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Differential contributions of vision and proprioception to movement accuracy

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Abstract

We examined the relative roles of visual and proprioceptive information about initial hand position on movement accuracy. A virtual reality environment was employed to dissociate visual information about hand position from the actual hand position. Previous studies examining the effects of such dissociations on perception of hand location have indicated a bias toward the visually displayed position. However, an earlier study, which employed optical prisms to dissociate visual and proprioceptive information prior to targeted movements, suggested a bias in movement direction toward that defined by the actual hand position. This implies that visual and proprioceptive information about hand position may be differentially employed for perceptual judgments and movement planning, respectively. We now employ a virtual reality environment to systematically manipulate the visual display of the hand start position from the actual hand position during movements made to a variety of directions. We asked whether subjects would adjust their movements in accord with the virtual or the actual hand location. Subjects performed a series of baseline movements toward one of three targets in each of three blocks of trials. Interspersed among these trials were "probe" trials in which the cursor location, but not the hand location, was displaced relative to the baseline start position. In all cases, cursor feedback was blanked at movement onset. Our findings indicated that subjects systematically adjusted the direction of movement in accord with the virtual, not the actual, start location of the hand. These findings support the hypothesis that visual information about hand position predominates in specifying movement direction.

Keywords

Sensorimotor integration; Reaching; Motor control; Sensory distortion; Motor planning

Introduction

Previous research has suggested that information about the initial location of the hand is critical for accurate movement planning (Favilla et al. 1989; Ghez et al. 1991, 1997; Gordon et al. 1987a, b, 1994a, b; Rosenbaum 1980; Rossetti et al. 1995). Such information can be

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derived from different sources of sensory information, including vision and proprioception. In order to examine how these sources of information are combined to perceive a single hand position, researchers have employed sensory distortion techniques to dissociate the normally veridical relationship between vision and proprioception through the use of optical prisms or virtual reality environments. Under such conditions, subjects perceive their hand in a location that is between that specified by vision and the “actual” hand position, specified through proprioception (Harris 1965; Hay et al. 1965; Pick et al. 1969; Van Beers et al. 1996, 1999; Warren 1980; Warren and Cleaves 1971). A similar perception occurs when a distortion in proprioception is introduced through vibratory stimulation (DiZio et al. 1993; Juta et al. 1979; Lackner and Levine 1979). Most studies have indicated that, whether visual or proprioceptive information is perturbed, the perceived position of the hand is biased toward the position indicated by vision.

As exemplified by the studies of Goodale and coworkers (1992), spatial perceptions do not necessarily predict the way in which subjects act upon objects. For example, Haffenden et al. (2001) demonstrated a clear dissociation between perceptual judgments and grasp scaling by examining responses to the Ebbinghaus illusion, in which three circles of equal size are each surrounded by circles of a different size. Subjects perceive the size of the center circle to differ depending on the surround conditions, but grasp aperture is not affected by this illusion. The perceptual illusion does not affect the movement system. This raises the question of whether the illusory perception of hand position that results from a dissociation between visual and proprioceptive feedback influences the movement production system. An earlier study by Rossetti et al. (1995) suggests that the effect of visual/proprioceptive discrepancies on movement is opposite to the previously reported effects on perception. In that study, prisms were used to distort hand position information prior to targeted reaching movements. As a result, movement directions were only partially (~30%) adjusted to the altered visual start location, but remained biased toward the actual start location of the hand. This suggested that limb position information is determined prior to planning movement direction, by combining the conflicting information from both modalities. The apparent bias toward the actual location of the hand is discrepant with the research on position perception described above.

Recent findings from our laboratory suggest that position information supplied by each modality might play a specialized role in the planning of movement direction and movement distance, respectively (Sainburg et al. 2003). We employed a virtual reality environment to dissociate visual and proprioceptive information about initial finger location during a planar reaching task. Regardless of the discrepancy between visual and proprioceptive information, subjects altered the distance of their movements in accord with the actual, not the visually displayed, position of the hand. In contrast, subjects consistently made movements in accord with the direction indicated by the visual display, and not the actual hand location. Thus, our findings suggested a strong bias of initial position information toward the virtual display of the hand. However, in this task we always maintained the visual display of start location constant while altering the actual start location of the finger. We were thus unable to assess whether subjects utilized changes in the virtual location of the finger, indicated visually, to actively plan new movement directions.

We now directly examine the hypothesis that visual information about start position predominates in specifying movement direction. In this study, we systematically alter the virtual position of the hand while maintaining the actual hand position constant. We are thus able to ask whether subjects plan a direction that originates from the virtual start location, from the actual hand location, or between these points. Based on our previous results, we predict that movement direction will vary substantially with the visually presented target.

Materials and methods

Experimental set-up

Figure 1 illustrates the general experimental set-up used for this experiment. Subjects sat with the dominant arm supported over a horizontal surface, positioned just below shoulder height (adjusted to subjects' comfort), by a frictionless air jet system. A start circle, target, and cursor representing finger position were projected on a horizontal back-projection screen positioned above the arm. A mirror, positioned parallel and below this screen, reflected the visual display, so as to give the illusion that the display was in the same horizontal plane as the fingertip. Calibration of the display assured that this projection was veridical. A bib, running from the subjects' neck to the edge of the mirror, blocked view of the shoulder and upper arm. All joints distal to the elbow were immobilized using an adjustable brace. In addition, movements of the trunk and scapula were restricted using a butterfly-shaped chest restraint. Position and orientation of each limb segment was sampled using the Flock of Birds (Ascension-Technology) magnetic 6-DOF movement recording system. The maximum 3-D position error that we measured during calibration of this system was 2.1 mm^3. A single 6-DOF sensor was attached to each arm segment by a plastic splint. The digital data (103 Hz) from each sensor were transmitted to a Macintosh computer through separate serial ports and were stored on disk for further analysis. Custom computer algorithms for experiment control and data analysis were written in REAL BASIC (REAL Software), C, and Igor Pro (Wavemetric).

The following method was used to record limb segment positions relative to the Flock of Birds sensors. The position of the following three bony landmarks was digitized using a stylus that was rigidly attached to a Flock of Birds sensor: (1) index finger tip, (2) the lateral epicondyle of the humerus, and (3) the acromion, directly posterior to the acromio-clavicular joint. A single 6-DOF sensor was attached to a rigid plastic forearm/hand splint and to a rigid plastic upper arm cuff. The position of the bony landmarks relative to the sensors attached to each arm segment thus remained constant throughout the experimental session. As sensor data was received from the Flock of Birds, the position of these landmarks was computed by our custom software. The 2-D position of the index finger tip was used to project a cursor onto the screen. This position was updated at 103 Hz, as data was received by the computer's serial ports.

Kinematic data

The 3-D position of the index finger, elbow, and shoulder was calculated from sensor position and orientation data. Then, elbow and shoulder angles were calculated from these data. All kinematic data was low-pass filtered at 12 Hz (3rd order, no-lag, dual pass Butterworth), and differentiated to yield angular velocity and acceleration values.

Each trial usually started with the hand at zero velocity, but small oscillations of the hand sometimes occurred within the start circle. In this case, the onset of movement was defined by the last minimum (below 8% maximum tangential velocity) prior to the maximum in the index finger's tangential velocity profile. Movement termination was defined as the first minimum (below 8% maximum tangential finger velocity) following the peak in tangential finger velocity.

Subjects

Subjects were five right-handed adults (three female, two male) from 18 to 27 years old. All subjects were right handed, as indicated by laterality scores of 100 on the 10-item version of the Edinburgh Inventory (Oldfield 1971). All of the subjects were free of neurological and orthopedic diseases or disorders and had normal (or corrected to normal) vision. Subjects were recruited from the university community and were paid for their participation. Informed consent was solicited prior to participation, which was approved by the Institutional Review Board of the Pennsylvania State University.

Experimental task

Three experimental blocks were provided per session, each block consisting of 250 movements to a single target. For the first 50 trials within a block, subjects made consecutive movements toward the single target. Prior to movement, a start circle and one of three target circles (18 cm distance) were displayed. A cursor, providing veridical feedback about the tip of the index finger, was to be positioned in the start circle (1 cm diameter) for 300 ms. At the presentation of an audiovisual "go" signal, the cursor was blanked. Subjects were instructed to move the finger to the target using a "single, uncorrected, rapid motion." Audiovisual feedback and points were awarded for accuracy for movements performed within a specified time window of 400–550 ms. Final position errors of less than 1 cm were awarded 10 points, while errors between 1 and 2 cm were awarded 3 points, and errors between 2 and 3 cm were awarded 1 point. Points were displayed following each trial, along with a tone that was specific to each point value, 1, 3, or 10. Between trials, cursor feedback was only provided when the tip of the index finger was within a 3-cm radius of the center of the start circle. This was done to prevent adaptation to altered visual feedback following "probe" trials.

Following 50 consecutive trials within each block, the relationship between the cursor and the index finger was altered prior to movement on occasional (every 6–10) probe trials. Maximum points (10) were awarded for these trials, regardless of accuracy. In order to place the cursor into the new displaced start circle on probe trials, subjects had to reposition their finger into the start location that had been previously experienced during the "baseline" (non-displaced) conditions, while the shift in the start circle position was associated with a new relationship between the cursor start position and the target.

Start location changes

For each of the three target directions (45°, 90°, 135°), 5 different visual displaced start positions for the cursor were defined by the altered relationship between finger and cursor position (15 total cursor start locations). During probe trials, hand position was the same as that during baseline trials, while visual information of cursor location had changed. The schematic shown in Fig. 1B (left) depicts the veridical arrangement between cursor and finger during baseline trials, whereas Fig. 1B (right) depicts the relationship of the subject's hand to the cursor during a probe trial. To position the cursor into the displaced start circle required the hand to return to the hand location experienced for all non-displaced (baseline) trials. As shown in Fig. 1C, two rows of 3 start locations each, were arranged either 3.5 cm anterior to the start circle relative to the axis of the target, laterally displaced relative to the axis of the target, or both (~5-cm displacement).

Experimental sessions

Each subject performed sessions to each of the three targets, with probe trials for positions A, AR, AL, L, and R. Each subject performed three blocks, one toward each target. The order of the blocks was randomized between subjects. Within each block, 50 consecutive movements were performed before beginning probe trials. Within the remaining 200 trials per block, probe trials were pseudorandomly presented every 6–10 trials. The design of this study produced an average of 6 probe trials for each of the displaced cursor start positions. Subjects had no prior information about the change in start circle position. On repositioning the cursor in the new start circle, subjects only received cursor feedback when the hand was within 3 cm of the baseline hand location.

Measures of task performance

Three measures of task performance were calculated from hand trajectory data: relative initial movement direction, relative final movement direction, and radial distance. Radial distance was calculated as the 2-D distance between the start location of the fingertip and the final location of the fingertip. Relative final direction was calculated as the angular difference between the following displacement vectors: vector 1 was defined from the start location of the finger to the position of the finger at movement termination, while vector 2 was defined from the center of the start circle to the center of the target circle. Relative initial direction was similarly determined, but with vector 1 ending at the position of the finger at the time of peak tangential finger velocity.

Hand path averaging

For averaging of hand trajectories (see Fig. 2), the following methods were used: First, the X and Y hand displacement profiles were time normalized to 100 points. Each series of either X or Y displacement profiles were point averaged to yield a mean and standard error value for each consecutive point. As shown in Fig. 2, the mean X and Y values were plotted against one another to yield a mean 2-D hand path profile. The standard error for X displacements and Y displacements are displayed in Fig. 2 as horizontal and vertical error bars, respectively.

Statistical analysis

Analysis of variance (ANOVA) was used to test for effects of target direction and initial start location on experimental measures. A 3-target location × 6-start location ANOVA was conducted on measures of initial direction error, final direction error, and movement distance. Significant interactions of target and start locations were decomposed by analyzing the simple main effects of start location for each target. Main effects of both target and location were tested using Bonferroni/Dunn corrected pairwise comparisons.

Results

Movement direction varies with cursor location

Figure 2 shows average hand paths for a representative subject, demonstrating the general results of the experiment for movements to each target. The initial hand position was the same for all trials, regardless of visual displacement of the start circle and cursor. Hand paths for trials in which the cursor start location was altered were consistently made parallel to the line between the visually displayed start circle and target. Overall, movements substantially overshot the target, which is typical for rapid horizontal reaching movements made in a low friction environment (see Sainburg et al. 1999). The fact that minimum points were awarded for up to a 3-cm (17%) error likely contributed to this tendency. Nevertheless, there is no clear relationship between the target distance, relative to the cursor start location and the movement distance.

Figure 3 shows the mean relative directions, calculated as the difference between the baseline target vector and the hand path displacement vectors, taken at either final position (top) or peak tangential finger velocity (middle). For trials in which the cursor start position was displaced to either side of the finger start position, the relative direction of the displayed target vector is represented as a horizontal black line. For all three target directions, final movement direction varied systematically with the displayed target vector. Thus, our 3 (target) × 6 (start position) ANOVA showed a main effect for start location (ANOVA: $P<0.0001$). The amplitude of these movement direction changes varied with target direction, yielding a significant main effect for target (ANOVA: $P=0.001$), as well as an interaction between target and start position (ANOVA: $P=0.0047$). We expect that this interaction reflects direction-dependent direction errors, which have been previously well documented (Gordon et al. 1994a, b).

It has previously been shown that the initial direction of rapid reaching movements, computed at peak tangential finger velocity, largely reflects feedforward mechanisms (Sainburg et al. 1999). We thus asked whether changes in initial direction predicted final direction accuracy, which would indicate that planning mechanisms were adapted to the altered initial cursor locations. As depicted in Fig. 3 (middle), variations in initial relative movement direction showed a similar pattern to those of final relative movement direction. Accordingly, our 3 (target) × 6 (start position) ANOVA showed a main effect of start location (ANOVA: $P<0.0001$), a main effect of target (ANOVA: $P=0.0099$), and an interaction between target and start location (ANOVA: $P=0.0019$). Whereas the movements tended to be gently curved, variations in initial movement direction predicted final movement direction. The scattergram in Fig. 3 (bottom) shows the dependence of final relative direction on initial relative direction. On average, 84% of the variance in final direction was predicted by variations in initial direction (R^2: mean=0.84, SD=0.08). Thus, the visual projection of initial cursor position seems to have induced systematic changes in the planning of movement directions even though the hand position was not displaced.

Specification of movement distance did not vary when initial hand location remained constant

Figure 4 shows the radial distance (top), tangential velocity (middle), and tangential acceleration (bottom) for all movements across the six cursor positions for each of the three targets. As can be seen in Fig. 4 top, radial distance showed very little change across cursor start locations. Accordingly, our 3 (target) × 6 (start position) ANOVA showed no main effects of start location (P=0.7698), no effect of target (P=0.9569), and no interaction between start location and target (P=0.9979). Nevertheless, it can be seen in the figure that the mean distance of movements made when the start cursor was displaced to any of the anterior positions appeared to be slightly, though not significantly, shorter than the other conditions.

Previous research has indicated that when subjects plan to make movements that cover a range of movement extents, peak tangential finger velocity and acceleration vary in amplitude with movement distance (Atkeson and Hollerbach 1985; Ghez et al. 1991, 1997; Gordon and Ghez 1987b; Gordon et al. 1994b). We therefore asked whether the slight trend to shorten those movements in which the cursor was displaced anterior relative to the target was attributable to such preplanning mechanisms. Figure 4 middle and bottom, show peak tangential finger acceleration and velocity for all movements across the six cursor positions for each of the three targets. If the trend to reduce the distances of movements with anterior displaced cursor positions is attributable to preplanning mechanisms, we would expect to see a trend toward smaller velocities and accelerations for these movements, which did not occur. It must, however, be emphasized that subjects tended to grossly overshoot the targets in this paradigm, indicating that distance regulation was not a primary emphasis of this task. Thus, the 3.5-cm displacements in the cursor start location may have simply been an inadequate stimulus to elicit substantial modifications in movement distance.

Discussion

In this study, subjects performed a series of baseline movements toward one of three targets, in each of three blocks of trials. Interspersed within each block were probe trials in which the cursor location, but not the finger location, was displaced relative to the baseline start position. In all cases, cursor feedback was blanked at movement onset. We were thus able to assess the relative contributions of initial position information, as provided by proprioceptive and visual input, to movement accuracy. We predicted that this manipulation would result in systematic variations in movement direction in accord with the displaced cursor position. We also predicted that movement distance would not vary with the position of the cursor because the initial location of the hand remained constant.

Our results confirmed the first of these hypotheses by demonstrating that movement direction varied with the visually displayed vector between the altered cursor start location and the target. When the cursor position was altered, no significant changes in movement distance, acceleration, or velocity occurred. However, a trend to decrease movement amplitude in accord with the virtual finger location was evidenced. These findings provide support for the idea that visual information about initial hand location predominates in specifying movement direction. Such findings are consistent with previous reports, employing optical prisms, which indicate a larger influence of visual information in hand location perception (Harris 1965; Hay et al. 1965; Pick et al. 1969; Warren 1980; Warren and Cleaves 1971). However, our findings extend these reports to indicate that visual information about hand location also predominates in specifying the direction of targeted movements. Further research is necessary to determine whether the systematic alterations in perception of hand position, induced by visual/proprioceptive discrepancies, are quantitatively consistent with the effects on movement production shown here.

Our findings appear contradictory with those of Rossetti et al. (1995), who employed optical prisms to displace the visual display of a finger LED prior to targeted reaching movements. In that study, the fingertip was positioned by a haptic cue on the tabletop. Thus, visual information about start position was displaced while proprioceptive *and* haptic information about finger location was not. Consistent with our findings, subjects adjusted movement direction in accord with the vector between the displaced LED position (virtual position) and the target. However, the change in movement direction was only one third of that required to bring the cursor to the target under the altered feedback conditions, substantially less than that seen in the current study. Using a *weighted fusion* algorithm in which proprioceptive information had the largest influence, the authors concluded that both proprioception and vision contributed to direction specification. In the current study, movements associated with most target/cursor position pairs showed nearly complete direction adjustment to the vector between cursor and target. This indicates a predominant influence of visual information in specifying movement direction. It is plausible that the discrepancy in findings may result from the additional haptic information available in Rossetti's study.

Previous psychophysical studies have provided evidence that movement direction and extent are specified relative to the initial location of the hand. Our current findings support this idea by demonstrating that movement direction is altered predictably by providing an illusory display of initial hand location. Early evidence in favor of distinct programming of movement direction and extent, relative to an origin at the hand, was provided by Rosenbaum (1980) by examining reaction times in a precued reaching task. These ideas were further supported by Favilla et al. (1989), using a cued reaction paradigm during a targeted force pulse task. Gordon et al. (1994b) extended these concepts using a planar, center out reaching task performed at different amplitudes. The finding that movement endpoints were clustered in elliptical patterns, with the major axis of the ellipse oriented along the direction of movement, suggested that movements were planned from an origin at or near the hand (see also Ghez et al. 1991). This vector hypothesis has been supported by electrophysiological studies in primate cortex, which indicate that neuronal activity varies with the direction of intended hand motion (Georgopoulos 1994, 1995, 1996, 2000; Kakei et al. 1999; Kalaska 1988; Kalaska et al. 1983). However, electrophysiological evidence for independent coding of direction and distance in the CNS remains controversial (Fu et al. 1993, 1995; Messier and Kalaska 2000).

Our findings both support and extend the vector hypothesis by showing that changes in information about initial finger location have substantial effects on movement direction. When the virtual start position was displaced from that of the finger, subjects adjusted movement direction in accord with the visual display. This indicates that the new movement directions were planned from an origin at or near the virtual start location. A previous study (Sainburg et al. 2003) further suggested that movement distance planning is most influenced by proprioceptive information. However, because the current paradigm did not emphasize distance regulation, we cannot with certainty determine whether changes in the virtual start position substantially influence movement distance.

An alternative interpretation is introduced by the findings of Van Beers et al. (1996, 1999, 2002), suggesting that, under conflicting feedback conditions such as those employed here, the perceived position of the hand is biased toward the modality with the best resolution in the region of space considered. These studies suggest that the contributions of each modality to position information are direction specific, with greater proprioceptive weight given to displacements along the anterior/posterior axis and greater visual weight given to displacements along an orthogonal axis. It is plausible that such direction-dependent weighting of each modality may explain our current findings as well as our previous findings which indicate a strong influence of proprioceptive information in specifying movement distance (Sainburg et al. 2003). However, further research is necessary to dissociate whether the contributions of vision and proprioception are best characterized by differential contributions to direction and distance specification, or rather, by direction dependent variations in modality-specific resolution.

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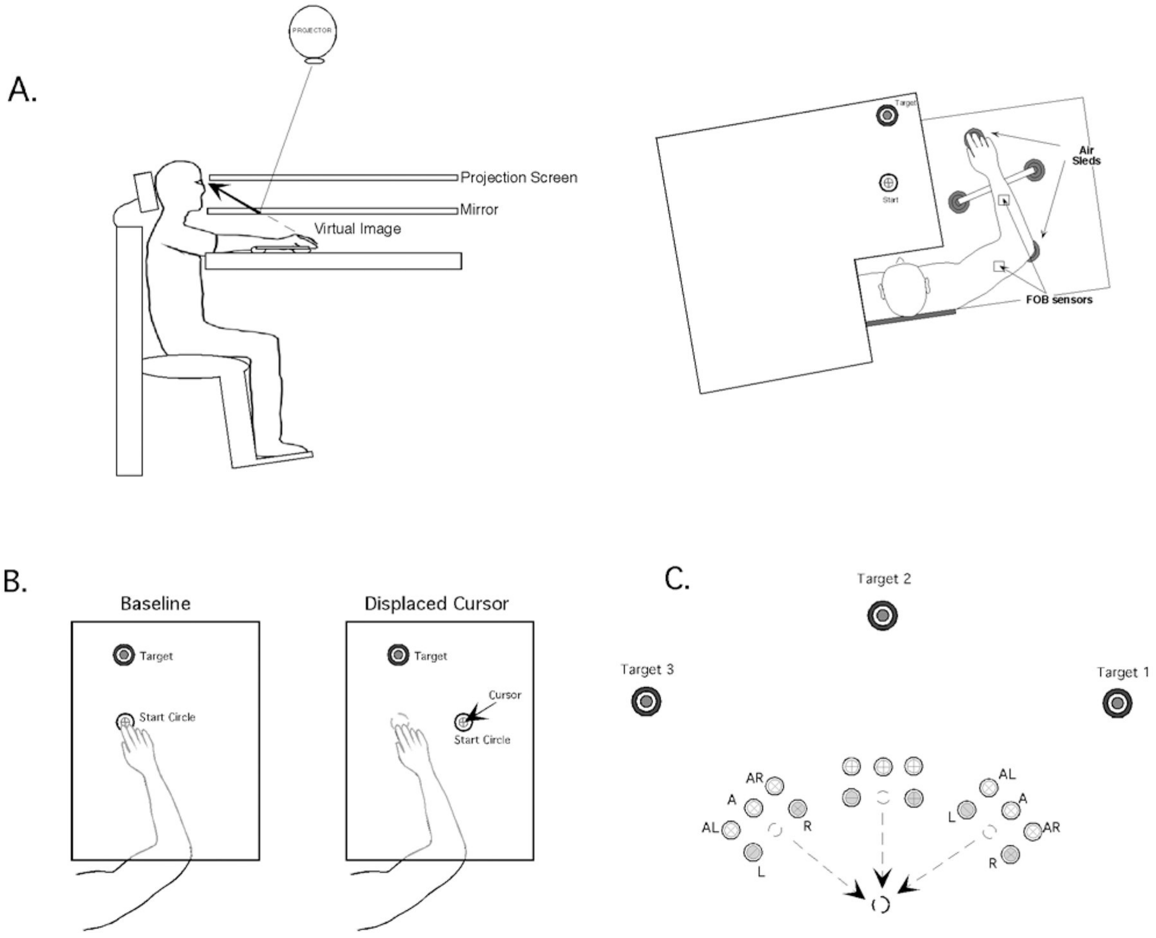

Fig. 1.

A–C Experimental set-up. **A** The subject's dominant arm was supported on a horizontal surface by a frictionless air-sled system. Two sensors (Flock of Birds) were attached to the upper arm and forearm. All joints distal to the elbow were splinted with a brace. Positioned above the subject was a VGA projector, which projected an image of a start circle, target, and a cursor representing finger position onto a back projection screen and mirror, thus giving the illusion that the cursor was at finger level. **B** (*left column*) Position of the hand for a Non-Displaced (baseline) trial. **B** (*right column*) Position of the new visual start circle for a Displaced (probe) trial. **C** Schematic of the five cursor start locations used in the probe trials for each target direction. The central location corresponds to the location of the hand (*dashed circle*)

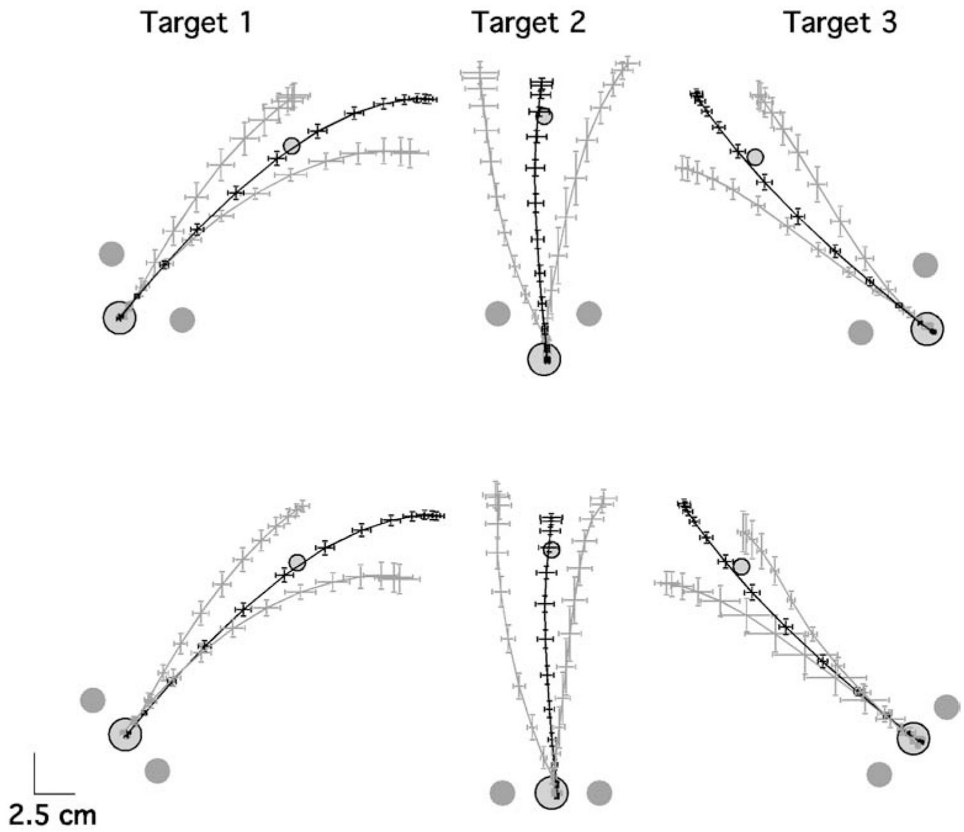

Fig. 2.

Averaged hand paths. Target direction is indicated in the center of each column. *Top panel* Baseline (*BL*) and anteriorly displaced visual start positions for each target (*AL*, *AR*). *Bottom panel* Baseline (*BL*) and laterally displaced start positions for each target (*L*, *R*). Movement time has been normalized. Notice that the movements with a displaced start circle location show substantial changes in movement direction compared to baseline. *Bars* in the X and Y directions show standard errors for trajectories

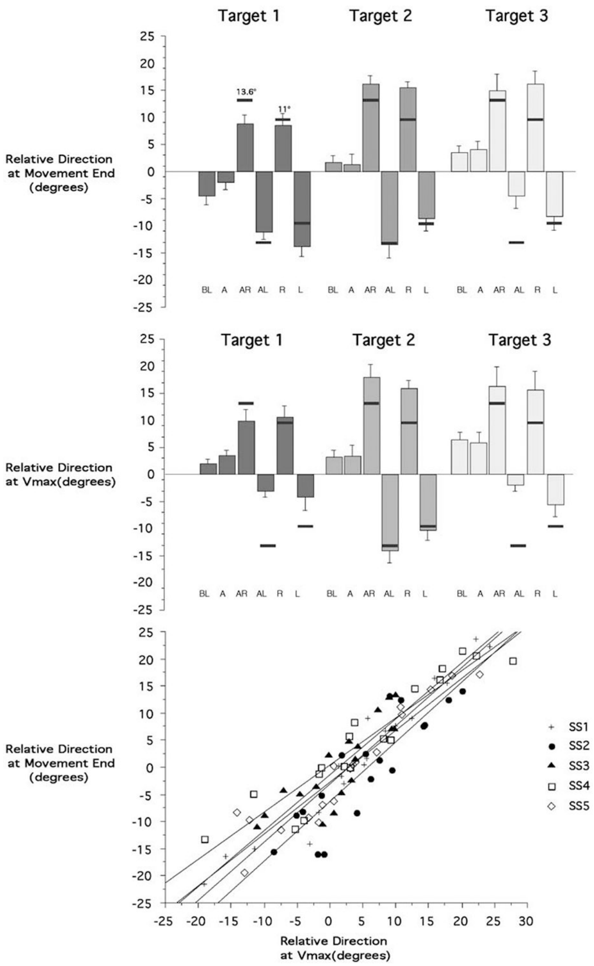

Fig. 3.

Relative movement direction, averaged separately for each target start location, and grouped by target (mean ± SE). *Top panel* Final relative direction. *Middle panel* Initial relative direction. *Bottom panel* Dependence of final relative direction on initial relative direction. *Solid lines* show simple linear regressions for each subject

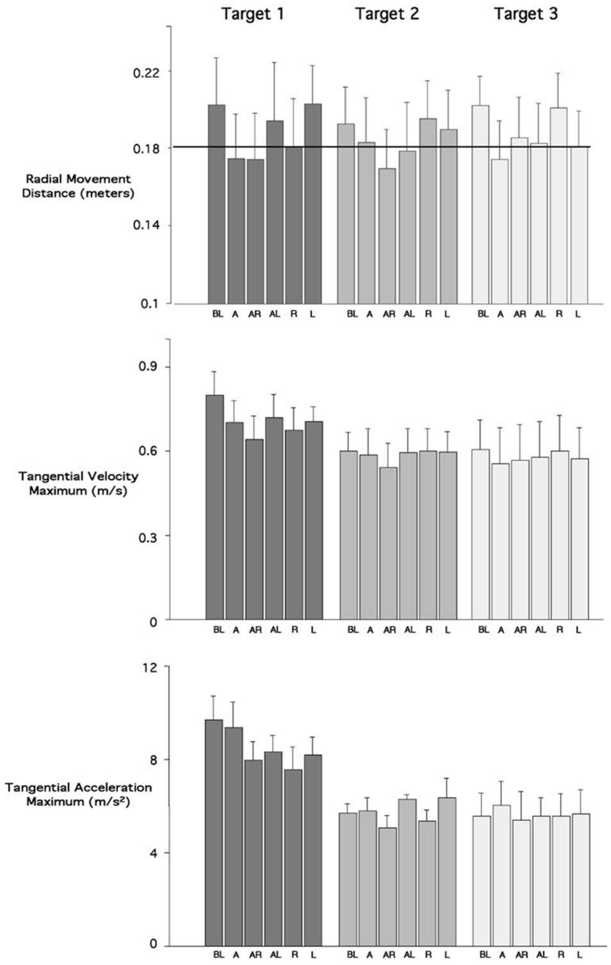

Fig. 4.

Radial distance (*top*), peak tangential velocity (*middle*), and peak tangential acceleration (*bottom*), averaged separately for each cursor start location, and grouped by target (mean ± SE). *Solid line* indicates target distance (*top*)