Contribution of execution noise to arm movement variability in three-dimensional space

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Apker GA, Buneo CA. Contribution of execution noise to arm movement variability in three-dimensional space. J Neurophysiol 107: 90–102, 2012. First published October 5, 2011; doi:10.1152/jn.00495.2011.—Reaching movements are subject to noise associated with planning and execution, but precisely how these noise sources interact to determine patterns of endpoint variability in three-dimensional space is not well understood. For frontal plane movements, variability is largest along the depth axis (the axis along which visual planning noise is greatest), with execution noise contributing to this variability along the movement direction. Here we tested whether these noise sources interact in a similar way for movements directed in depth. Subjects performed sequences of two movements from a single starting position to targets that were either both contained within a frontal plane (“frontal sequences”) or where the first was within the frontal plane and the second was directed in depth (“depth sequences”). For both sequence types, movements were performed with or without visual feedback of the hand. When visual feedback was available, endpoint distributions for frontal and depth sequences were generally anisotropic, with the principal axes of variability being strongly aligned with the depth axis. Without visual feedback, endpoint distributions for frontal sequences were relatively isotropic and movement direction dependent, while those for depth sequences were similar to those with visual feedback. Overall, the results suggest that in the presence of visual feedback, endpoint variability is dominated by uncertainty associated with planning and updating visually guided movements. In addition, the results suggest that without visual feedback, increased uncertainty in hand position estimation effectively unmask the effect of execution-related noise, resulting in patterns of endpoint variability that are highly movement direction dependent.

Vision; planning; execution; reference frames

Noise pervades every stage of sensorimotor processing and contributes to movement variability, a hallmark of human motor behavior (Faisal et al. 2008). This noise can be attributed in part to neural processes associated with transforming sensory signals into motor commands (“planning noise”) and to processes associated with transforming motor commands into movements (“execution noise”) (van Beers et al. 2004). Planning noise includes noise arising during the initial sensing of limb and target position, as well as noise that arises during the central integration of these signals, and is thought to result in variability in movement direction and amplitude, as well as speed (Churchland et al. 2006a, 2006b; Gordon et al. 1994; McIntyre et al. 1997, 1998; Vindras and Viviani 1998). Execution noise also arises from both peripheral and central mechanisms and can have profound effects on movement variability (Buneo et al. 1995; van Beers et al. 2004). Understanding how planning- and execution-related noise interact is critical not only for explaining movement variability that is observed in neurologically intact human subjects but also for comprehending the exaggerated variability that arises following nervous system damage (Contreras-Vidal and Buch 2003; Hermsdorfer and Goldenberg 2002; Longstaff and Heath 2006; Thies et al. 2009). In addition, the effects of this interaction are relevant to understanding such diverse sensorimotor functions as position estimation (van Beers et al. 1998, 1999, 2002b), cue integration (Kording and Wolpert 2004), and motor adaptation (van Beers 2009).

The effect of noise manifests differently depending on whether it is execution or planning based. For example, noise associated with execution is thought to result in movement variability that is most pronounced along the direction of movement, particularly its terminal component (van Beers et al. 2004). In contrast, noise associated with sensing the position of the limb (a component of movement planning) has different spatial characteristics that arise from the unique properties of the sensors. For example, localization of the hand by proprioception is reportedly more precise when the hand is closer to the body and is also more precise in depth than in azimuth (van Beers et al. 1998, 2002b). Vision is also more precise for positions closer to the eyes/body but is more precise in azimuth than in depth. These differing workspace dependencies predict that patterns of movement variability arising from planning noise will depend on whether hand position is sensed through proprioception alone or via both senses (Shi and Buneo 2009). In either case, the effects of this noise will be both movement direction and arm configuration dependent (Shi and Buneo 2009).

As a result of the different behavioral consequences of execution- and planning-related noise, determining the source or sources of movement variability that arises during a particular experiment can be problematic. For instance, patterns of variability following movements made from a starting position near the body to targets further away in depth have often been found to be significantly elongated along the depth axis (Carrozzo et al. 1999; McIntyre et al. 1997, 1998; van Beers et al. 2004). These results could be interpreted as resulting from noise in execution (van Beers et al. 2004), noise in visual estimation of the target and/or hand (van Beers et al. 1998; Viguier et al. 2001), or both processes. This is due to the fact that the axes along which execution noise and visual planning noise are thought to dominate (the terminal movement axis and depth axis, respectively) are aligned when movements are directed in depth. Additionally, the elongated pattern of variability could also arise due to noise associated with other aspects of movement planning (McIntyre et al. 1997, 1998, 2000).
In most instances, however, movement variability likely arises from the interaction of noise sources (Thaler and Todd 2009). In support of this idea, sensory and execution noise have been shown to interact “near-optimally” in the temporal domain to determine overall levels of behavioral variability (Faisal and Wolpert 2009). In a recent study of unconstrained reaching movements to targets in the frontal plane, we (Apker et al. 2010) argued that this may also be the case in the spatial domain. In particular, we showed that visually related planning noise played a dominant role in determining patterns of endpoint variability in three-dimensional (3-D) space, with execution noise contributing to this variability in a direction-dependent manner (i.e. along the movement vector). However, since movements in this experiment were designed to be confined largely to the frontal plane, it was unclear if planning and execution noise interacted in the same way for movements requiring large components along the depth axis. In addition, in these experiments, the role of uncertainty in hand position estimation in determining patterns of movement variability in 3-D could not be adequately determined. That is, although we found that patterns of endpoint variability were larger and more isotropic in the absence of hand vision, due to the use of predominantly frontal plane movements we were unable to fully interpret the roles of execution and planning noise in shaping these distributions.

In the present investigation, we studied the interaction of planning and execution noise during the performance of movement sequences with or without a substantial terminal component in depth. As in Apker et al. (2010), planning and execution noise were accentuated by randomizing target positions from trial to trial and by switching the final target position during movement, which required rapid, online changes in movement planning and execution. The switching of targets was performed in such a way that the resulting sequences of two reaches were either both chiefly contained within a frontal plane (“frontal sequences”) or involved an initial reach within the frontal plane and a second that was directed toward or away from the subject (“depth sequences”). In addition, on half of the trials movements were made without visual feedback of the hand, a manipulation designed to increase uncertainty in hand position estimation (Franklin et al. 2007). We hypothesized that variability would be more anisotropic and more strongly aligned with the depth axis when the dominant axes of execution noise and visual planning noise were more aligned, i.e., during depth sequences. We found that when visual feedback was available, patterns of endpoint variability were for the most part anisotropic, with the principal axes of variability being closely aligned with the depth axis regardless of sequence type (and therefore movement axis). In the absence of visual feedback, variability associated with depth sequences exhibited similar spatial characteristics while movements made primarily within the front plane were considerably more isotropic and were more strongly influenced by the primary axis of movement. These results confirm previous suggestions that anisotropically distributed visual planning noise plays a dominant role in determining patterns of arm movement variability in 3-D space. In addition, the findings suggest that in the absence of vision, increased uncertainty in hand position estimation results in patterns of endpoint variability that are more influenced by execution noise than those with visual feedback.

METHODS

Subjects. Ten (10) subjects (3 women and 7 men) between the ages of 21 and 27 were recruited to perform the experiment. The experiment complied with and was approved by the Arizona State University Institutional Review Board before subject recruitment and data collection. All subjects read and signed an Institutional Review Board approved informed consent form before participating. 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.

Apparatus. An experimental apparatus was constructed to allow control of task parameters during 3-D movements; the arrangement of the different components of this setup is illustrated in Fig. 1A. A large, standing frame supported a stereoscopic 3-D monitor (Dimension Technologies, Rochester, NY) that projected images onto a mirror that was visible to the subjects. The mirror was embedded within a metal shield, which was oriented at a 45° angle with respect to the monitor. This shield also served to block the arm from view. During the experiment, subjects were seated with their head positioned on a chin rest. A large, overhead display mirror was used to allow subjects to view their own hands reaching to targets in the 3-D space. The experimental set-up was controlled by a computer running custom software written in Visual Basic for Applications (Microsoft Office 2007). The software controlled the generation of target positions, movement sequences, generation of auditory feedback, and data collection. All subjects read and signed an Institutional Review Board approved informed consent form before participating. 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.

Fig. 1. Experimental apparatus and target layout. A: experimental apparatus. B: frontal and sagittal plane views of the 4 potential movement sequences associated with T1 up. The second movement in the sequence was directed to 1 of 4 secondary targets located clockwise (T2 cw), counterclockwise (T2 ccw), inward (T2 in), or outward (T2 out) from its associated T1. C: frontal and horizontal plane views of the 4 potential movement sequences associated with T1 right.

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chinnest in such a way that the eyes were aligned with the center of the mirror.

**Motion tracking.** An active-LED-based motion tracking system was used to track movements of the fingertip (Visualeyz VZ-3000 motion tracker; Phoenix Technologies, Burnaby, British Columbia; 150-Hz sampling rate; 0.5-mm spatial resolution). During the experiment, a single LED was positioned on the subject’s fingertip and its position was fed back to the subject in near real-time via a virtual reality environment developed in Vizard (WorldViz, Santa Barbara, CA). Fingertip position, target positions, and the starting position were displayed on the 3-D monitor as green spheres and were ~5 cm in diameter when presented in the vertical plane defined by the starting position and T1 target positions. To aid in depth perception, a wireframe cube was also rendered in the virtual environment. The cube was centered on the starting position but was large enough that all of the targets and movements were completely contained within it.

An examination of the efficacy of the depth cues in our environment indicated that subjects can perceive depth with an accuracy and precision similar to that exhibited by subjects in real environments (Viguié et al. 2001) over the range of target depths used in this study.

**Experimental design.** The task was to execute a sequence of two reaches to targets that were arranged on the surface of an 18-cm diameter sphere centered on a single starting position. There were four primary targets (T1) located along the x (lateral) and y (vertical) axes cutting through the center of the sphere. Each T1 was associated with four potential secondary targets (T2) located 45° clockwise, counterclockwise, closer in depth (inward), or further in depth (outward) from a given T1 and at a straight-line distance of ~6.4 cm (see Fig. 1, B and C). As a result of this target arrangement, the second movement in a sequence was either largely contained with the same frontal plane as the first movement (in the case of clockwise/counterclockwise movements) or had a large component parallel to the depth axis (for inward/outward movements). This allowed a more comprehensive examination of the interactions between execution noise and planning noise than was previously attempted (Apker et al. 2010). Movement sequences were performed either with visual feedback of fingertip position throughout the movement [visual (V) condition] or without visual feedback [nonvisual (NV) condition].

Individual trials began with the illumination of the starting position, which cued the subjects to visually align their fingertip with this position (visual feedback was always present during this epoch). After holding for 350 ms within a 4-cm window centered on the starting position, a T1 would be illuminated, cueing the first movement. Coincident with the fingertip leaving the start position window, T1 would disappear and an adjacent T2 would appear cueing the second movement. Note that the size of the start position window was chosen such that this target jump occurred very close to peak hand velocity to T1, which was designed to obviate saccadic suppression. On V trials, vision of the fingertip was available throughout the movement. On NV trials however, coincident with the appearance of T1, visual feedback [nonvisual (NV) condition] or had a large component parallel to the depth axis (for inward/outward movements). This allowed a more comprehensive examination of the interactions between execution noise and planning noise than was previously attempted (Apker et al. 2010). Movement sequences were performed either with visual feedback of fingertip position throughout the movement [visual (V) condition] or without visual feedback [nonvisual (NV) condition].

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Subjects had no knowledge of the trial parameters before trial onset and were instructed to move as quickly and accurately as possible to the presented targets. Subjects were also instructed to avoid adjusting their fingertip position at the end of a sequence. These aspects of the experiment design were incorporated to accentuate planning- and execution-related noise processes rather than to minimize them (as in some previous studies), thereby facilitating a characterization of their interaction. Trials were considered successful if the subject moved to the target quickly and remained within an acceptable window around the target (5-cm radius along each axis) for 350 ms. Knowledge of results was provided in terms of an auditory tone that signaled that subjects were successful but this information could not be used to further adjust endpoint position. When the endpoints did not fall within this window, the trial was aborted and repeated later during the session. If a subject was having repeated difficulty acquiring a particular target, the 5-cm window was temporarily enlarged for that target so that the requisite number of trials could be completed. The decision to increase the window radius in these limited cases was based on concerns that the length of the experimental session would lead to increased difficulty in elevating the limb off of the table and that this fatigue would affect performance on subsequent trials. Only position data for successful trials were retained for analysis.

**Data analysis.** Movements were first sorted according to subject, feedback condition, and target sequence (i.e., combination of T1 and T2). Movement data were then smoothed offline using a digital low-pass filter (5-point moving average), and the instantaneous tangential velocity was calculated by differentiating the position data along the movement path. Movement endpoints were identified as the point at which the tangential movement velocity fell below 5% of its peak value for movements to T2. In a limited number of instances, recorded movement endpoints were allowed to fall outside of the 5-cm target window during data acquisition, in order for subjects to complete a full set of trials to each target location. However, these trials were excluded from analysis and only accounted to a very small fraction of total trials (26/4,800 trials; 0.5%).

To assess movement accuracy, constant errors were calculated by subtracting the known T2 target position from the measured endpoint of the hand. However, since constant errors tend to be idiosyncratic (Berkinblit et al. 1995; Darling and Miller 1993; Foley and Held 1972; Soechting and Flanders 1989), we did not explore their nature in detail here. Instead, analysis focused on the variable errors, which provide more direct information about planning- and execution-related noise (McIntyre et al. 1998; Carrozzo et al. 1999; van Beers et al. 2004). Variable errors associated with a given axis and T2 position (σi) were calculated as follows:

\[
\sigma_i = \frac{1}{n_i} \sqrt{\sum_{t=1}^{n_i} (h_i - \bar{h}_i)^2}
\]

where \(h_i\) represents the mean endpoint position for a given T2 position \(t\), \(\bar{h}_i\) represents the corresponding endpoint position on trial \(i\), and \(n_i\) represents the number of trials.

Principal component analysis (PCA) was also used to analyze the endpoint distributions associated with frontal and depth sequences. The 95% tolerance ellipsoids associated with each endpoint distribution were first computed as follows (McIntyre et al. 1998; Morrison 1990):

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

where the dimensionality \(q = 3\), the number of target positions \(k = 1\), and \(H\) is the covariance matrix. The resulting eigenvalues and eigenvectors (obtained from the matrix \(T\)) were used to quantify the sizes, shapes and orientations of the endpoint distributions (see below). For visualization purposes, 95% confidence ellipses and ellipsoids were calculated using Matlab code based on the Khachiyan algorithm (Khachiyan 1996; Khachiyan and Todd 1993), as implemented by Nima Moshtag.

Endpoint distributions associated with frontal and depth sequences were compared by analyzing differences in the sizes, shapes, and orientations of their corresponding tolerance ellipsoids. The size of each ellipsoid was quantified by its volume (V):

\[
V = \frac{4}{3} \pi abc
\]

where \(a\) represents the radius of the major axis of the 95% confidence ellipsoid and \(b\) and \(c\) represent the radii of the minor axes. The aspect ratio was used to characterize the shape of each ellipsoid, defined as...
the ratio of the radius of the major axis of the ellipsoid to the sum of the radii of the minor axes. Lastly, the general orientation of each ellipsoid was defined by the absolute values of the components of the first eigenvector derived from the PCA (Carrozzo et al. 1999; McIntyre et al. 1997, 1998).

Statistical analyses. To determine whether the distributions derived from PCA were isotropic or anisotropic a $\chi^2$ test of the form used by Morrison (1990) and McIntyre et al. (1997) was used, which determined whether any two eigenvalues were significantly different from each other. The nonparametric Mann-Whitney $U$-test was used to test whether individual components (lateral, vertical, or depth) of the first eigenvectors differed between endpoint distributions. Lastly, ellipsoid volumes and ellipsoid aspect ratios associated with frontal and depth sequences were compared using two-way ANOVAs with factors “sequence type” (frontal vs. depth) and “T1 location.” The latter factor was chosen to assess any differences that may have arisen due to differences in the initial and final movement directions in a sequence. The significance level for all statistical tests used in this study was $\alpha = 0.05$.

RESULTS

Variable errors with visual feedback. Figure 2 illustrates average movement paths and individual movement endpoints for the four sequences associated with each T1. Ellipses represent two-dimensional projections of the 95% confidence ellipsoids calculated for each endpoint distribution. Data from a single subject are shown and are viewed from the bottom up for T1$_{up}$ and T1$_{down}$ and from the subject’s left for T1$_{left}$ and T1$_{right}$. These plots show that, although endpoint distributions appeared to vary somewhat in size and shape for the different sequences, these distributions were generally anisotropic in the V condition. In addition, for many of the distributions, the largest component of variability appeared to be aligned with the depth axis. This is most evident for the distributions associated with inward and outward sequences (red), where the average movement paths were also largely parallel to the depth axis. However, this trend can also be observed for some of the distributions associated with clockwise and counterclockwise sequences (black), most notably those associated with T1$_{up}$. This is despite the fact that the average movement paths for these frontal plane sequences were roughly orthogonal to the depth axis. These trends were consistent across subjects in the V condition; across the population, variable errors were largest along the depth axis for 99% of the inward/outward sequences (79/80) and 95% of the clockwise/counterclockwise sequences (77/80).

The tendency for movement variability to be particularly large along the depth axis can be best appreciated from the orientations of the first eigenvectors derived from PCA. Figure 3 shows the size of each component of these eigenvectors for each type of movement sequence, grouped by T1. Data for a single subject are shown (the same subject shown in Fig. 2). The proportion of variance accounted for by the first eigenvector (indicated by the numbers at the top left of each plot) was typically large for this subject and was also reasonably consistent across the different types of movement sequences (means: 74 ± 15%). Although the variance accounted for was often higher for inward/outward sequences for this subject, this was not a consistent finding across the population (see below). Figure 3 also illustrates that the orientations of these eigenvectors were very consistent. That is, these vectors generally had their largest components along the depth axis for both the clockwise and counterclockwise sequences as well as for the inward and outward sequences. The lone exception to this observation is the counterclockwise sequence associated with T1$_{down}$ which had its largest component along the lateral axis. The fact that the clockwise and counterclockwise sequences typically had...
their largest components of movement variability along the depth axis might seem surprising as by design these sequences did not require significant movement components in depth. However, this observation is consistent with the findings of Apker et al. (2010), which were obtained under similar conditions. Moreover, these investigators showed that this trend was not related to the orientation of the terminal components of the average, executed movements in the frontal plane, which were largely orthogonal to the depth axis in that study and the present one (see Fig. 2).

The main findings illustrated in Fig. 3 were also observed at the population level. Figure 4 shows the average size of the components of the first eigenvectors associated with each type of endpoint distribution. As with the single subject shown in Fig. 3, the average proportion of variance accounted for by the first eigenvector was generally large and very consistent across subjects and sequence types (mean: 77 ± 4%), consistent with other studies of endpoint variability in 3-D space (Apker et al. 2010; McIntyre et al. 1997, 1998). In contrast to the single subject data, there was little difference between the average amount of variance accounted for by the eigenvectors for the clockwise/counterclockwise sequences and the eigenvectors for the inward/outward sequences (78 and 76%, respectively). Figure 4 also clearly shows that at the population level the first eigenvectors were strongly biased along the depth axis: looking across all sequence types, the mean component of the eigenvector along this axis was never <0.8. Interestingly, even though the clockwise and counterclockwise sequences (and likewise the inward and outward sequences) were directed along axes that differed somewhat in orientation (due to the fact that targets were on the surface of a sphere), the average components of their associated eigenvectors were typically very similar. This was confirmed statistically as well: no statistically significant differences were found between the magnitudes of the individual eigenvector components associated with clockwise and counterclockwise sequences (P > 0.05, Mann-Whitney U-test conducted separately on the lateral, vertical, and depth axes). Similarly, no differences were found between the magnitudes of the individual eigenvector components associated with inward and outward sequences (P > 0.05, by Mann-Whitney U-test).

Size, shape, and orientation of endpoint distributions with visual feedback. Given previous findings (Apker et al. 2010), we hypothesized that in the V condition endpoint distributions associated with depth-directed movements (i.e., inward/outward sequences) would be more anisotropic and more strongly aligned with the depth axis than endpoint ellipsoids associated with frontal plane movements (clockwise/counterclockwise sequences). Instead, our analysis of the first eigenvectors associated with individual endpoint distributions suggested that the orientations of these distributions were very similar at the population level. To further examine the similarities and differences between the different types of sequences, we also compared their endpoint distributions in terms of their sizes (volumes) and shapes (aspect ratios), which take into account variability along axes other than those defined by the first eigenvector. Since the first eigenvectors for counterclockwise and clockwise sequences were statistically indistinguishable from each other at the population level for each T1 (see above), we combined the distributions corresponding to these sequences together for this analysis and refer to the combined error distributions as frontal sequences. Similarly, distributions for the inward/outward sequences (which were also statistically indistinguishable from each other at the population level) were grouped together for this analysis and are referred to as depth sequences.

Figure 5A shows a horizontal plane view of the population ellipsoids and first eigenvectors for the frontal and depth
sequences associated with each T1. The main axes of the ellipsoids, as well as the first eigenvectors, appear to be strongly aligned with the depth axis, as would be expected given the results shown in Figs. 2–4. In addition, the ellipsoids appear fairly consistent in size (volume) and shape across the different T1s and types of sequences. To further illustrate the consistency in volumes, Fig. 5B plots the average ellipsoid volumes associated with frontal and depth directed sequences for the population, grouped by the different T1s. This figure shows that ellipsoid volumes were typically small in the V condition, averaging between 15 and 20 cm$^3$ (approximately equivalent to the volume of a golf ball). Ellipsoid volumes were also generally consistent across the different T1s and between sequence types. At the population level we found no statistically significant effects of T1 location, sequence type (depth vs. frontal), or their interaction on ellipsoid volume ($P = 0.71$, $P = 0.35$, and $P = 0.75$, respectively, by two-factor ANOVA). Thus for the most part 3-D endpoint distributions associated with frontal and depth sequences did not appear to differ in size (volume) when vision of the hand was available throughout movement.

Endpoint distributions associated with frontal and depth sequences were also similar when analyzed in terms of their shapes. Figure 5C shows the aspect ratios of the ellipsoids associated with frontal and depth-directed sequences, grouped by T1. These aspect ratios reveal that, on average, variability along the first eigenvector (which is proportional to the length of the longest radius of the ellipsoid) was $\sim 1.5$ times greater than that along the other eigenvectors for both types of sequences. Similar to the analysis of ellipsoid volume, Fig. 5C also shows that the shapes of the ellipsoids were similar between frontal and depth-directed sequences and across the different T1s. This was confirmed statistically as well: here again we found no statistically significant main or interaction effects of T1 location or sequence type on ellipsoid aspect ratio ($P = 0.51$, $P = 0.91$, and $P = 0.42$, respectively, by two-factor ANOVA). We conclude therefore that the shapes of the endpoint ellipsoids also did not vary in a consistent manner between frontal and depth sequences in the V condition.

The similarities in ellipsoid volumes and shapes extended to the ellipsoid orientations. Figure 5D shows the average components of the first eigenvectors of the endpoint distributions associated with frontal and depth sequences, grouped by T1. This figure strongly suggests that both types of sequences had their largest components along the depth axis in agreement with the analyses shown in Figs. 3 and 4. This was in fact the case; depth components of the first eigenvectors were significantly different from both the lateral or vertical components for both the frontal and depth sequences ($P < 0.05$, by Mann-Whitney U-test). Some small but significant differences were observed between components for some axes ($P < 0.05$, by Mann-Whitney U-test). For example, lateral components were somewhat larger for the frontal sequences for T1$\text{up}$ and T1$\text{down}$, while for T1$\text{right}$ the opposite trend was observed (there was no difference in these components for T1$\text{left}$). These differences likely reflect the influence of execution noise, a point we will return to later. Overall, however, Fig. 5 and its associated statistical analyses strongly suggest that in the presence of visual feedback, endpoint distributions associated with frontal and depth-directed movement sequences did not appear to differ substantially in size, shape, and orientation. In addition, the results suggest that for both sequence types, variability was predominantly anisotropic and strongly aligned with the axis along which uncertainty associated with planning and updating visually guided movements would be expected to dominate, i.e., along the depth axis.

**Variable errors without visual feedback.** As in Fig. 2, Fig. 6 shows average movement paths, individual movement end-
points, and confidence ellipses for the four endpoint distributions associated with each T1. Data from a single subject in the NV condition are shown. As expected, endpoint distributions were often larger in this condition, which likely resulted from the increased uncertainty associated with estimating the position of the hand in the absence of visual feedback. In comparison to the V condition, variable errors in the NV condition appeared to be somewhat less anisotropic and the nature of this anisotropy also appeared to differ among the different types of sequences. That is, although the variability associated with depth-directed sequences (red) still appeared to have a very large component along the depth axis, this was less consistently observed for the frontal sequences (black). In Fig. 6, these observations are most evident for sequences associated with T1_{down} and T1_{right}. Here the distributions for the inward/outward sequences appear anisotropic and aligned with the depth axis, while the distributions for the clockwise and counterclockwise sequences appear either isotropic or do not appear to be aligned with the depth axis.

Figure 7 shows the average first eigenvectors associated with each type of endpoint distribution in the NV condition, grouped by T1. There are noticeable differences between these eigenvectors and those in the V condition. First, the proportion of variance accounted for by the first eigenvector was typically smaller in this condition (mean: 66 ± 5%) and was somewhat smaller for the frontal sequences than for the depth-directed sequences (61 vs. 72%), a finding that was not observed in the V condition. These observations suggest that the endpoint distributions were in fact more isotropic in this condition, particularly those associated with frontal sequences, as was also suggested by Fig. 6. Regarding the components of the eigenvectors, for virtually all sequence types the average magnitudes of the lateral, vertical, and depth components were more similar in this condition than in the V condition. For example, although the eigenvectors for the clockwise and counterclockwise sequences associated with T1_{right} and T1_{left} showed a slight tendency toward having larger components in depth, this was not the case for T1_{up} and T1_{down}. In fact for T1_{down}, these components were relatively uniform in magnitude for both the counterclockwise and clockwise sequences. Thus there was not a consistent pattern of variability between sequence types in the NV condition, unlike what was observed in the V condition.

Fig. 5. Analysis of endpoint ellipsoids associated with frontal and depth sequences in the V condition. A: horizontal plane views of the ellipsoids and first eigenvectors associated with each T1. All ellipsoids are plotted on the same scale. Coordinate axes at the bottom left also serve as scale bars (2 cm). B: ellipsoid volumes (sizes), for frontal and depth sequences associated with each T1. C: aspect ratios of the endpoint ellipsoids (shapes) for frontal and depth sequences associated with each T1. D: average absolute values of the axial components of the first eigenvectors (orientations) associated with each T1. In general, volumes, aspect ratios, and ellipsoid orientations did not vary substantially between frontal and depth sequences in the V condition.
Figure 7 shows that the inward/outward sequences did tend to have their largest components along the depth axis, as was observed in the V condition. However, the lateral and vertical components were relatively larger in this condition than in the V condition, suggesting the endpoint distributions were not as well aligned with the depth axis in the absence of hand vision. Overall, Figs. 6 and 7 suggest that movement variability in the NV condition, rather than being dominated by visual planning noise, more strongly reflected the effects of execution noise and/or an interaction between execution noise and visual planning noise. This appeared to be particularly true for the movement sequences performed in the frontal plane where the endpoint distributions were more isotropic and apparently less clearly aligned with the depth axis.
Size, shape, and orientation of endpoint ellipsoids without visual feedback. As was the case in the V condition, the first eigenvectors for counterclockwise and clockwise sequences at each T1 in the NV condition were statistically indistinguishable from each other at the population level (\( P > 0.05 \), by Mann-Whitney U-test applied along each axis). This was also true for the inward/outward sequences in the NV condition. As a result, we again grouped the data together for the clockwise and counterclockwise sequences at each T1 (frontal sequences) and also grouped the data together for inward and outward sequences (depth sequences). Figure 8A shows a horizontal plane view of the resulting population ellipsoids and first eigenvectors for the frontal and depth sequences associated with each T1. In contrast to the ellipsoids in the V condition, these appeared to differ somewhat in size and shape between sequence types (e.g., for T1\text{up} and T1\text{down}). The most striking difference, however, was with regard to the orientations of the ellipsoids. Although the ellipsoids and eigenvectors for the depth sequences were strongly aligned with the depth axis (as in the V condition), this was not the case for the frontal sequences. For T1\text{up} and T1\text{down}, these appeared to be oriented largely laterally, reflecting the fact that the clockwise and counterclockwise sequences associated with these T1s had large lateral components of movement. For T1\text{right} and T1\text{left}, the eigenvectors and ellipsoids appear to be rotated out of the horizontal plane to some degree, consistent with the fact that the clockwise and counterclockwise targets associated with these T1s had large vertical components of movement.

As in the V condition, we quantified the sizes, shapes, and orientations of the endpoint ellipsoids associated with the frontal and depth sequences in the NV condition and compared them. Figure 8B shows the average ellipsoid volumes. Ellipsoid volumes were generally much larger in the NV condition than in the V condition, averaging between 50 and 100 cm\(^3\). Figure 8A suggested that the ellipsoid volumes for the frontal sequences were larger than those for the depth sequences, particularly for T1\text{up} and T1\text{down}. Although some slight differences in the average ellipsoid volumes can be observed both across T1s and between sequence types in Fig. 8B, ellipsoid volumes tended to be quite variable across subjects. As a result, these differences were not statistically significant at the population level (\( P = 0.68, P = 0.31, \) and \( P = 0.35 \), by two-factor ANOVA, for main effects of T1, main effects of sequence type, and interaction effects, respectively). Thus similar to the V condition, endpoint distributions associated with frontal and depth sequences did not differ significantly in volume in the NV condition.

Figure 8C shows the average aspect ratios of the endpoint ellipsoids in the NV condition, grouped again by T1 and sequence type. Some similarities and some differences can be
observed between the results of this analysis and the analogous one shown in Fig. 5. In terms of similarities, aspect ratios were generally consistent in magnitude across the different T1s, as they were in the V condition. However, aspect ratios were somewhat smaller under NV conditions, averaging between 1 and 1.25. (In contrast, the average aspect ratio in the V condition was ~1.5.) This again suggests that endpoint variability was more isotropic without hand vision than with hand vision, as was also suggested by Figs. 6 and 7. Another difference between the V and NV conditions was the tendency for aspect ratios to be somewhat larger for depth sequences than for frontal sequences in the NV condition. In Fig. 8C, this can be observed for nearly all the T1s (the exception being T1right) and is consistent with Fig. 7, which indicated that the proportion of variance accounted for by the first eigenvector was typically less for the frontal movement sequences than for the depth sequences. When examined statistically, although no significant main effect of T1 location on aspect ratio was found, a significant main effect of sequence type (frontal vs. depth) was identified (P = 0.66 and P = 0.04, respectively, by two-factor ANOVA; P = 0.22 for interaction effects). Post hoc tests (Tukey’s honestly significant difference) indicated that this difference arose largely due to differences associated with T1down although again Fig. 8C suggests that aspect ratios for most of the other T1s were trending in that direction. Overall, these results suggest that in the NV condition, depth sequences were associated with slightly more elongated endpoint distributions than those associated with frontal sequences and that both types of sequences were less elongated than those in the V condition.

Substantial differences were observed between the orientations of the endpoint distributions in the NV condition. Figure 8D shows the average components of the first eigenvectors derived from PCA for the frontal and depth sequences, grouped by T1. This figure suggests that depth sequences had their largest components of variability directed along the depth axis, as in the V condition. Statistical analyses confirmed that the depth components of the first eigenvectors differed from both the lateral or vertical components for all of the T1s (P < 0.05, by Mann-Whitney U-test). However, this was not the case for the frontal sequences: only for T1right was the depth component significantly different from both the lateral and vertical components.

Not surprisingly then there were differences between the two sequence types along certain axes, and, moreover, these differences were larger than those in the V condition and more consistent in nature. For example, lateral components were larger for the frontal sequences for T1up and T1down and vertical components for the frontal sequences were larger for T1right and T1left (P < 0.05, by Mann-Whitney U-test). These differences were consistent with differences in the required movement axes used to approach the final target positions. That is, for frontal sequences, T1up and T1down were associated with large lateral terminal components of movement while those for T1right and T1left were associated with large vertical components. In contrast, depth sequences were not generally associated with either large lateral or vertical terminal movement components. Therefore, we conclude that in the absence of visual feedback, endpoint distributions differed in orientation (and to a lesser degree shape) between frontal sequences and depth sequences. These differences in orientation appear to reflect differences in the directions of the movement vectors used to approach the final target positions, suggesting an enhanced role for execution noise in determining patterns of endpoint variability when vision of the hand is unavailable.

Comparisons between feedback conditions yielded results that were similar in many ways to those described in Apker et al. (2010) but with several important additional findings. That is, a t-test performed on the combined data for all T1s found that endpoint distributions (ellipsoid volumes) in the NV condition were larger than their V condition counterparts for both sequence types (P < 0.05). In addition, aspect ratios of ellipsoids in the V condition were significantly larger than those in the NV condition for both sequence types (P < 0.05). These results were similar to those described in Apker et al. (2010). Regarding differences in orientation, the orientation of the ellipsoids of depth sequences was generally similar between feedback conditions. That is, of the 12 comparisons made between axial components of the eigenvectors across all T1s, only 1 difference (8%) was found between feedback conditions. In contrast, for frontal sequence ellipsoids, 9/12 components (75%) differed significantly between the V and NV conditions across all T1 location, including significantly differing depth components for each T1 location (P < 0.05, by Mann-Whitney U-test). As a result, ellipsoids in the NV condition were more strongly biased along the lateral and/or vertical axes, consistent with a greater effect of the movement vector on these endpoint distributions.

Start-position corrected endpoint analysis. Variability in finger position at the starting position was analyzed to ensure that differences in endpoint variability did not arise from differences in variability at the starting position between frontal and depth sequences. A Levene’s test confirmed that variability in the starting position was not significantly different along any axis between the frontal or depth sequences associated with a given T1; this was the case for both feedback conditions (P > 0.05). As an added measure, we also reran our statistical analyses using start-position-corrected endpoint positions. The results of only 2/32 (6%) of our statistical tests differed following this correction: Differences in the first eigenvector components along the horizontal and depth axes for T1right in the V condition, which were previously shown to be statistically significant, were not significant following correction. Importantly, these exceptions do not alter the conclusions of this study; in fact they strengthen the conclusion that frontal and depth sequences were similar in the vision condition.

DISCUSSION
In this experiment, we quantified patterns of endpoint variability associated with movement sequences performed in the frontal plane and compared these patterns to those associated with sequences containing a large movement component in depth. For both types of sequences, movements were performed with and without vision of the hand. We hypothesized that for both visual conditions endpoint distributions would be more elongated and more aligned with the depth axis for sequences containing large movement components in depth. We found that when visual feedback of the hand was available, patterns of variability at the endpoint of both sequence types were highly anisotropic, with the primary axis of variability...
being strongly aligned with the depth axis, suggesting that
the executed movement direction (and therefore execution
noise) played only a minor role in shaping endpoint distri-
butions in this condition. However, when visual feedback of
the hand was not available, patterns of endpoint variability
differed significantly for the two types of sequences. More
specifically, while endpoint distributions associated with
depth sequences were very similar to those observed with
visual feedback of the hand, endpoint distributions for fron-
tal sequences were more isotropic and not generally well
aligned with the depth axis. These results emphasize the
primacy of visual planning noise in determining patterns of
endpoint variability in 3-D space and also suggest that the
removal of visual feedback (and resulting increased uncer-
tainty in estimating hand position) effectively unmasks the
effects of execution-related noise (and planning noise as
well) leading to patterns of variability that can differ sub-
stantially for movements performed along different axes in
3-D space.

Relation to previous findings. Although previous studies
have examined the relations between movement variability and
sensing noise (Osborne et al. 2005; Shi and Buneo 2009; van
den Dobbelsteen et al. 2001; Vindras et al. 1998), planning
noise (Churchland et al. 2006a; Gordon et al. 1994; McIntyre
et al. 1997, 1998; Vindras and Viviani 1998), and execution
noise (Buneo et al. 1995; van Beers et al. 2004), the relative
importance of these noise sources in determining patterns of
arm movement variability in 3-D space remains a matter of
debate. For planar (2-D) arm movements, it has been argued
that movement variability is dominated by noise associated
with execution (van Beers et al. 2004). In a previous study
of 3-D arm movement sequences performed in the frontal plane
(Apker et al. 2010), we argued that patterns of arm movement
variability were largely determined by visually derived noise
associated with planning movements in depth. That is, end-
point distributions were aligned with the depth axis and were
only minimally influenced by the executed movement direc-
tions, suggesting a lesser role for execution noise. However,
the fact that movement directions were predominantly orthog-
onal to the dominant axis of visual planning noise in this study
made it difficult to distinguish the effects of execution noise
from uncertainty in hand position, as each would be expected
to manifest in roughly similar ways for these types of
sequences.

The findings of Apker et al. (2010) were reminiscent of
those of McIntyre et al. (1997, 1998), who also demonstrated
that for point to point reaches initiated from starting positions
near the body to targets further away in depth, endpoint
distributions were highly anisotropic and strongly aligned with
the depth axis. In these studies, the primary axis of variability
evolved toward the sight line for movements performed in
different workspaces with respect to the body, providing
strong evidence that these patterns of variability arose from
noise associated with visual estimation of the hand and/or
target. The present findings for the V condition, and for the
depth sequences in the NV condition, are consistent with the
findings of both Apker et al. (2010) and McIntyre et al. (1997,
1998). However, the observation that endpoint distributions
for frontal sequences were strongly influenced by the primary axes
of movement in the NV condition suggests that execution noise
can play a more significant role in determining patterns of
endpoint variability when visual feedback of the hand is
unavailable (Gordon et al. 1994; van Beers et al. 2004).

To ascertain the specific role of hand vision in determining
patterns of variability in 3-D space, Carrozzo et al. (1999)
analyzed movement endpoints as human subjects made reach-
ing movements with and without vision of the hand but with
full vision of the target. These investigators observed that patterns of endpoint
variability in the presence of hand vision were consistent with
those reported here for the V condition, i.e., they were highly
anisotropic and strongly aligned along the depth axis. In the
absence of hand vision, patterns of variability were more
isotropic and less aligned with the depth axis, consistent with
the NV endpoint distributions for the frontal sequences in the
present study but not with those for the depth sequences.
These observations can be explained by certain methodological dif-
ferences between the two studies. In the study of Carrozzo et
al. (1999), movements were similar to the frontal sequences in
the present study in that final target positions were approached
largely using varying degrees of vertical and lateral move-
ments. It is not surprising therefore that the endpoint distribu-
tions in the two studies had some similar properties. In Car-
rozzo et al. (1999), movements also had components in depth,
but these were very different from the depth-directed se-
quences used here. In the present study, subjects were required
to pass through (or near) an intermediate target that was at the
same lateral and vertical position on the way to the final target.
As a result, final target positions were approached using
movements with much larger depth components than those in
Carrozzo et al. (1999), which likely explains why the depth-
directed sequences were more aligned with the depth axis in
the present study.

Interaction between planning and execution noise. Since
movement directions were designed to be orthogonal to the
depth axis in Apker et al. (2010), it was unclear if the inter-
action of execution and planning noise would manifest in a
similar way for movement sequences that were directed along
the depth axis. Given our previous results, as well as those of
McIntyre et al. (1997, 1998), we hypothesized here that end-
point distributions would be more anisotropic and more aligned
with the depth axis under these conditions, reflecting the fact
that the dominant axes of execution noise and visual planning
noise were aligned. In fact when visual feedback was present,
endpoint distributions associated with both frontal plane and
depth-directed sequences were anisotropic and aligned pre-
donominantly with the depth axis and did not differ in terms of
their overall sizes (volume), shapes or orientations. Thus, even
when execution noise was directed along the depth axis, it did
not appear to significantly alter overall patterns of movement
variability. This supports the idea that uncertainty associated
with planning and updating visually guided movements plays a
dominant role in determining patterns of endpoint variability in
3-D space.

While the effect of execution noise was only minimally
apparent in the V condition, its effect could be easily observed
in the NV condition, particularly during the performance of
frontal plane movement sequences. Endpoint distributions
appeared relatively isotropic for frontal plane movement se-
quences in the NV condition and were also not well aligned
with the depth axis, appearing to be more strongly influenced
by the primary axes of movement. Note that this also appeared
to be the case in Apker et al. (2010), although due to the fact that only frontal plane movement sequences were used in that study, we were unable to fully explain these patterns. In contrast, endpoint distributions for depth sequences in the NV condition more closely resembled those in the V condition, being largely anisotropic and oriented in depth. Based on these differences, we believe that patterns of endpoint variability in the absence of online visual feedback results from increased uncertainty in estimating the position of the hand, which effectively unmasks the effects of execution-related noise and planning noise.

The removal of visual feedback would be expected to result in greater uncertainty in estimating hand position, as estimates that depend only on a single sense (proprioception in this case) are generally less precise than those derived through multisensory integration (van Beers et al. 2002a). This increased uncertainty would be expected to have two effects. First, movement planning would be adversely affected, resulting in errors in planned movement directions and extents (Buneo et al. 1995; Franklin et al. 2007; Shi and Buneo 2009). These errors would be compounded by noise associated with visual estimation of the targets as well as central planning noise, with the resulting effects on behavior being difficult to predict. However, it is likely that variability would be increased along all axes leading to generally more isotropic distributions. Second, in the absence of online visual feedback increased hand position uncertainty near the end of the movements would be expected to effectively increase the influence of execution noise (by failing to mitigate it, as when vision is available), thereby elongating the endpoint distributions along the movement direction (van Beers et al. 2004). For frontal sequences, this would result in endpoint distributions that reflected a combination of enhanced execution noise and visual planning noise, which was observed in the present study (see Fig. 8D). For depth sequences, this interaction would be less apparent, as the executed movement directions were not orthogonal to but aligned with the primary axis of visual planning noise. Even so, the observation that ellipsoids were larger and less elongated under these conditions is consistent with effectively increased levels of both planning and execution noise during performance of these sequences.

Given that endpoint distributions of 3-D movements are highly dependent on planning noise, it would be interesting to know if this endpoint variability arises due to planning noise at the beginning of movement or is more related to uncertainty towards the end. Execution noise is most evident in the terminal phases of movement (van Beers et al. 2004); it may also be the case therefore that the influence of planning noise largely reflects feedback conditions nearer the end of movement. This could be tested by removing visual feedback at various times throughout the movement. Conversely, it would also be of interest to observe the effect of returning visual feedback at various points in the terminal movement. Recently, Faisal and Wolpert (2009) demonstrated that temporal characteristics of sensory and execution noises integrate in a “near optimal” manner. Varying the timing and/or duration of visual feedback would help integrate this finding with the present results to develop a better sense of the spatiotemporal nature of the influence of planning and execution noises.

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DISCLOSURES

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AUTHOR CONTRIBUTIONS


REFERENCES


