction appeared consistent throughout the duration of the movement, with no significant difference in movement direction at peak acceleration and the end of the movement [$F(1,8)=0.3515$, $P=0.5696$], as shown in Figure 8. Peak acceleration occurred on average 0.145 s ± 0.0752 s following movement onset. Therefore, the specification of movement direction appears to occur before or soon after movement onset.

These results suggest that movement direction is largely dependent on last-seen visual information on hand position, supporting Hypothesis 1. As vision is removed and drift induced, subjects planned their new movements based on their initial start position. This specification seems to occur at movement onset as direction is consistent early on at peak acceleration.
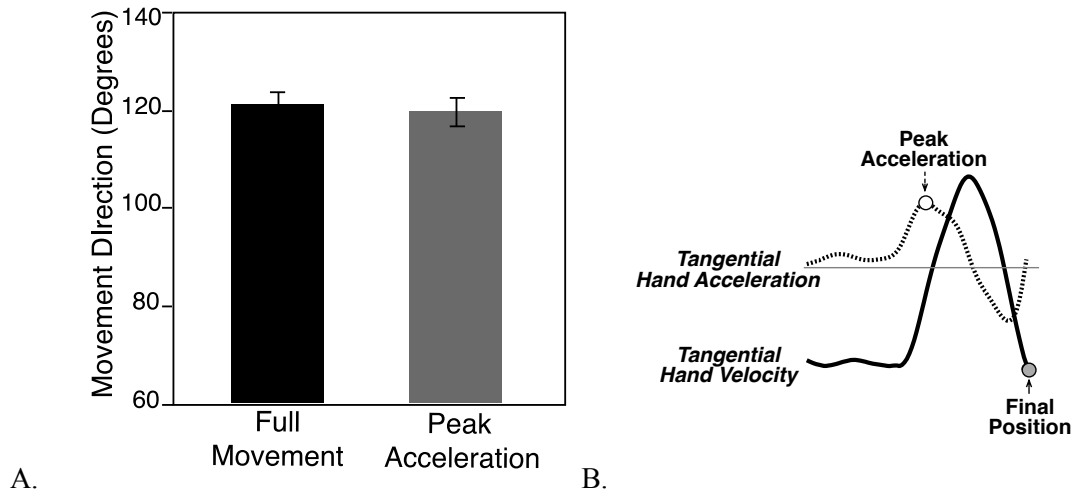
Figure 8. Movement Direction at Different Time Points. The direction of the movement at movement's end (full movement) and early on in the movement (peak acceleration) are displayed in black and gray, respectively. (B) Velocity and Acceleration Plot. Movements followed a normal acceleration profile and a normal velocity profile. Peak acceleration is marked by a white circle and final position is marked by a gray circle.

Movement Distance Reflects Drifted Hand Position

We then looked to see how movement distance was specified when moving to a new target following limb position drift. Movements from the drifted position largely overshot the target by 3.870 cm ± 1.0184 cm (M ± SE), which is typical of movements in a low friction environment in the absence of vision. As Figure 5 illustrates, movements were often twice the length necessary to reach the target.

There was no significant effect of target on movement distance [$F_{(5,40)}= 0.6347$, $P= 0.6744$], so we collapsed across target to perform a repeated measures 1 Way ANOVA, revealing a main effect of movement condition [$F_{(2, 16)}= 5.8593$, 0.0123]. Movement distance, although overshot, averaged at 10.364 cm ± 0.883 cm (M ± SE). This distance from the drifted position was significantly different from

the distance from the initial start (T=3.977, P= 0.0011), but there is not enough evidence to suggest that it is different from the current hand position to target distance (T=1.931, P= 0.0714), as displayed in Figure 8.

While movement distance was not significantly different from that of the hand start to target distance, Figure 9 shows that there is no clear similarity, still differing by 1.92 cm ± 0.996 cm (M ± SE). Movement distance therefore appears to be influenced by the current hand position, supporting Hypothesis 2 for distance, but is not completely dependent.

We then explored how the extent of drift may influence distance planning. As the extent of drift increases, or the participant limb position is displaced further from its initial start position, distance error relative to the initial start position increases as well (T= 3.92, P=0.0058), displayed in Figure 10A. As participants drift further, the reliability of their visual input decreases, overshooting the target more and more relative to the initial start position with increasing drift or uncertainty. Relative to the hand position, however, Post-hoc analysis (T-test) revealed that there is no significant change in distance error with increasing drift, shown in Figure 9B (T= -1.06, P= 0.323). Distance error relative to the hand position is maintained, demonstrating that positional information, or proprioception, of the hand is used to detect location and program movements accordingly, even if these distances are consistently overshot. The specification of movement distance is linked to distance information from the current hand position, utilizing proprioceptive input, and further supporting the predictions of Hypothesis 2.
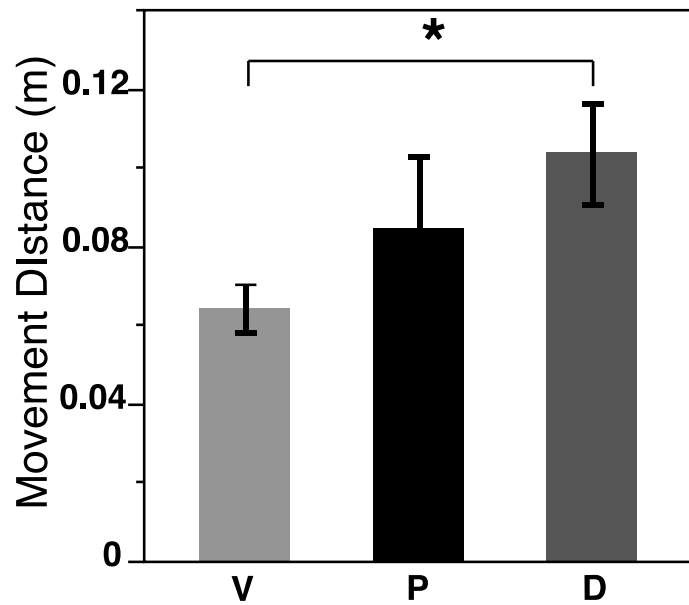
Figure 9. *Movement Distance Conditions. Initial position (V) to target distance and hand position (P) to target distance are baseline measurements from session 2. Drifted position (D) to target distance was measured during session 1.*
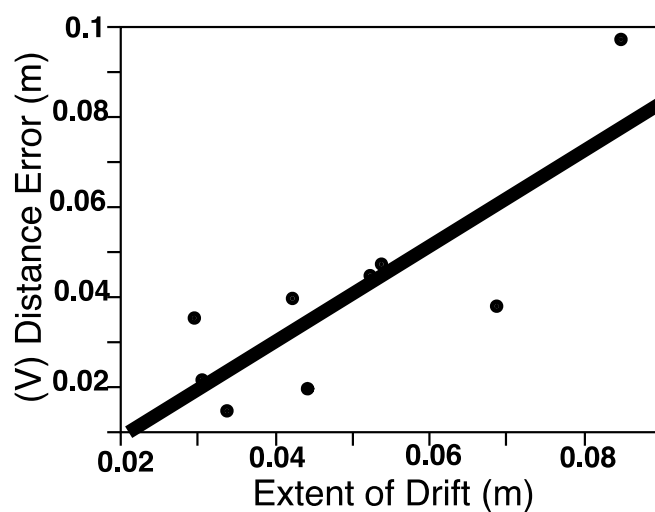
A.
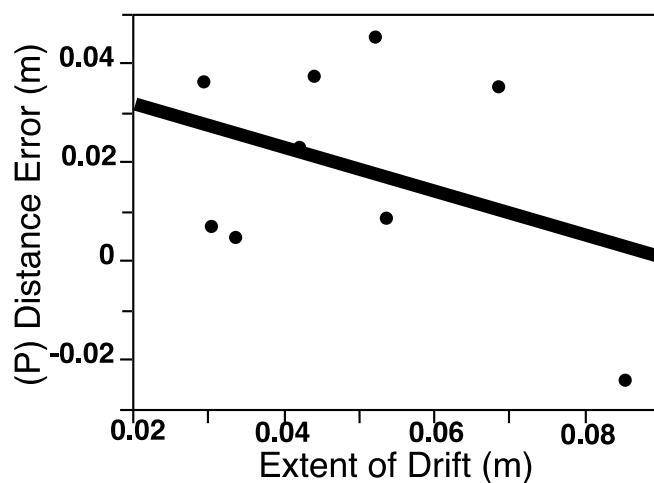
B.

Figure 10. *Distance Error and Drift. (A) Drifted position (D) movement distance – initial position (V) distance varies as drift increases. (B) Drifted position (D) movement distance – hand position (P) distance does not significantly vary with drift.*

Similar to movement direction, movement distance appears to be specified early on in the movement. Post-hoc analysis (T-test) revealed a main effect of movement condition on peak velocity in the drifted position movement versus the initial position baseline (T= -2.585, P= 0.010). This is not the case relative to the baseline hand position movements (T= -0.8232, P= 0.2112). Peak velocity, which can be used as a measurement of movement planning, more closely resembles that of movements originating from drifted hand position, suggesting that the same sensory input, proprioception, is utilized to plan the

movement distance early on, and continues to influence movement distance specification for the movement's entirety.

These results suggest that movement distance specification takes into the current, drifted hand position. Proprioceptive inputs inform movement distance specification, and thus support Hypothesis 2. These results support previous findings that suggest movement distance specification relies on proprioceptive input.

Chapter 4

Discussion

The aim of this study was to examine whether limb position drift might reflect a misalignment in visual and proprioceptive maps by examining the specification of new movements from a drifted position. Limb position drift was induced by having participants perform repetitive out and back movements between two targets in the absence of visual feedback of their dominant right hand, in the horizontal plane. Following 44 repetitive movement cycles, participants made movements towards one of six "new" targets without pause and without vision. Participants returned for a control session where they made movements towards the same targets from session 1 from varying start positions: their initial start position from session 1 along with 6 positions that matched their previously drifted start positions from session 1. The baseline movements in session two reflected movements from the initial position as well as from the drifted positions but with veridical visual and proprioceptive information about initial start position. These three movement conditions, veridical initial position information during movements made from the initial start position (visual), and from the drifted hand positions (proprioceptive), and from the "unknown" drifted hand positions were compared.

We first confirmed the replication of limb position drift following repetitive movements in the absence of visual feedback. Movement distance and direction were maintained throughout the movement, demonstrating that, in spite of drift, participants were able to accurately update their control strategy to account for drift-dependent variations in limb posture (Brown et al., 2003). However, proprioception in the absence of simultaneous visual feedback was not adequate to prevent limb position drift.

We next examined the effects of position drift on movements made to new target directions. Movements towards a series of six new target directions exhibited differential influence of vision and proprioception on direction and distance specification. Movement direction clearly reflected visual input, and was not significantly different from the direction of baseline movements made under veridical conditions from the initial hand position. This represented the last seen visual position of the hand, and

thus we labeled this position "visual". On the other hand, movement distance was influenced by the drifted location of the hand, not the last seen 'visual' position. Movement distance from the unknown drifted position was not significantly different from the baseline proprioceptive hand position to target movement distances suggesting the use of proprioceptive input of the current hand position to influence distance specification.

We conclude that position drift results from a progressive misalignment between accurate visual and proprioceptive representations of hand position in space. Continuous or occasional veridical display of vision is apparently required to update the alignment between these representations. When participants' hand positions drift, the visual representation is used to specify movement direction, while the control strategy is updated using proprioceptive information to specify movement commands that are appropriately adjusted to the drifted hand positions. In contrast, movement distance is specified according to the current proprioceptive information about the drifted hand positions. These findings are consistent with previous research indicating a differential influence of vision for movement direction specification and of proprioception for movement distance specification (Sainburg 2003; Lateiner 2003; Rosenbaum 1980; Gordon et al., 1994).

If proprioception is accurately employed to plan new movements, why is the drift, which depends on positional uncertainty, occurring in the first place? Brown et al. previously showed through inverse dynamic analysis that during drift, participants exploited proprioceptive information about limb configuration to modify joint torque patterns in order to maintain the distance and direction of repetitive movements. We now show that this updating extends to the planning of new movements. We conclude that during limb position drift visual and proprioceptive maps of the task-space and body coordinates, respectively, are not distorted or fused, rather we propose that these maps become misaligned. Previous research using prism glasses used limb position matching experiments to test how declarative information of limb position was altered when a discrepancy between visual feedback and proprioceptive feedback is introduced (Desmurget et al., 1995; van Beers et al., 1996). The results indicated that under these

dissociated conditions, participants reported hand positions that were in between the visual feedback positions and the actual (proprioceptive) hand positions, with a bias toward the visual position. They proposed that the two representations became fused into a single visual-proprioceptive map.

The apparent difference between these experiments and the current experiment is the difference between using visual and proprioceptive information for declarative report of limb position or perception, and using the information to specify movements, or action. Classically, these two aspects of limb position information have been described as conscious and unconscious proprioception, which have been proposed to be mediated by different neural pathways, such as dorsal columns and spinocerebellar tracts, respectively (Kaas et al., 2008; Jansen et al., 1967; Ross et al., 1979). This distinction between sensory processing for declarative perception and action has been proposed previously (Goodale et al., 1992; Jeannerod and Rossetti 1993; Schwartz et al., 2004). In fact, a clear dissociation of perception and action was found by Haffenden et al. (2001) when participants' judgments of object size were affected by the Ebbinghaus illusion, which surrounds circles of equal size with circles of a different size, yet their grasp aperture when reaching for the objects remained accurate, unaffected by the illusion. This distinction is further made by evidence for dorsal and ventral processing streams, which represent different areas in the brain and are responsible for producing action and for object recognition, respectively (Goodale and Milner 1992; Deubel et al., 1998).

We now propose that the integration of visual with proprioceptive information is carried out differently for the purposes of perception versus action. While Van Beers et al., suggested that a weighted and fused representation of limb position is used for declarative judgments about limb position, we now propose that limb configuration information for action depends on the alignment of two independent, but accurate representations. This idea is supported by the work of Sober and Sabes (2003), in which visual information was used to specify a desired movement vector, but proprioceptive information was used in a module that specified configuration dependent movement dynamics. They estimated the contributions of each modality to the position estimate that was formed at each planning stage. In these studies, subjects

made reaches in a virtual reality environment in which vision and proprioception were dissociated by shifting the location of visual feedback. The relative weighting of vision and proprioception at each stage was then determined using computational models. They determined that the position estimate used for movement vector planning relied almost exclusively on visual input, whereas the estimate used to compute the joint-based motor command relied on proprioceptive signals. In a related set of studies, Lateiner and Sainburg (2003), showed that when visual and proprioceptive feedback of initial hand position was dissociated using a virtual reality environment, specification of direction depended entirely on visual information. However, when they performed inverse dynamic analysis, they showed that subjects adjusted joint torque strategies to the actual (proprioceptively sensed) configuration of the limb to achieve these visually-specified directions. Thus, these two lines of evidence are consistent with our current findings indicating that accurate representations in each modality are used for different aspects of motor planning, but that misalignment of these maps is associated with limb position drift.

The idea that the alignment of independent representations of limb position derived from vision and proprioception is supported by the findings of Mutha et. al. (2014). They showed that focal lesions of left hemisphere posterior parietal cortex specifically prevented the ability to adapt to visuomotor rotations. This adaptation paradigm has received a great deal of attention over the last few decades, as a method for studying multisensory integration for motor adaptation (Flanagan et al. 1995, Wang and Sainburg 2005, Seidler et al., 2006). Participants make pointing movements toward a range of targets, usually on a horizontal surface, from a central starting location. A rotation of the cursor relative to the start location is introduced, such that the cursor moves in a different direction than the hand. Participants readily adapt to this type of visual distortion, and they generalize this adaptation to different regions of space, as a vectorial representation of their motion (Wang and Sainburg 2005). The fact that this adaptation reflects a realignment of movement vectors is reflected by the fact that participants specify rotated vectors from various locations in space, without errors in direction. More importantly, Mutha et al. (2014) showed that specific lesions to posterior parietal cortex can disrupt this adaptation, without

altering the ability to make accurate movements to visual targets, under baseline conditions. This supports

the idea that visual specification of movement direction as well as the process of specifying configuration

dependent movement dynamics, each remains intact. This, in turn, emphasizes that the representation of

position with each modality remains intact. However, the ability to rotate one's visual map relative to

one's proprioceptive map is specifically disrupted by this lesion. There is, in fact, substantial evidence for

distinct brain areas for processing visually guided movement, namely the ventral intraparietal cortex and

ventral premotor area F5; proprioceptively guided movement, namely the dorsal medial bank of the

intraparietal sulcus and ventral premotor area F4; and the integration of vision and proprioception, namely

the posterior parietal cortex (Gregoriou and Savaki 2003; Mutha et al., 2011; Ghilardi et al., 2000).We

suggest that limb position drift demonstrates that these independent representations of visual and

proprioceptive space require constant recalibration (Ghilardi et al., 1995; Rossetti et al., 1995; Wann and

Ibrahim 1993). Our current findings on limb position drift support this point of view.

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<center>ACADEMIC VITA</center>
Jacqueline Patterson

EDUCATION

The Pennsylvania State University, The Schreyer Honors College   **University Park, PA**
Eberly College of Science, Braddock Scholar   *Graduation: May 2016*
Bachelor of Science Biology, concentration in neuroscience

RESEARCH EXPERIENCE

Movement Neuroscience Laboratory   **University Park, PA**
Honors Thesis in Kinesiology   *August 2014-Present*
- Investigate the differential roles of vision and proprioception in movement planning and execution
- Involved in experimental design, participant recruitment, data collection, data analysis, and presented preliminary findings at the Annual Society for Neuroscience Conference in Chicago in October, 2015
- Skilled at computer programming including C++ for kinematic and statistical analysis

EuroScholars Program at Universiteit Utrecht   **Utrecht, the Netherlands**
Researcher with Dr. Chris Dijkerman   *February 2014 – June 2014*
- Studied the role of vision and proprioception in body schema adaptation by measuring obstacle avoidance of the dominant hand during reaching within the MIRAGE multisensory illusion system
- Shadowed doctors and physical therapists in the neurologic rehabilitation department at Utrecht University Medical Center

Motivation Laboratory   **University Park, PA**
Undergraduate Researcher   *January 2013 -September 2013*
- Studied sedentary behavior and motivations in exercise by exploring literature guidelines for optimal active breaks from sitting
- Helped in the development of an mobile application that increases motivation to exercise through priming

Center for Neurodegenerative Disease Research, University of Pennsylvania   **Philadelphia, PA**
High school summer intern under Dr. Virginia Lee   *June 2011 - August 2011*
- Observed doctors and researchers in the diagnosis of Alzheimer's and other neurodegenerative diseases in deceased patients
- Participated in the autopsy, tissue processing, tissue staining, diagnosis by microscopy, and presenting research

LEADERSHIP EXPERIENCE

The Coding Space   **New York, NY**
Parent Happiness Manager   *January 2016 – Present*
- Communicate with parents about their child's progress learning code and developing problem solving skills through weekly lesson updates and facilitate feedback and improvement within the company to better serve families.

PSU Know How   **University Park, PA**
Private Instructor   *March 2015 – January 2016*
- Assist students in achieving their educational goals in biology, chemistry, and statistics through effective learning strategies to master challenging concepts and to confidently approach exams.

Career Development Program   **University Park, PA**
Senior Mentor   *September 2015 - Present*
- Guide new freshman as they adapt to college and start to plan their education and career goals by meeting biweekly in a casual setting to answer any questions, explore tools for success, and share experiences.

Penn State Dance Marathon (THON)   **University Park, PA**
Information and Publications Coordinator   *September 2015 - Present*
Alternative Fundraising Executive   *April 2014 - April 2015*
- Construct the monthly THON Newsletter and biweekly Volunteer Update received by thousands to communicate policies and upcoming events, while empowering individuals to take action in the fight against childhood cancer

AWARDS

Edward C. Hammond Jr. Memorial Scholarship	*August 2014-present*
Women in Science and Engineering Research grant	*January 2013 - September 2013*
Eberly College of Science Braddock Scholarship	*August 2012 - present*
Schreyer Honors College Academic Excellence Scholarship	*August 2012 - present*