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Interacting Noise Sources Shape Patterns of Arm Movement Variability in Three-Dimensional Space

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Apker GA, Darling TK, Buneo CA. Interacting noise sources shape patterns of arm movement variability in three-dimensional space. *J Neurophysiol* 104: 2654–2666, 2010. First published September 15, 2010; doi:10.1152/jn.00590.2010. Reaching movements are subject to noise in both the planning and execution phases of movement production. The interaction of these noise sources during natural movements is not well understood, despite its importance for understanding movement variability in neurologically intact and impaired individuals. Here we examined the interaction of planning and execution related noise during the production of unconstrained reaching movements. Subjects performed sequences of two movements to targets arranged in three vertical planes separated in depth. The starting position for each sequence was also varied in depth with the target plane; thus required movement sequences were largely contained within the vertical plane of the targets. Each final target in a sequence was approached from two different directions, and these movements were made with or without visual feedback of the moving hand. These combined aspects of the design allowed us to probe the interaction of execution and planning related noise with respect to reach endpoint variability. In agreement with previous studies, we found that reach endpoint distributions were highly anisotropic. The principal axes of movement variability were largely aligned with the depth axis, i.e., the axis along which visual planning related noise would be expected to dominate, and were not generally well aligned with the direction of the movement vector. Our results suggest that visual planning-related noise plays a dominant role in determining anisotropic patterns of endpoint variability in three-dimensional space, with execution noise adding to this variability in a movement direction-dependent manner.

INTRODUCTION

Limb movements are inherently variable. This variability is the result of noise arising during the transformation of sensory signals into motor commands (planning noise) and noise generated during the transformation of commands into movements (execution noise; van Beers et al. 2004). Planning noise includes uncertainty arising during the sensing process (Fig. 1), and several studies have pointed to visual and/or proprioceptively derived uncertainty as an important source of movement variability (Osborne et al. 2005; Shi and Buneo 2009; van den Dobbelen et al. 2001; Vindras et al. 1998). Although Fig. 1 emphasizes the feed-forward aspects of planning noise, this process continues to affect reaching performance throughout the movement as on-line feedback control of the hand requires constant modification of the movement plan. Noise generated during other stages of planning, e.g., during coordinate transformations or during the specification of the required move-

ment vector, have also been shown to contribute significantly to movement variability in humans (Gordon et al. 1994; McIntyre et al. 1997, 1998; Vindras and Viviani 1998). In addition, a recent neurophysiological study in nonhuman primates has shown that variability in neural activity before movement onset can account for nearly one half of the variability in movement speed (Churchland et al. 2006), further emphasizing the strong contribution of planning noise to movement variability. As indicated above, execution related noise can also profoundly affect movements (Buneo et al. 1995); in fact, it has been suggested that in many circumstances patterns of arm movement variability are largely determined by execution-related noise (van Beers et al. 2004).

The interaction of planning and execution noise during natural movements is poorly understood, despite being essential for understanding the exaggerated variability that results from damage to the nervous system. At least two factors have contributed to this lack of understanding. First, in many psychophysical studies, behavioral constraints are built into the experimental procedures that serve to reduce the effect of noise at one stage of movement production from interfering with those under study, thereby obviating analysis of the interaction of noise sources. Second, analysis of endpoint distributions, a chief method for quantifying movement variability, is often confounded by the inherently similar behavioral consequences of planning and execution related noise in certain contexts. For example, in the studies by McIntyre et al. (1997, 1998), movements were made from starting positions near the body to targets located further in depth. The resulting endpoint errors were found to be elongated along the depth axis, which could conceivably have resulted from noise in execution (as movements had relatively large depth components), noise in visual estimation of the target or hand (as vision is relatively unreliable along the depth axis), or noise occurring during other stages of planning, as argued by the investigators. It is equally possible that the interaction of two or more of these sources contributed to the observed endpoint variability (Thaler and Todd 2009).

Recently, it has been argued that planning and execution-related noise combine in a “near-optimal” manner (Faisal and Wolpert 2009). However, the relative contribution of each noise source to endpoint variability depends on a number of factors, including variations in the relative reliability of sensory information across the reaching workspace. For example, estimation of hand position depends on both visual and somatic cues. The precision of these cues is anisotropic in nature, being more reliable along azimuthal axes than in depth for vision and vice versa for somesthesia (van Beers et al. 1998, 1999, 2002). In addition, the absolute precision of both cues appears to vary

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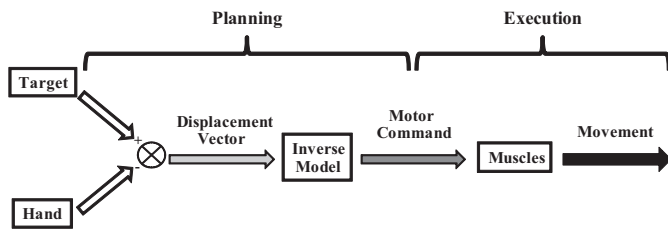


FIG. 1. Simplified schematic representation of the processes involved in reach planning and execution. Planning noise arises from noisy sensor estimates of hand and target position and during the coordinate transformations required to produce a displacement vector. Additional noise is added at later stages of processing, including at the levels of the neuromuscular junction and muscles (execution noise) to produced observed patterns of behavioral variability. Note that only the feed-forward component of movement planning is illustrated here. A similar process is also involved in on-line feedback control of the limb, thus the effects of sensory and planning noise are evident throughout the movement.

with position in the workspace, being less precise further from the body surface. These findings suggest that the contribution of sensor noise, and thus planning noise, to overall movement variability should vary with the position of the hand in the workspace.

Studies of planar arm movements have shown that execution-related noise results in patterns of endpoint variability that depend on the required movement direction (van Beers et al. 2004). As a result, endpoint variability will vary not only with the position of the hand in the workspace but also with the path that the hand took to reach that position. Execution noise can be traced in part to noise in the commands to the muscles, the lengths and moment arms of which vary substantially with arm configuration. Thus patterns of movement variability might even be expected to vary for the same movement vector executed at different positions in the workspace. This is particularly true for unconstrained movements in three-dimensional (3D) space, which necessitate more complex sensorimotor transformations than those that are more constrained (Desmurget et al. 1997).

In this study, we studied the interaction of planning and execution noise across a large portion of the 3D workspace of the arm. Seven human subjects performed reaches to targets arranged in three vertical planes separated in depth, and movements were made with and without visual feedback of the hand. In contrast to previous studies, starting positions were contained within the same vertical planes as the targets. As a result, required movement vectors were perpendicular to the depth axis, i.e., the axis along which visual planning noise would be expected to dominate. Planning and execution noise were accentuated by randomizing target positions from trial to trial and by switching the final target position during movement, requiring rapid, on-line changes in movement planning and execution. We hypothesized that movement variability would be largely dominated by execution noise and that this dominance would be most apparent under visual conditions, where visual planning noise was relatively low. We found that, in the presence of hand vision, patterns of endpoint errors were anisotropic, with the principal axis of variability being largely oriented along the depth axis. In contrast, in the nonvision condition, endpoint errors were larger and more isotropic. In both conditions, patterns of endpoint errors were only well aligned with the movement vector when movements were directed primarily along the depth axis. The results suggest that

visual planning-related noise determines the anisotropic nature of reach movement endpoints in 3D space, with execution noise acting to amplify or reduce this anisotropy in a direction-dependent manner.

METHODS

Subjects

Seven subjects (4 women, 3 men) between the ages of 21 and 25 yr were recruited to perform the experiment. Before the experiment, subjects were briefed on the experimental procedures and what to expect when moving within the virtual environment but were naïve to the purpose of the study. The experiment complied with and was approved by the Arizona State University Institutional Review Board before subject recruitment and data collection, and all subjects read and signed an informed consent form before participating.

Apparatus

The experimental apparatus consisted of a large, standing frame that supported a stereoscopic 3D monitor (Dimension Technologies, Rochester, NY), a metal shield, and a chinrest (Fig. 2A). The monitor projected down through an opening in the frame onto a mirror embedded within the metal shield, which also served to block the arm from view. The shield was suspended from the frame at a 45° angle

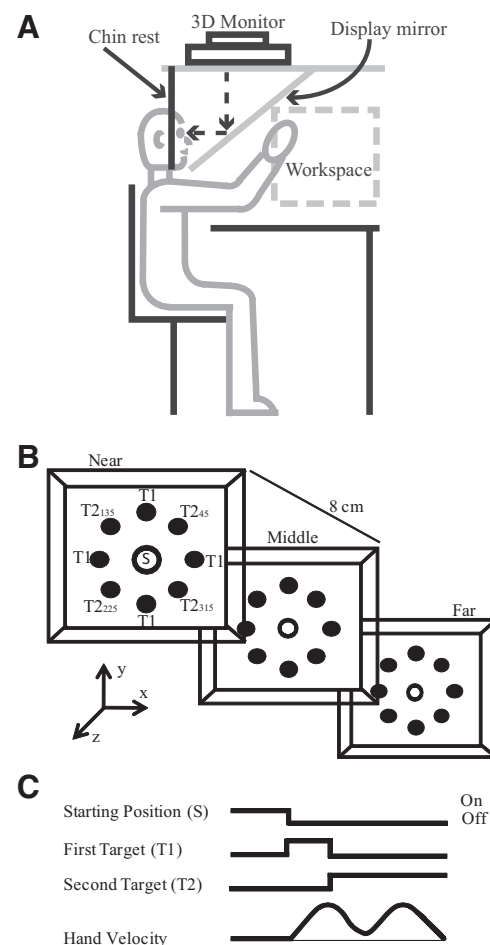


FIG. 2. *A*: experimental apparatus. *B*: target layout for each experimental depth. T1s represent position of initial targets and T2s the position of secondary targets. Each T2 is approached from both adjacent T1s for 8 movement sequences per target plane. *C*: trial sequence showing T1 and T2 onset and idealized tangential velocity profiles.

with respect to the monitor. Subjects were seated directly in front of the shield with their head positioned on the chinrest in such a way that the eyes were aligned with the center of the mirror.

Motion tracking

During an experiment, an LED was positioned on the subject's fingertip to monitor the position of the hand throughout the reach. LED position was continuously monitored by a Visualeyex VZ-3000 motion tracker (Phoenix Technologies, Burnaby, British Columbia, Canada) at a rate of 150 Hz (0.5-mm spatial resolution). The position data were fed back to the subjects via a virtual reality (VR) environment developed in Vizard (WorldViz, Santa Barbara, CA) and displayed on the 3D monitor as a green sphere of ~5 cm diam in the near depth plane. This system provided feedback of the hand within the virtual workspace in near real time. In addition, a large cube was rendered in the virtual environment to provide additional depth cues. Movement data were smoothed off-line using a regressive/low-pass filter to reduce sampling noise, and instantaneous tangential velocity was calculated by differentiating the position data along the movement path.

Experimental design

The task was to execute a sequence of two reaches to targets located in each of three vertical planes positioned at different distances from the body (i.e., in depth; Fig. 2B). The VR environment was calibrated in such a way that the nearest plane of targets was located ~20 cm from the body surface, with each successive target plane located 8 cm farther in depth, making the respective depths of the planes 20, 28, and 36 cm. The targets, as well as the centrally located starting position, were rendered as green spheres of ~5 cm diam in the near plane. This target size was chosen such that depth discrimination between target planes in the VR environment was clearly apparent, facilitating judgment of target depth. As shown in Fig. 2B, targets were arranged on a circle in each vertical plane and were positioned 8 cm from the centrally located starting position. There were four primary targets (T1), located along the x (horizontal) and y (vertical) axes of the display. Each T1 was associated with two potential secondary targets (T2) located immediately clockwise or counterclockwise from a given T1. As a result, each T2 was approached from two different T1s, which allowed a comparison of the endpoint variability at a given T2 when this target was approached from two different directions. Note that starting locations for each vertical target plane were also varied in depth. As a result, required movement sequences were perpendicular to the axis along which visual planning noise would be expected to dominate, i.e., along the depth axis, in contrast to previous studies of reach endpoints in 3D space (McIntyre et al. 1997, 1998).

Movement sequences (i.e., combinations of T1 and T2) were performed with full visual feedback throughout the movement [visual (V) condition] or without visual feedback after movement onset [nonvisual (NV) condition]. Each trial began with the illumination of the starting position (Fig. 2C). This cue also defined the depth at which the subsequent targets would appear. Between trials, subjects had ample time (1.5 s) to visually align their hand with the starting position. After a 350-ms holding period within the starting window, T1 would appear, cueing the first movement. On leaving a predetermined window ($r = 4.5$ cm) around the starting position, T1 would disappear and an adjacent T2 would appear, cueing the second movement. The size of this window was chosen such that T2 appeared very close to peak hand velocity to T1. This was done to minimize the effects of saccadic suppression, which was not the focus of this research and a potential confound to analysis. On NV trials, coincident with the appearance of T1, the visual feedback of the moving hand was removed for the duration of the trial. On V trials, vision of the hand was always allowed. For each trial, the feedback condition (V, NV), depth plane, and the locations of T1 and T2 were all

pseudorandomly selected such that each combination of variables was sampled seven times. The subject had no prior knowledge of any of these trial parameters before trial onset.

Selection of target positions was randomized both within and across depth planes on a trial by trial basis. In addition, subjects were instructed to move as quickly and accurately as possible to the presented targets. These aspects of the experiment design were incorporated to accentuate planning and execution related noise processes rather than to minimize them, thereby allowing a characterization of their interaction. Subjects were also instructed to avoid correcting their position at the end of a sequence. Knowledge of results was provided by means of an auditory tone that signaled that subjects were in an acceptable window around the target (± 5 cm along each axis), but this information could not be used to further adjust endpoint position. The trial was considered a success if the subject moved to T2 in under 1,400 ms and remained within the target window for 350 ms.

Data analysis

Analysis focused on movement errors at the end of each sequence (i.e., at each T2). Movement endpoints were defined as the point at which the tangential movement velocity fell below 10% of its peak value for movements to T2. To assess accuracy, constant errors were calculated by subtracting the known target center (T) from the measured endpoint of the hand (h) on each trial. More specifically, constant errors along a given axis were calculated as

$$e_d = \frac{1}{n_d} \sum_{i=1}^{n_d} h_d^i - T_d \quad (1)$$

where T_d is the location of the target at depth plane d , h_d^i is the endpoint position of the hand for this target for trial i , and n_d is the corresponding number of trials. Similarly, precision was assessed by calculating the variable errors along a given axis for each target position as follows

$$\sigma_d = \frac{1}{n_d} \sqrt{\sum_{i=1}^{n_d} (h_d^i - \bar{h}_d)^2} \quad (2)$$

where \bar{h}_d represents the mean endpoint position for a given target at a particular workspace depth.

Movement endpoints were arranged according to subject, feedback condition, target sequence, and depth plane. Levene's test (a conservative test of equality of variances) was used to analyze the separate effects of workspace depth, feedback condition, and movement direction on the endpoint variability along each axis (for a given sequence). Where sample sizes were larger (e.g., after grouping endpoints across workspace depths for a given sequence), Bartlett's test of uniformity was applied. This also allowed us to assess more specific differences in variability (e.g., lesser or greater variance).

Principal components analysis (PCA) was used to quantify the size, shape, and orientation of the endpoint distributions. For this analysis, we first calculated the 95% tolerance ellipsoids associated with each endpoint distribution as follows (McIntyre et al. 1998; Morrison 1990)

$$T_{95\%} = q \frac{(n+1)(n-k)}{n(n-q-k+1)} F_{0.05, q, n-q-k+1, H} \quad (3)$$

where the dimensionality $q = 3$, the number of target positions $k = 1$, F refers to the F statistic, and H is the covariance matrix of endpoint position h . Eigenvalues and eigenvectors were determined from the matrix T . The eigenvalues determined the size of the distributions, the ratio of the eigenvalues associated with each eigenvector determined the shape of the distributions, and the eigenvectors themselves determined the orientation. A χ^2 test of the form used by Morrison (1990); and McIntyre et al. (1997) was used to test whether any two eigenvalues were significantly different from each other, to ascertain

whether the distributions were isotropic or anisotropic. For visualization purposes, 95% confidence ellipses and ellipsoids were calculated for the endpoint distributions using Matlab code based on the Khachiyan algorithm (Khachiyan 1996; Khachiyan and Todd 1993), as implemented by Nima Moshtagh.

In a recent examination of the role of execution noise in movement variability, it was observed that movement variability (endpoints and initial movement directions) varied systematically with movement direction (van Beers et al. 2004). Moreover, when movements in a single direction but different distances were examined, endpoint ellipses were better aligned with the last part of the movement trajectory than with the straight line joining the starting position to the target, a finding attributed largely to execution noise. To estimate the contribution of execution noise in this experiment, we consequently related endpoint variability to both the total movement vector between T1 and T2 (vector connecting T1 and T2 endpoints) and the terminal movement vector, i.e., the difference between the T2 endpoint and the hand position 200 ms before the end of movement. More specifically, to evaluate the degree of alignment between execution and endpoint variability, we calculated the angle in space (α) between the movement vector (both total and terminal) and the first eigenvector derived from PCA.¹

RESULTS

Subjects generally produced stereotyped reaching trajectories under both feedback conditions. Figure 3 shows endpoint positions and average movement paths for clockwise sequences in the frontal plane. Data for a single subject at each workspace depth are shown. Although movements in both conditions were very stereotyped, movements in the NV condition (red) often undershot T1 and were followed by a slightly more curved and variable movement to T2. In contrast, when vision was available (blue), subjects moved completely to T1 and then executed the movement to T2 in a more direct and consistent manner. This behavior is consistent with previous findings under similar feedback conditions (Prablanc et al. 1979).

Temporal aspects of the movement trajectories also differed somewhat between feedback conditions, but, as with the movement paths, these differences were consistent across depths. Peak velocities to T1 in the NV condition were significantly slower than their V counterparts for many sequences ($P < 0.05$). The reduced velocities and durations on NV reaches suggest a misestimation of the movement amplitudes required to reach T1. With respect to movements to T2 (which remained visible throughout), there were no significant differences in peak velocities and movement times between the V and NV conditions. Regarding workspace depth, no significant effect of depth on peak velocities and movement times to T2 was noted for either condition.

Endpoints in the V condition were in general more accurate and less variable than those in the NV condition. However, in both feedback conditions, variability was generally most pronounced along the depth axis. This can be readily appreciated in Fig. 4, which shows a top-down view of the movements and endpoints shown in the middle plot of Fig. 3. Variable errors were larger along the depth axis than along the horizontal for both the upper (*left*) and lower (*right*) T2s. This was true in both feedback conditions, although the endpoint distributions were larger without vision. The mean of the endpoint distributions (constant errors) were also occasionally biased outside the target plane, although the nature of this bias (under or overshoot) was both target and subject dependent. Such idiosyncratic behavior with regard to constant errors has been reported elsewhere (Berkinblit et al. 1995; Darling and Miller 1993; Foley and Held 1972; Soechting and Flanders 1989); thus these errors were not explored in detail. Instead, we will focus our discussion on the variable errors, which provide more direct information about planning and execution-related noise. We first consider the endpoint variability in the V condition and then consider these errors in the absence of visual feedback.

¹ The online version of this article contains supplemental data.

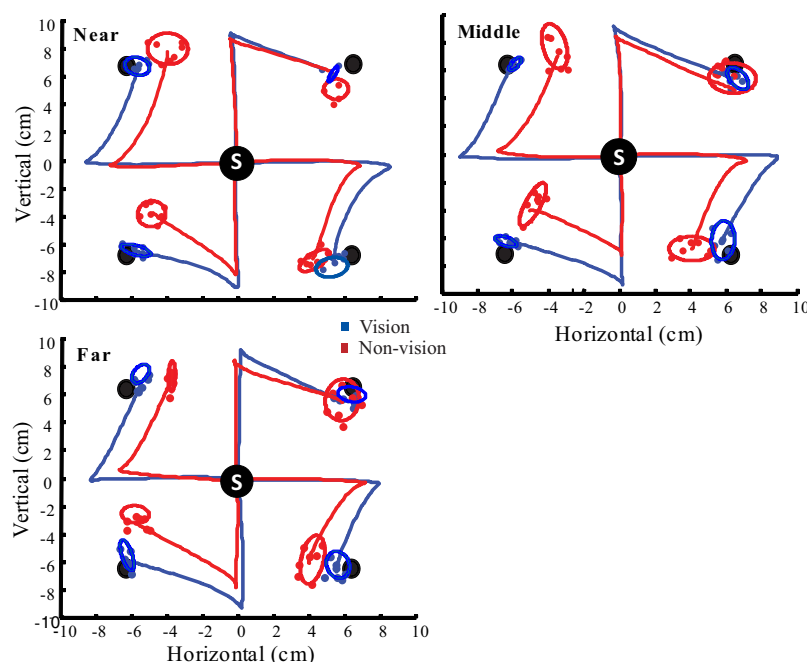


FIG. 3. Mean trajectories and endpoint positions to clockwise T2s at each depth for 1 subject. Each colored dot represents the endpoint for 1 trial to the target in a given feedback condition. Open ellipses represent 95% confidence ellipses for the endpoint distributions in each feedback condition. ●, target locations. Performance generally varied between visual (V) and nonvisual (NV) conditions but did not vary with depth for a given T1-T2 sequence.

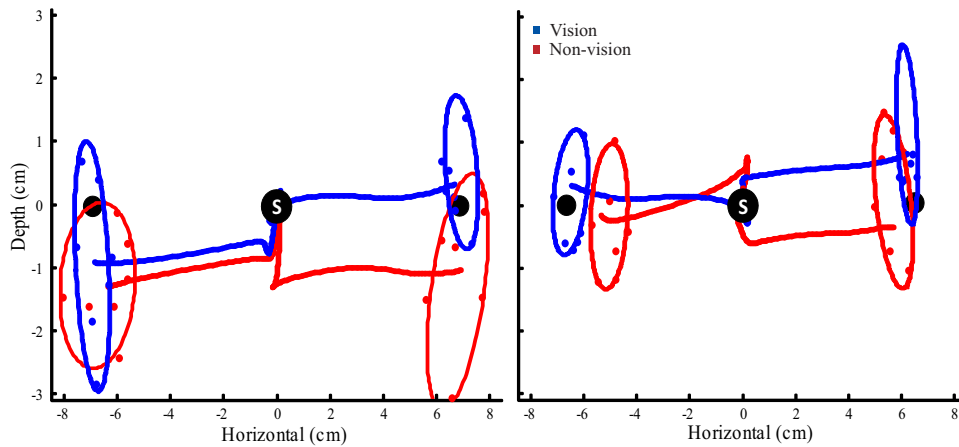


FIG. 4. Mean trajectories and endpoint positions in the horizontal plane to upper (left) and lower (right) T2s for the movements shown in the middle workspace depth of Fig. 3. Other figure conventions as in Fig. 3. Variability along the depth axis was generally similar in magnitude between V and NV conditions.

Endpoint variability under visual feedback

The pattern of endpoint variability associated with a given movement sequence was relatively consistent across workspace depths and subjects. Figure 5 shows bar plots of the variable errors along each axis for the clockwise movement sequences in a single subject (the same subject as in Fig. 4). Data for identical movement sequences (i.e., same T1-T2 combination) executed at different workspace depths are shown in each panel. As indicated above, variable errors tended to be larger along the depth axis than along the horizontal or vertical axes; this is most evident for T2₁₃₅

and T2₂₂₅. In addition, the relative distribution of endpoint variance associated with a given movement sequence was generally consistent across depths. This was quantitatively assessed by comparing the variance along a given axis as a function of workspace depth. When data from all subjects and sequences were analyzed, only 14 of 168 (8%) sequence axes showed an effect of workspace depth (Levene's test, $P < 0.05$). Thus we conclude that the endpoint variability associated with identical movement sequences was not significantly affected by changes in workspace depth in this experiment.

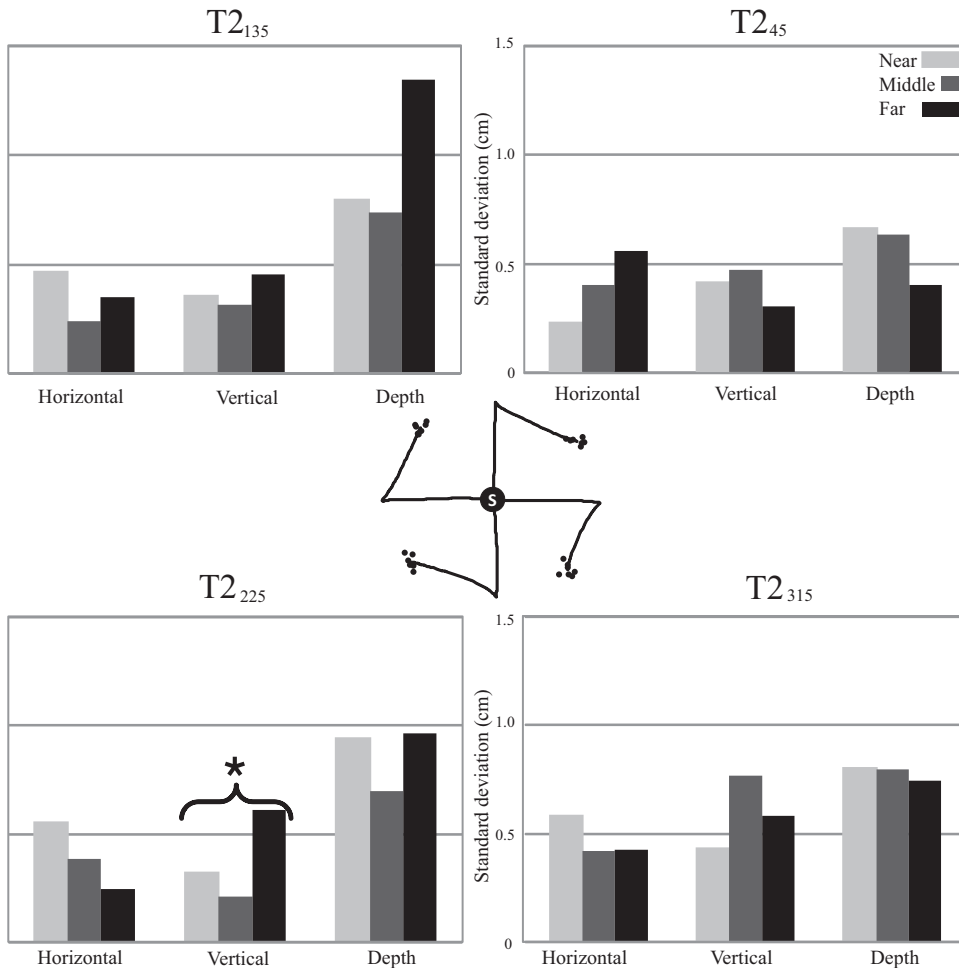


FIG. 5. Single subject variable errors for clockwise sequences performed at each workspace depth. Axis-specific errors were compared across workspace depths for identical sequences using Levene's test. Stars demarcate statistically significant differences ($P < 0.05$). A significant result along any 1 axis resulted in the entire sequence being classified as being workspace dependent. When all subjects and sequences were considered, only 14/168 sequence axes (8%) were classified in this way.

For planar arm movements, patterns of endpoint variability have been shown to be better related to the terminal phases of the hand trajectory (which include any curvature) than to the vector connecting the initial hand position to the target (van Beers et al. 2004). This has been used to argue that endpoint variability is better related to execution than planning noise. Thus a key question concerns how well the orientations of terminal movement vectors in this experiment can explain the observed patterns of endpoint variability. To aid in comparing the terminal movement vector with the distribution of observed variable errors we used PCA. The first eigenvector typically accounted for 60–75% of the total variance in endpoint position, and the first two eigenvectors typically accounted for nearly 95% of the variance, consistent with other studies of endpoint variability in 3D space (McIntyre et al. 1997, 1998). To assess the role of execution-related noise, we used the first eigenvector as our estimate of the orientation of endpoint variance and compared that to the orientation of both the total movement vector and the terminal movement vector (see METHODS). The rationale is that, if execution related noise were largely responsible for producing the anisotropic distribution of errors observed in this task, the first eigenvectors and movement vectors should be roughly aligned in 3D space.

Visual inspection of movement paths suggested that neither the total movement vector nor the terminal vector could account for the generally large out-of plane (depth) component of the first eigenvectors. This can be appreciated from Fig. 6, which shows, for a single subject, the average movement paths (blue lines) and 95% confidence ellipsoids for sequences in the middle plane. Black lines cutting through each ellipsoid represent the first eigenvector for that sequence, centered on the mean endpoint. In the frontal plane (Fig. 6A), ellipsoids and

eigenvectors suggest some degree of elongation of the endpoint variability along the mean T1-T2 path. This is consistent with our expectation that execution noise plays a role in determining endpoint variability, especially when visual planning uncertainty is reduced. However, for most sequences, only a small portion of the eigenvector is observed to project onto the frontal plane. Instead, for many sequences, the first eigenvector was oriented perpendicular to the plane containing the starting position and targets. This is most evident in Fig. 6B, which shows top-down views of the same movements and ellipsoids. For both upper (*top*) and lower (*bottom*) T2s, the orientations of the ellipsoids and eigenvectors were clearly biased along the depth axis. Moreover, they are clearly not well aligned with the average movement paths, which were largely horizontally directed.

Figure 6 suggests that the principal axis of movement variability was not well explained by the orientation of either the total or terminal movement vectors in this experiment. This was generally the case. First, on average, the first eigenvector had a significantly larger component along the depth axis than along the horizontal and vertical axes (Kruskal-Wallis test, $P < 0.001$; Fig. 7A). In contrast, the components of the mean terminal movement vector were not significantly different from each other, which suggests that eigenvectors and terminal movement vectors were often misaligned. To verify this, we calculated the angle (α) between the total/terminal movement vector and the first eigenvector for each sequence. For the terminal vector, the mean angular difference across sequences was $58 \pm 21^\circ$, which is much larger than one would expect if the movement vector (and therefore execution-related noise) were largely responsible for the observed anisotropy in endpoint position. With respect to the total movement vector, a

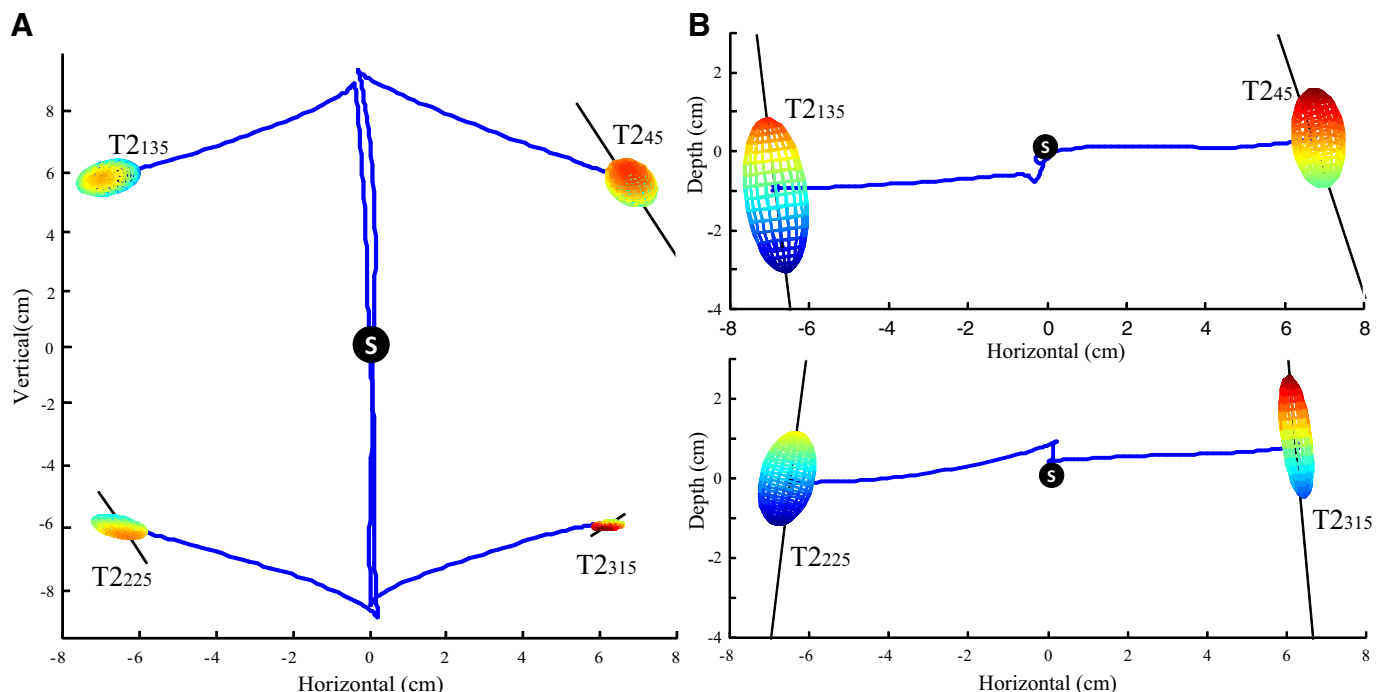


FIG. 6. *A*: frontal plane view of the mean trajectories and endpoint positions for clockwise sequence in the middle workspace. Data from 1 subject in the V condition are shown. Also shown are 95% confidence ellipsoids for each endpoint distribution and the 1st eigenvectors derived from principal components analysis of these distributions (black lines). In this view, ellipsoids appear to be aligned to some degree with the mean trajectory. *B*: top-down view of the same movements shown in *A* for the upper (*top*) and lower (*bottom*) T2s. Eigenvectors and ellipses appear largely oriented along the depth axis and not with the mean trajectory.

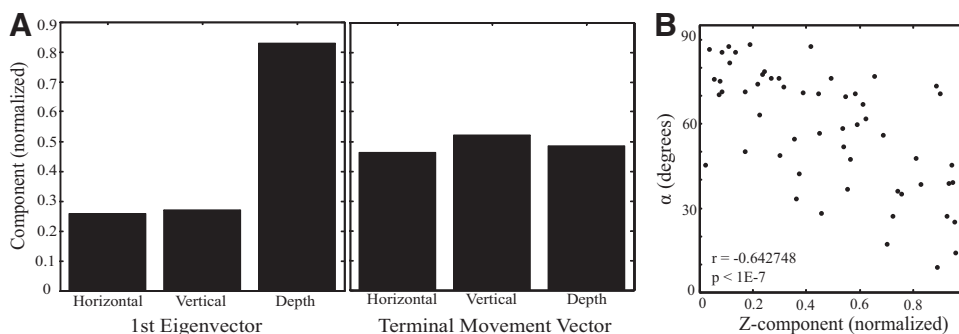


FIG. 7. Comparison of eigenvectors and terminal movement vectors. *A*: axial components of the 1st eigenvector (*left*) and terminal movement vector (*middle*), averaged across all subjects and sequences. Eigenvectors were significantly biased along the depth axis ($P < 0.001$), whereas terminal movement vectors were not biased along any axis. *B*: scatterplot of the depth component of the terminal movement vs. α (the angle between the 1st eigenvector and the terminal movement vector). Significant negative correlation indicates that larger components of movement in depth resulted in greater alignment of movement and eigenvectors.

mean α of $69 \pm 19^\circ$ was observed, indicative of even poorer alignment. The terminal movement vector was better than the total vector at explaining patterns endpoint variability in virtually all analyses and in both conditions. As a result, we will focus the rest of our discussion of execution noise on this vector.

It is important to emphasize that the movement vector did affect endpoint variability in this experiment; it just did so in an axially dependent manner. This was ascertained by correlating α with the degree of movement along each axis. Because a given movement sequence resulted in largely identical patterns of movement variability at each workspace depth, we combined the variable errors for identical sequences across depths for this analysis. This also served to increase our statistical power. For the terminal vector, α was uncorrelated with movement along the vertical axis ($r = 0.06$; $P = 0.66$) and was only weakly correlated with horizontal movement ($r = 0.426$; $P < 0.01$). However, α was strongly correlated with movement along the depth axis ($r = -0.643$; $P < 0.001$; Fig. 7C). In fact, when the component of the terminal movement vector was >0.75 (i.e., when it was oriented largely along the depth axis), α was on average $36 \pm 17^\circ$, indicating a relatively high degree of alignment. Note that, although we combined data across workspace depths for this analysis, these basic trends were clearly observable without such grouping. Thus in this condition, anisotropies in endpoint position seem to be largely related to misestimating the final position in depth, with a smaller contribution from execution-related noise processes.

We also assessed the influence of execution noise by comparing the endpoint distributions for pairs of movement sequences associated with different T1s but the same T2. The average angle between terminal movement vectors to a common T2 was $85 \pm 32.5^\circ$. Given this disparity, we predicted that a strong influence of execution noise would result in significant differences in the endpoint variability associated with different movements to the same T2. We found that for 43% (12/28) of the possible comparisons, endpoint distributions differed significantly along at least one axis (Bartlett's test, $P < 0.05$). This indicates that the movement path did affect endpoint distributions to some degree in this experiment, which could reflect the influence of execution-related noise.

Endpoint variability without on-line visual feedback

Similar to the V condition, patterns of endpoint variability in the NV condition were relatively consistent across workspace depths and subjects. In this condition, we did not observe as strong a tendency for variable errors to be elongated along the depth axis. That is, neither the average terminal movement vector nor the average first eigenvector was biased along a particular axis. However, patterns of endpoint variability associated with a given sequence were still generally similar across workspace depths. That is, when data from all subjects and sequences were analyzed, only 15 of 168 sequence axes (9%) showed an effect of workspace depth (Levene's test, $P < 0.05$). Thus similar to the V condition, endpoint variability associated with identical movement sequences was not significantly affected by changes in workspace depth.

Figure 8 shows average movement paths and 95% confidence ellipsoids for a single subject in the NV condition. Here, ellipsoids appear larger and more isotropic than those in the V condition. This is consistent with the prediction that an increase in sensor uncertainty would lead to more variability overall. Similar to the V condition, first eigenvectors in this condition had large components in depth. However, this was less consistently observed than for movements with visual feedback. Also similar to the V condition was the tendency for the eigenvectors and movement vectors to be misaligned. This can be seen in both the frontal (Fig. 8A) and horizontal plane views (Fig. 8B). These observations are consistent with the idea that the removal of visual feedback results in an increase in sensor uncertainty (and therefore planning noise). Consequently, more isotropic patterns of movement variability were observed in this condition than when vision of the hand was available. The overall increase in planning noise was such that evidence of execution related variability was less evident in the observed endpoint distributions in this condition.

The above observations regarding endpoint variability in the NV condition were consistent across subjects and for the majority of sequences. In general, endpoint distributions were more isotropic without hand vision, and the first eigenvectors describing these distributions were still generally not aligned with the terminal movement vector. These conclusions were based on the following: first, as stated above, the components of the mean eigenvector across subjects and sequences were not significantly different from one another in this condition,

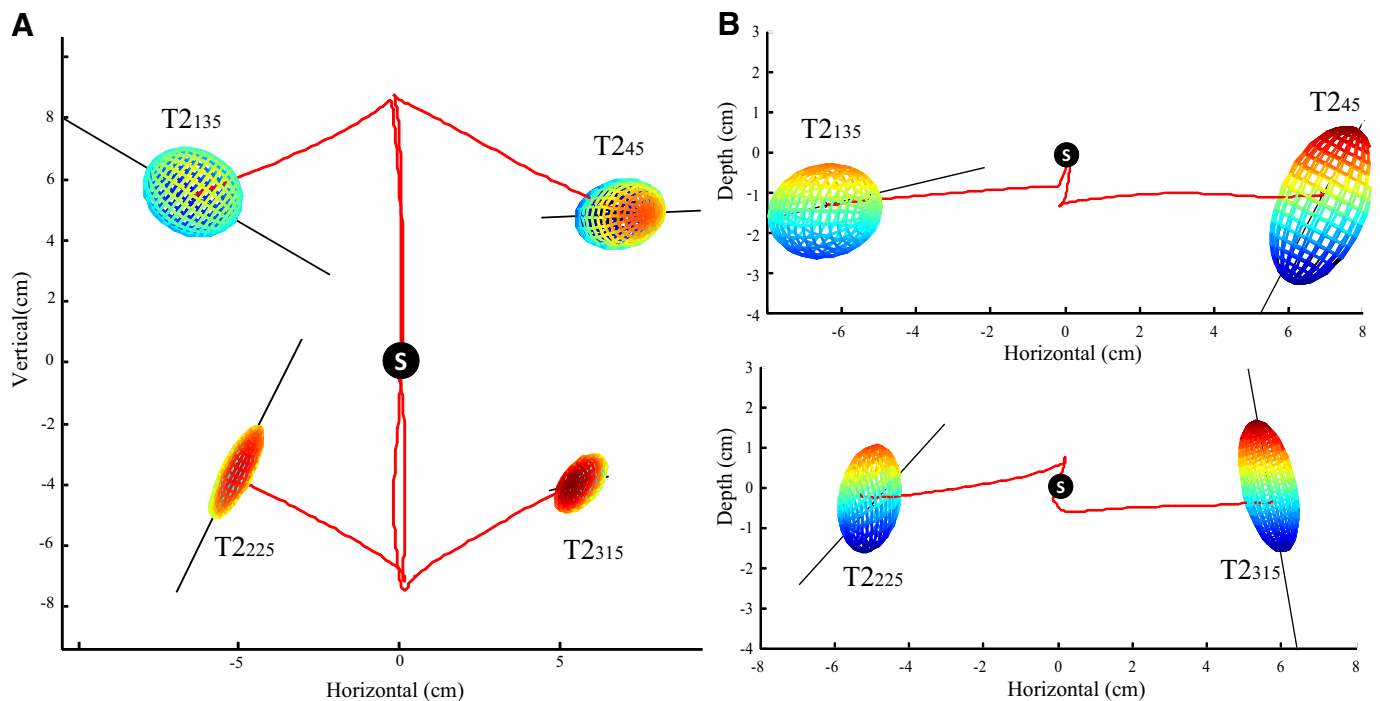


FIG. 8. *A*: frontal plane view of the mean trajectories and endpoint positions for clockwise sequence in the middle workspace (NV condition). Figure conventions as in Fig. 6. Ellipsoids are generally larger and more isotropic than those of the V condition (Fig. 6). *B*: top-down view of the same movements shown in *A* for the upper (*top*) and lower (*bottom*) T2s. As in the V condition, eigenvectors and ellipsoids appear largely oriented along the depth axis and not with the mean trajectory.

which indicates a lack of consistent anisotropy in the endpoint data. Mean movement vectors were also not biased along a given axis. In addition, the angle between the terminal movement vector and first eigenvector was still generally quite large ($54 \pm 23^\circ$), showing lack of consistent relation between the orientations of the terminal movement vectors and the primary axis of movement variability. Similar to the V condition, alignment between the first eigenvectors and movement vectors was not correlated with the degree of movement along the vertical axis ($r = -0.003$; $P = 0.98$) and was only weakly correlated with horizontal movement and movement in depth ($r = 0.314$; $P < 0.05$ and $r = -0.420$; $P < 0.01$, respectively).

Effects of on-line visual feedback

These results may also be interpreted with respect to the role of vision in the on-line control of arm movements in 3D space. To evaluate the effect of on-line visual feedback, we compared endpoint variable errors between the two visual feedback conditions. Because we rarely observed a significant effect of workspace depth on variable errors, endpoints were combined across workspaces for identical sequences. Figure 9 shows the variable errors in both conditions for clockwise sequences from a single subject. In general, endpoint variability in the V condition was significantly reduced along the vertical and horizontal axes but not along the depth axis (Bartlett's test, $P < 0.05$). This pattern was consistently observed across sequences and subjects. This observation suggests visual feedback reduces sensor and planning noise along the horizontal and vertical axes (relative to NV conditions) but does not reduce sensory uncertainty in depth, consistent with observations obtained in studies of hand position estimation in the horizontal plane (van Beers et al. 1998).

Interestingly, despite allowing subjects >1 s to visually align their hand with the starting position, we observed a similar pattern of variability at this position. Although variability was smaller overall at the starting position, subjects were slightly less precise at positioning their hands along the depth axis compared with either the horizontal or vertical axes. In addition, the variability along the horizontal and vertical axes was similar in magnitude. Given that subjects acquired this position under conditions where execution-related noise was relatively reduced, we interpret this finding as further evidence that the observed endpoint variability was largely a product of sensor/planning uncertainty.

Coordinate frames

Analyses of endpoint variability are often used to infer the reference frame or frames used to plan movements (Gordon et al. 1994; McIntyre et al. 1997, 1998; Vindras and Viviani 1998). The bias in errors along the depth axis begs the question as to whether their orientation supported movement planning in an eye/head or trunk/arm based reference frames. To probe this, we again combined our data across workspace depths for identical sequences and examined the orientation of the resulting ellipses and eigenvectors. As shown in Fig. 10, when viewed in both the sagittal and horizontal planes, these eigenvectors appeared to have their largest components along the depth axis, as previously discussed. This is consistent with reduced visual precision along this axis and could be interpreted as supporting an eye-centered reference frame for movement planning. However, in the sagittal plane, these vectors did not in most cases point toward the nominal sight line (i.e., inferiorly for upward targets, superiorly for lower targets). In the horizontal plane, these eigenvectors also did not seem to

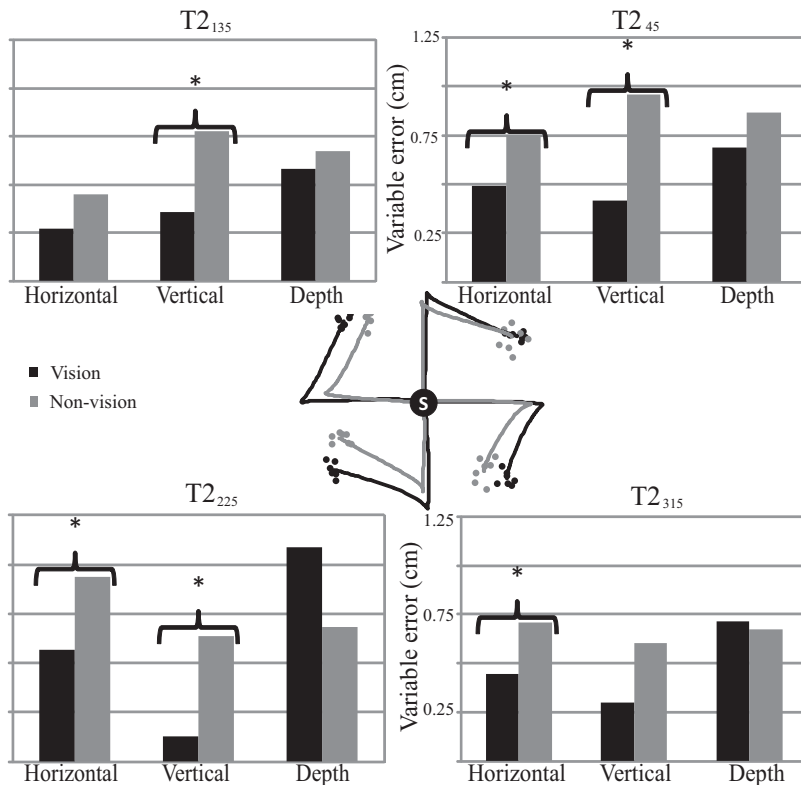


FIG. 9. Single subject variable errors along each axis for clockwise sequences in both conditions. Endpoints were combined across depths for each sequence before calculating errors. Bartlett's test of uniformity was used to determine whether vision reduced variable errors along a given axis (stars). Variability in the NV condition was significantly larger along the horizontal and vertical axes for almost all sequences. Variable errors along the depth axis did not vary significantly between feedback conditions.

converge toward the sight line nor were they rotated in the direction of the shoulder of the pointing (right) arm, a key element of the most prominent body-centered scheme (Flanders et al. 1992). Thus patterns of endpoint variability in this experiment likely reflect the influence of multiple reference frames, a point we discuss further below.

DISCUSSION

Subjects produced movement sequences to targets arranged in three vertical planes separated in depth, approaching each target from two different directions. These movements were conducted with visual feedback (V condition) and without vision (NV condition). This design provided a means to probe the interaction of execution noise and planning noise with respect to reaching variability. Endpoint variable errors in the V condition were relatively small along the horizontal and vertical axes but were elongated along the depth axis, consistent with previously reported characteristics of visual reliability (McIntyre et al. 1997; van Beers et al. 1998, 2002; Viguier et al. 2001). Errors in the NV condition were generally larger and more isotropically distributed in space than those in the V condition but were similar in magnitude along the depth axis to those in the V condition. The large component of error in depth in both conditions suggests a prominent role for planning noise in determining endpoint variability for movements in three dimensions. We propose that this arises from visual uncertainty associated with localizing targets in depth or noise associated with combining target position with hand position to determine the required movement vector. This effect is likely compounded by execution noise when the terminal movement vector is also along this axis. Therefore we conclude that patterns of endpoint errors across the workspace arise from the

interaction of anisotropically distributed visual planning noise with noise related to execution. That is, the spatial interaction of these sources of variability occurs in a direction-dependent manner defined by the characteristics of noise arising within each process.

Relation to previous findings

The elongated pattern of endpoint errors in depth described here is reminiscent of the findings of McIntyre et al. (1997, 1998). In these experiments, subjects made movements from starting positions near the body to targets located further away from the body surface. The resulting endpoint distributions were consistent with a misestimation of endpoint position in depth and were interpreted as evidence for a viewer- or eye-centered planning frame during visually guided movements (McIntyre et al. 1997, 1998). More recently, van Beers et al. (2004) reported that for center-out reaching movements in the horizontal plane, endpoint variability was well accounted for by noise in the motor command. This noise resulted in patterns of variability that were elongated along the movement direction near the end of the trajectory. As a result, for movements directed toward or away from the body these errors appeared to be elongated in depth. Thus the patterns of variability described by McIntyre and colleagues could conceivably be explained as arising from either planning noise, execution noise, or both processes, because the axes along which these noise sources are expected to dominate were nearly collinear in these latter experiments.

Although planning and execution noise have traditionally been evaluated independently, the two inherently interact during the production of movement. Furthermore, these interactions can lead to ambiguity in interpreting patterns of move-

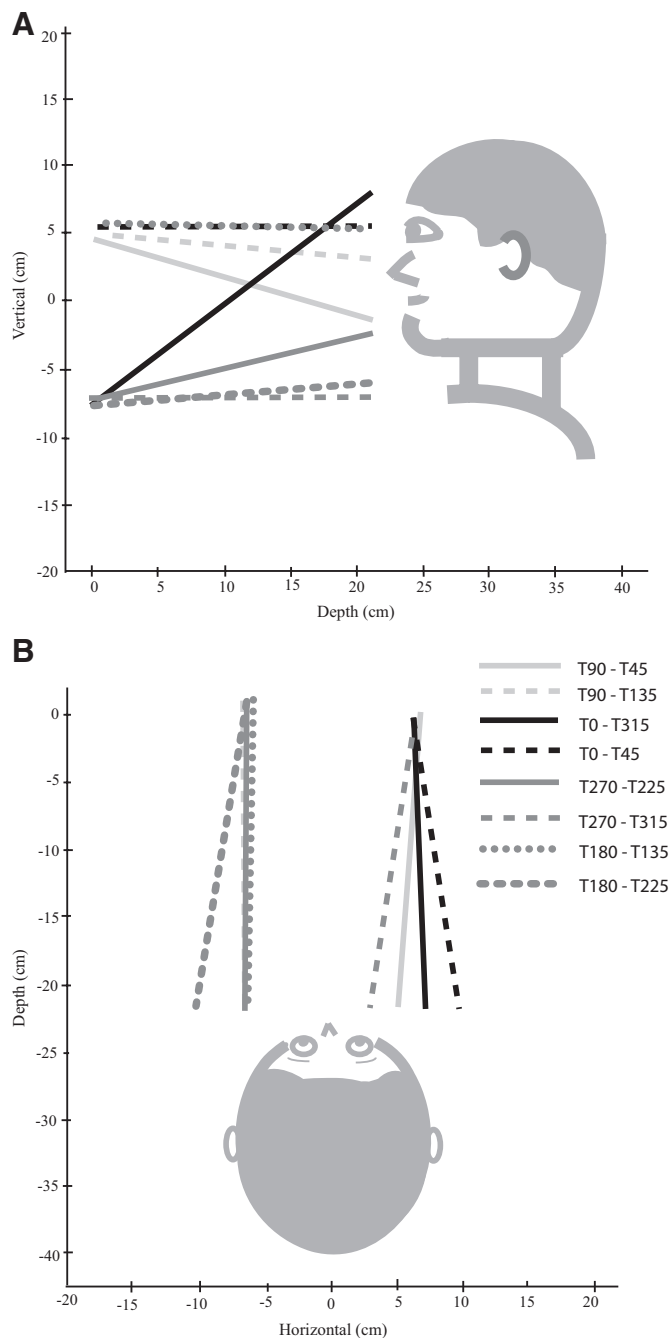


FIG. 10. Principle eigenvectors of endpoint distributions for movement sequences in the V condition from a single subject. Error distributions for each sequence were collapsed across depths before principal component analysis. Each eigenvector originates from the mean error of its endpoint distribution relative to the average target distance from the subject. Vectors were elongated to aid in visualization. *A*: projection of eigenvectors onto the sagittal plane. *B*: projections onto the horizontal plane. Neither view suggests a single frame of reference underlies the endpoint distributions.

ment variability, for reasons stated above. This task, which involved randomized target positions, workspaces, and visual conditions, as well as unpredictable changes in target location, was designed to accentuate both planning- and execution-related noise processes. In addition, by keeping starting positions in the same vertical plane as the targets, thereby requiring planned movements to be largely perpendicular to the depth

axis, we sought to disentangle the contributions of planning- and execution-related noise to endpoint variability. Indeed, we found that even though required movement directions were roughly orthogonal to the sight line in this experiment, patterns of endpoint variability were still largely elongated in depth, in agreement with previous findings obtained for movements in 3D space (McIntyre et al. 1997, 1998).

Although our endpoint distributions were largely aligned with the depth axis, they were still biased to some degree by the movement vector. The magnitude of this latter effect seems to be somewhat stronger than that described by McIntyre et al. (1997, 1998). The effect also seems to be stronger than one would expect based on other studies of variable and constant errors during pointing to visual and/or kinesthetic targets (Baud-Bovy and Viviani 1998; Flanders et al. 1992; van den Dobbelen et al. 2001; Vetter et al. 1999). There are at least three possible explanations for these differences, all of which relate to our experimental design. First, our use of an unpredictable change in target location likely involved larger levels of execution noise (relative to single reaches), as sequential movements seem to involve at least partial superposition of sequential motor commands (Flash and Henis 1991; Flash et al. 1992). This increased level of noise would manifest as a greater effect of the movement vector on the endpoint distributions. Second, the design allowed us to analyze variable errors associated with movements from different starting positions to the same target, as in the work of McIntyre and colleagues. However, the angles between movement vectors in the present study appear to be considerably larger than in these previous studies, which may have made effects of the movement vector more noticeable. Last, as discussed above, the experimental design was such that movement directions were largely orthogonal to the sight line in this experiment; this was not the case in previous studies and may also have made movement-related effects more evident than in previous studies.

Interaction between execution and planning noise

Recently, it has been argued that planning- and execution-related noise combine “near optimally” in the temporal domain (Faisal and Wolpert 2009). These investigators showed that overall task variability could be predicted from the sum of time-dependent sensory and motor variability. That is, when sensing times were small, and sensor uncertainty was therefore large, task variability was high. However, when sensing uncertainty was smaller (because of longer sensing times), variability became more indicative of the level of execution noise. Extending this scheme to the spatial domain, one would predict that the shape of a given endpoint distribution would reflect the relative amount of noise caused by planning and execution, as well as the spatial distribution of each noise source. The latter is believed to be determined by the natural coordinate axes of the relevant sensors and effectors (the eyes and arm, respectively).

In the V condition, vision of the hand was available at all times. Because visual estimation of hand position has been shown to be highly precise along the horizontal and vertical axes, planning noise throughout movement should have been relatively low in the vertical plane in the V condition. As a result, one might predict that patterns of variability in the

vertical plane would reflect largely execution related noise in this condition. Although execution noise was not the dominant source of variability in this experiment, its influence was most apparent in the vertical plane in the V condition, as suggested by the slight elongation of the confidence ellipsoids along the average movement direction in Fig. 6. In contrast, endpoint distributions appeared more isotropic in the NV condition when viewed in the vertical plane (Fig. 8). This would be expected if planning noise in this plane was considerably larger without visual feedback of the hand, a premise supported by previous findings (Carrozzo et al. 1999). Thus the observed patterns of variability in the two feedback conditions appear to arise from differences in the relative levels of planning noise between conditions, as well as the differing spatial distributions of uncertainty arising from planning and execution noise.

An important corollary to this discussion is that, when both levels of noise are similar and their underlying coordinate axes are aligned, their respective contributions to endpoint variability should be more difficult to distinguish. This was in fact the case in this experiment. In general, the principal axes of movement variability were better explained by known anisotropies in visual planning noise than by the orientation of the movement vector. However, as Fig. 7 indicates, when movements involved a significant depth component, endpoint distributions were relatively well aligned with the movement vector. This arises from the fact that when movements are directed in depth, the coordinate axes of visual uncertainty and execution noise are largely collinear and therefore contribute together to the elongated shape of endpoint distributions in depth.

A more quantitative estimation of the relative contributions of execution and planning noise, as has recently been performed in a different context (van Beers 2009), would require an in depth analysis of the variability associated with movement sequences performed along all three axes in space. Experiments of this nature could be a fruitful avenue for future studies. Similarly, probing the nature of visual planning noise will require more advanced experimental paradigms as well. As suggested by Fig. 1, this noise could arise at several stages of the planning process, including during the estimation of target and/or hand position and during computation of the required movement vector. The similar levels of variability along the depth axis in the V and NV condition suggest that estimation of hand position is not a major determinant; this could be a reflection of the more dominant role of proprioception in estimating hand position along this axis (see *Cue integration*). Instead, the large variability in depth reported here more likely resulted from visual uncertainty of target locations in depth or during the computation of movement vectors, which includes coordinate transformations and subsequent vector subtraction. Future experiments will seek to distinguish among these various possibilities.

Workspace dependence

Previous work has shown that proprioceptive reliability decreases as the hand moves further from the body (van Beers et al. 1998). Visual reliability on the other hand is relatively constant, at least for distances within the workspace of the arm (Viguier et al. 2001). As a result, we hypothesized that the weighting of vision and proprioception might vary with workspace depth, resulting in different patterns of errors for iden-

tical movement sequences performed in different depth planes. Contrary to our initial hypothesis, increasing workspace depth did not generally affect the endpoint variability associated with different movement sequences. This suggests that the interaction of planning and execution noise was generally consistent across the workspace.

The fact that planning noise did not seem to change with workspace depth may be partially related to our experimental design and apparatus. Our use of a shield to block view of the arm prevented evaluation of hand positions closer than ~20 cm from the body, where proprioception should be most precise (van Beers et al. 1998). In addition, we did not explore positions near the limits of the reaching workspace, where proprioception might be expected to show a sudden decrease in precision (Scott and Loeb 1994; Wilson et al. 2008). In other words, in this study, we may have explored a region of space where the reliability of somatic feedback (like visual feedback) is relatively constant, leading to only minor effects on movement planning. These small changes in somatic reliability along this axis might also have been masked by the additional but larger visual uncertainty associated with target localization along this axis.

Cue integration

As previously mentioned, we observed similar degrees of error in depth in both feedback conditions. In fact, variability along this direction was almost always greater than variability along the horizontal or vertical axes. We attribute this to the increased planning noise associated with localizing targets in depth (McIntyre et al. 1997; Viguier et al. 2001). However, variability along the horizontal and vertical axes differed greatly between conditions, with errors being significantly smaller with hand vision than without. This suggests an anisotropic effect of vision in this experiment, as predicted by recent “optimal” cue integration schemes. Recent work in cue integration has argued that multiple sensory cues are combined in such a way that the contribution of each input is proportional to its reliability (the inverse of uncertainty) (Ernst and Banks 2002; Jacobs 1999; Knill and Saunders 2003; Kording and Wolpert 2004; van Beers et al. 1999). Vision is highly reliable along the horizontal and vertical axes, but less so in depth. Proprioception, on the other hand, exhibits the opposite tendency. Thus an “optimal” integration of these senses would manifest as a stronger weighting of visual information along the horizontal and vertical than in depth. Our observation that vision assists hand localization in the horizontal and vertical axis but has little effect on reliability in depth is precisely the pattern predicted for a system executing optimal integration strategies.

Frames of reference

Variable errors and constant errors have historically been analyzed as a means to understand movement planning, particularly the reference frame or frame in which movements are planned. The rationale behind using variable errors is that the coordinate system used to encode endpoint positions would show itself as a lack of correlated variance along a set of coordinate axes that are linked to key “nodes” in the sensorimotor chain. Behavioral evidence supporting hand, body, and

eye-centered coding of reach endpoints has previously been presented (Flanders et al. 1992; Gordon et al. 1994; McIntyre et al. 1997, 1998; Vetter et al. 1999; Vindras and Viviani 1998). More recently, behavioral studies suggest that, under many circumstances, reaching errors reflect the influence of distinct movement-related processes and/or sensory signals that are encoded in correspondingly distinct reference frames (Ghez et al. 2007; McGuire and Sabes 2009), observations that have support in both the modeling and neurophysiological literature (Buneo et al. 2002; Deneve et al. 2001). These schemes typically invoke a mixture of reference frames, e.g., eye-centered coordinates with limb or body-centered ones, with the weighting being determined by the statistical properties of the signals being integrated (McGuire and Sabes 2009) or, more generally, the task conditions (Heuer and Sangals 1998).

These results are partially supportive of this general scheme. That is, principal eigenvectors in this experiment were influenced in part by the direction of hand movement, which could be interpreted as reflecting a movement plan in hand-centered coordinates. The influence of an eye-centered reference frame is implied by the elongation of variable errors along the depth axis (consistent with reduced visual precision along this axis). However, as Fig. 10 suggests, we did not find strong evidence for a convergence of the eigenvectors, as would be expected for eye-centered coding (assuming subjects were fixating the target, which is reasonable). In addition, when viewed in the sagittal plane, these eigenvectors did not always point along the sight line, which is also inconsistent with an eye-centered coding scheme. Strong evidence for the encoding of endpoints in a single body-centered reference was also not found, as mentioned in RESULTS. Thus interpreted in the context of the coordinates of movement planning, these results point to a role for both relative (hand) and absolute (eye/body) coordinates, although the origin of the latter is equivocal.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

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