Chapter 2

Endpoints of arm movements
to visual targets

Reaching out for objects with an unseen arm involves using both visual and kinaesthetic information. Neither visual nor kinaesthetic information is perfect. Each is subject to both constant and variable errors. To evaluate how such errors influence performance in natural goal-directed movements we asked subjects to align a real 5-cm cube, which they held in their hand but could not see, with a three-dimensional visual simulation of such a cube. The simulated cube was presented at one of four target locations at the corners of an imaginary tetrahedron. Subjects made successive, self-paced movements between these target locations. They could not see anything but the simulated cube throughout the experiment. Initial analysis of the spatial dispersion of movement endpoints demonstrated that the major source of errors under these conditions was visual. Further analysis of the relationship between variability of the starting positions and endpoints showed that the errors were primarily in judging the endpoint, rather than the direction or amplitude of the required movement vector. The findings support endpoint control of human goal-directed movements.

Introduction

In daily life we come across many tasks that require reaching to, manipulating and displacing objects. In spite of the apparent ease with which we perform these simple motor tasks, the control of such targeted movements is rather complex. Although this issue has received considerable attention in both psychophysical and neurophysiological studies (for a review, see Lacquaniti and Caminiti 1998) the principles for controlling the movements are still largely unknown. A simple movement could either be controlled in terms of the intended endpoint (position coding; Polit and Bizzi 1979), or in terms of the required displacement from the initial arm posture (vector coding; Desmurget et al. 1998, De Graaf et al. 1996, Bock and Eckmiller 1986). In both cases it has been suggested that the coding is in terms of distance and direction (Rosenbaum 1980, Georgopoulos 1991). The endpoints of movements are thought to be coded as either the target's distance and direction relative to the body (Flanders et al. 1992) or the distance and direction of the required movement of the hand (Gordon et al. 1994).

A number of different techniques have been used to investigate the way goal-directed movements are controlled. One approach is to characterise the endpoint distributions of repetitions of the same intended movements. Higher variability in the distance from the subject than in the orthogonal direction suggests that errors in the intended endpoint play an important role (Carrozzo et al. 1999, McIntyre et al. 1998, 1997, Berkinblit et al. 1995, Flanders et al. 1992, Soechting and Flanders 1989a, 1989b). Similarly, greater variability along the axis of movement than along the orthogonal axis suggests that errors in the intended displacement play an important role (Messier and Kalaska 1999, 1997, Vindras and Viviani 1998, Gordon et al. 1994). Other support for the notion that movements are programmed as the vectorial difference between the initial and final hand positions comes from studies that show that endpoint accuracy is affected by information about the initial hand position (Vindras et al. 1998, Desmurget et al. 1997b, Rossetti et al. 1995, 1994). Moreover, errors for sequential movements accumulate (Bock and Arnold 1993, Bock and Eckmiller 1986).

The analysis of movement endpoints is complicated by the fact that their distributions reflect a combination of localising the target and executing the movement. It relies on both visual and kinaesthetic localisation, each with its own anisotropies (Haggard et al. 2000, Van Beers et al. 1998). Moreover, the experimental procedures often involve removal of vision of the hand to avoid corrections based on simultaneous vision of the hand and the target (Bock 1986, Prablanc et al. 1986, 1979). Occluding the arm removes the information that could be used to keep vision and kinaesthesia

in register, allowing them to drift apart (Wann and Ibrahim 1992). In the present study we attempt to separate these influences.

We examine the dispersion of endpoints when the target, but not the hand, is visible throughout the movement. In the experiment, subjects positioned a real 5-cm cube, which they held in their hand but could not see, at the location of a three-dimensional simulation of such a cube. They made self-paced movements between different target locations in a manner that allowed us to separate movement direction from viewing direction and arm configuration. We addressed the question whether the nervous system uses the initial hand position to encode the intended final hand position. We used an analysis that enabled us to evaluate possible effects of drift.

Materials and Methods

Apparatus

Images were generated by a Silicon Graphics Onyx computer at a frame rate of 120 Hz. The images were displayed on a Sony 5000 ps 21" monitor (30.0 cm × 40.4 cm; 816 pixels × 612 pixels), located in front of and above the subjects' head, and viewed by way of a mirror (see figure 2.1). Subjects saw a three-dimensional rendition of a cube beneath the mirror. They also held a 2-cm-diameter rod attached to a 5-cm cube (total weight: 145 g) in their unseen hand underneath the mirror. They held the rod with their hand touching the cube. Monitor and mirror were tilted 12° to increase the available workspace. The rationale behind using a cube on a hand-held rod instead of a hand-held cube was to reduce the conflict with occlusion that would otherwise arise when subjects fail to see their hand and therefore interpret the visible cube as being in front of the hand. Using liquid crystal shutter spectacles (CrystalEyes 2, weight 140 g., StereoGraphics Corporation, California), alternate images were presented to the two eyes for binocular vision. Images were corrected for the curvature of the monitor screen. A newly calculated image was presented to each eye every 16.7 ms. Standard anti-aliasing techniques were used to achieve sub-pixel resolution.

Sets of active infrared markers were attached to four sides of the real cube and to the shutter spectacles. A movement analysis system (Optotrak 3010, Northern Digital Inc., Waterloo, Ontario) registered the positions of these markers to within 0.1 mm at a sample frequency of 200 Hz. To create images with the appropriate perspective, eye position was inferred from the positions of the markers on the shutter spectacles (by eye position we mean eye position in space, not eye orientation in the orbit). This allowed the subject to move his head without introducing conflicts with information from motion parallax. The total delay between a movement of the subject's head and the presentation of the appropriate image was about 16 msec.
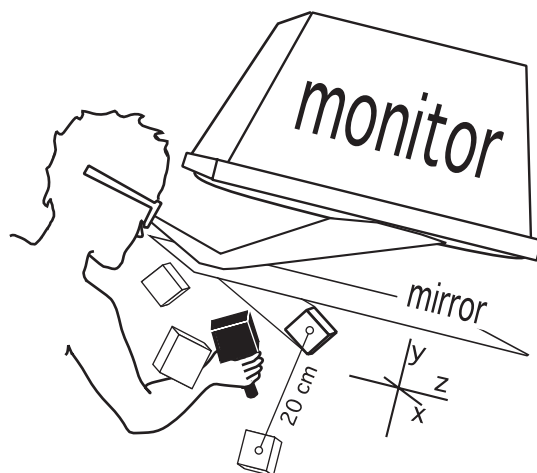
Figure 2.1 *Schematic view of the setup. Subjects stood in front of a monitor holding a cube attached to a rod. The only thing they could see was a three-dimensional rendition of the cube in one of four target locations. They were asked to align the position and orientation of the real cube with the position and orientation of the simulated cube.*

Stimuli

The simulated cube was presented in one of four positions beneath the mirror. These four positions were at the corners of an imaginary tetrahedron (each position was 20 cm from all others). Because the subjects were free to move their head, the distance from eye to target varied across subjects and movements. The overall average distance from eye to target was 44 cm. All target positions were well within reaching distance: the range was 33 to 62 cm. The orientation of the simulated cube was randomised. The luminance of each randomly textured, Lambertian surface of the simulated cube depended on the orientation relative to a virtual light-source above and to the left of the subject. There was also a virtual diffuse illumination to ensure that all surfaces facing the subject were visible. The virtual image of the cube was red because the liquid crystal shutter spectacles have least cross talk at long wavelengths. During the experiment the room was dark, so that subjects were unable to see anything but the virtual cube.

Subjects

Eight subjects participated in the experiment, including two of the authors. The local ethics committee approved the use of human subjects for this study. One subject used bifocal spectacles and responded overtly differently to the targets that were presented in his lower visual field. Therefore, this subject was excluded from the analysis. One subject used his left hand. Biases in the proprioceptively perceived position of the hand are known to be mirror symmetric for the left and right arm (Haggard et al. 2000). We thus mirrored the hand and head position data of the left-handed subject

in the off-line analysis. There were no evident differences between the data of the left-handed subject, the authors and the other subjects.

Procedure
Subjects were given the cube attached to the rod and asked to hold the rod with their hand touching the cube, so that they could feel the location and orientation of the real cube. They touched the edges of the real cube with their thumb to prevent rotation of the rod within the whole handgrip. They were instructed to move the cube as accurately as possible to a target position indicated by the simulated cube and to keep it there until the simulated cube was presented in another position. They were not only to bring the real cube to the target position, but also to align the orientation of the cube with the orientation of the simulated cube. No instructions were given about the speed of the movement, and the subjects received no feedback about their performance. The experiment started with the subject holding the cube beneath the mirror and the experimenter turning off the light in the room.

The total number of target presentations in the experiment was 120. As the starting position for the movement to the first target was not defined, we only analysed 119 movements. The sequence of target presentations was pseudo-random and consisted of 10 repetitions of the 12 possible movements between pairs of targets (movement configurations). For each movement, the starting position of the hand was the endpoint of the previous movement. A movement was considered to have come to an end when the subject moved the center of the cube less than 2 mm within 300 ms. The movements were smooth and all subjects reported that they were able to align the cubes before the next trial started. The whole experiment took less than 8 minutes per subject.

Analysis of movement endpoint variability
Variability was pooled over subjects after subtracting each subject's average movement endpoint (i.e. the constant error) for the relevant movement configuration from the individual movements. This prevented differences in constant errors between subjects from affecting our measure of variability. Endpoint variability is presented graphically as projections of oriented ellipsoids in 3D. For each movement configuration, this ellipsoid was determined by computing the normalised eigenvectors of the Jacobi transformed (McIntyre et al. 1997, Press et al. 1988) 3×3-matrix $\mathbf{A}$, whose elements are given by:

$$\mathbf{A}_{jk} = \sum_{i=1}^{n} \delta_{ij}\delta_{ik},$$

where the deviation $\delta_i = \vec{p}_i - \bar{\vec{p}}$, $\vec{p}_i$ is the endpoint of movement i along one of three orthogonal axes (rows and columns $j,k \in \{x,y,z\}$) and $\bar{\vec{p}}$ is the mean position over n trials. To determine the size and shape of the ellipsoid we computed the

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standard deviations of the endpoints along the axes described by these normalised eigenvectors. This is equivalent to taking the square roots of the eigenvalues; $SD_j = \sqrt{d_j / n}$, where d_j is the eigenvalue of the eigenvector j and n the number of trails. Each axis shows the mean ± the standard deviation of the endpoint settings along that particular axis.

The subjects were not constrained in any way. Therefore, head movements and possible variations in the distance of the targets as a result of body sway may affect movement endpoint variability. We evaluated the variability of the location of the eyes in the same manner as we analysed movement endpoint variability to see whether head movements contributed to endpoint variability.

Interpreting the variability

Vector coding

If movements are controlled as vectors, one assumes that two factors contribute to differences in endpoints between repeated movements: variability in the displacement and variability in the starting position of the hand. Moreover, these sources of variability should be independent. To establish whether this kind of encoding is important we constructed new (fictional) movement endpoints by combining observed displacements with observed initial positions of other movements that were made within the same movement configuration. If the two are independent, the variability in the fictional endpoints should be no different from the observed variability (see figure 2.2). Thus, finding a ratio of 3D variability of the measured endpoints and 3D variability of fictional endpoint (the explained variability) close to 100% would support the hypothesis of vectorial coding. As a measure of 3D variability in endpoints we calculated the volume of the ellipsoids that describe the variability in endpoints relative to the mean endpoint. The volume of this ellipsoid is given by: $V = \dfrac{4}{3}\pi r_1 r_2 r_3$,

where $r_{1,3}$ are half the standard deviations of the endpoints along the axes of the ellipsoid. Each movement configuration was repeated ten times so that all volumes for both the measured endpoints and the fictional endpoints were based on ten settings. We did this for each of the seven subjects and each of the 12 movement configurations resulting in 84 values for the variability of observed endpoints and 84 values for the variability of fictional endpoints.

Position coding

A comparable strategy can be used to determine whether the controlled variable is the desired endpoint. If so, variability in measured endpoints results solely from variability in the specification of the endpoint of the movement. Since variability in
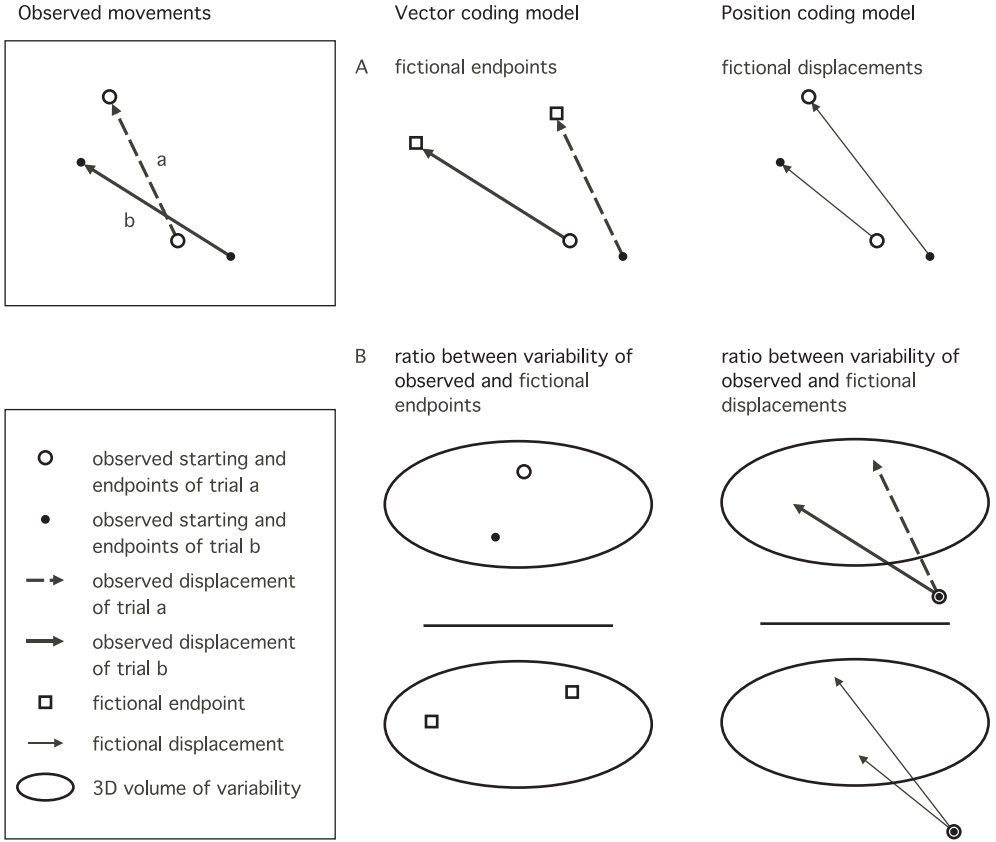
Figure 2.2 *Movement encoding models. The graph shows (using only two trials) the principles behind our method that uses the variability to study movement encoding models. A) Generation of fictional endpoints by combining observed starting positions with observed vectorial displacements from different trials (vector coding model), or of fictional vectorial displacements by combining observed starting positions with observed endpoints from different trials (position coding model). B) Ratios between volume of variability of observed and fictional data. The variability in the displacements (position coding model) was calculated by superimposing the initial positions and determining the variability in the endpoints. To evaluate whether the 3D variability in the fictional data is different from the variability in the observed data, we calculated the ratios of the volumes of the ellipsoids and expressed them as a percentage. We then averaged these values over all subjects and movement configurations.*

the initial position of the hand plays no part in the variability of endpoints, it should be independent of the latter, so that the vectorial displacements measured should be no different from ones constructed by combining arbitrary start- and endpoints. We tested this hypothesis by combining an observed endpoint of one movement with the initial position of one of the other movements to derive new (fictional)

vectorial displacements (see figure 2.2). Again we used combinations of start- and endpoints within the 12 movement configurations. The values for both the measured displacements and the fictional displacements were each based on ten settings. As a measure of 3D variability we calculated the volume of the ellipsoids that describe the variability in endpoints of the vectorial displacements relative to the mean endpoint, after superimposing the initial positions. We compared the 3D variability of the observed displacements with the 3D variability of the fictional displacements. The position coding model predicts that the ratio of 3D variability of fictional and observed data (the explained variability) is close to 100%.

Drift

Both the vector coding model and the position coding model assume that no other factors than the controlled variables and the constant errors affect the endpoints of movements. If this is so we could suffice with a much more simple analysis of our data (described in the appendix). However, in the current study, vision of the hand was prevented throughout the entire experiment. The constant errors might have changed over the course of the experiment due to drift between vision and kinaesthesia (Wann and Ibrahim 1992). This could also affect the results of the analysis we used, because we combine starting positions with endpoints of other movements, which took place some time earlier or later. We therefore combined initial positions with endpoint settings that were performed at specific times during the experiment, to evaluate the extent to which drift could have affected the results (also see the legend of figure 2.4).

Orientation matching

In order to minimise systematic effects of bio-mechanical factors (e.g. limb orientation) (Rosenbaum et al. 1999a, 1999b) on endpoint variability we asked subjects to align the orientation of the real cube with the orientation of the simulated cube, which was presented at random orientations. We analysed the errors in orientation matching to see whether the subjects successfully aligned the orientation of the real cube with that of the virtual cube. We limited our analysis to the 3D error in the orientation of the normal to one surface of the real cube relative to the normal to the nearest surface of the virtual cube. This gave one angle for each setting. Due to the symmetry of the simulated cube, the orientation error could not exceed 54.7° (orienting an axis at equal angles relative to three orthogonal axes gives the highest possible angle α, i.e. $\cos\alpha = 1/\sqrt{3}$).

Results

Subjects had no difficulty moving the real cube with their unseen hand toward the (continuously visible) targets. We analysed the spatial distribution of the movement endpoints. In figure 2.3 we show the projections of endpoint ellipsoids and target locations (squares) and the positions of the eyes, in the sagittal, fronto-parallel and horizontal plane. Each thick ellipsoid represents the variability in repeated responses for one of the 12 movement configurations. The two thin ellipsoids within the head show the variability in the position of the eyes over all movements.

The endpoint ellipsoids are close to the squares (i.e. most mean constant errors are less than 3 cm). The largest constant error (3.5 cm) was found for the most distant target. In this case the mean response is shifted toward the head. For most movement configurations the directions of highest variability converge toward the head of the subject (figure 2.3). Extrapolating the axes of highest variability enables us to determine the point in space for which the summed distance from all these lines is minimal. This position is slightly below and to the right of the subjects' eyes. Note that the directions of highest variability are sometimes almost perpendicular to the movement direction (e.g. for the movements from left to right and vice versa) and perpendicular to the variability of the position of the eyes.

Movement encoding

We analysed the variability in our data to see what it can tell us about the principles according to which a movement is encoded. Vector coding predicts that variability in the final hand position is the combined result of variability in the encoding of the displacement and variability in the initial hand position. We generated a collection of fictional endpoints, using observed displacements and initial positions, and contrasted them with the observed endpoints (see figure 2.2). The results are shown in figure 2.4 (filled squares). A value of 100% means that the volume of variability of observed endpoints is equal to the volume of variability of fictional endpoints. Lower values indicate that the observed variability is smaller than the variability of fictional endpoints. The observed variability is less than 30% of the newly synthesised variability, indicating that movements are not determined by independent variability in a vector and an initial position. The explained variability found is the same whether we constructed fictional endpoints from observed displacements and starting positions that were measured few (on average 12) or many (up to 60) trials apart.
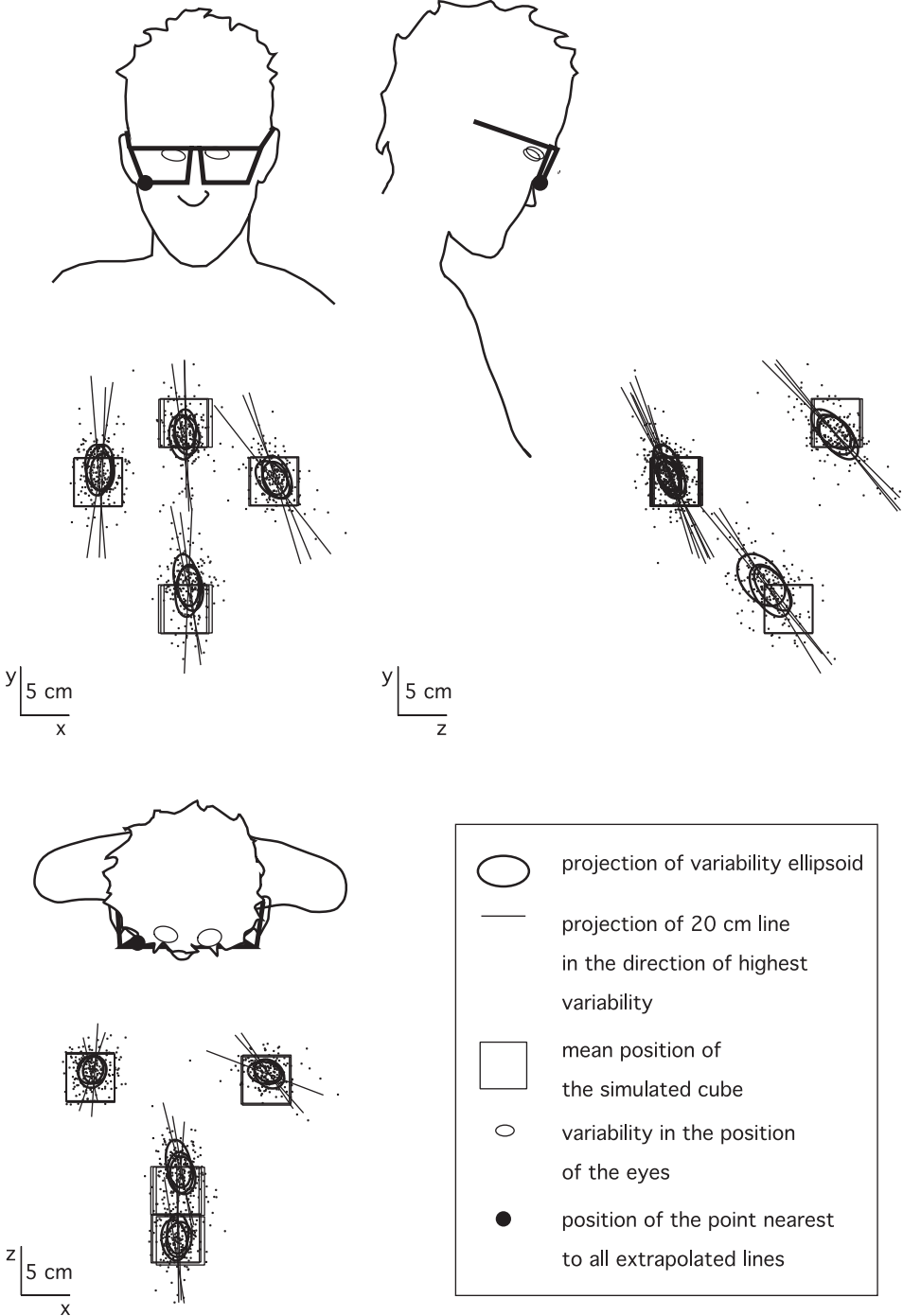
y | 5 cm
x

y | 5 cm
z

z | 5 cm
x

	projection of variability ellipsoid
	projection of 20 cm line in the direction of highest variability
	mean position of the simulated cube
	variability in the position of the eyes
●	position of the point nearest to all extrapolated lines

Figure 2.3 *Movement endpoints. Projections of endpoint ellipsoids and target locations in the sagittal, fronto-parallel and horizontal plane for each of the 12 movement configurations. For each movement configuration, we computed the average positions of both the simulated cube and the real cube relative to the cyclopean eye over all subjects. Squares show the mean location (and the size) of the simulated cube, relative to the observer. Variability of eye position is shown by the two thin ellipsoids. The positions of the targets relative to the eyes show small systematic shifts because subjects turn their head when shifting gaze. The positions of the thick ellipsoids relative to these targets show the constant errors pooled over subjects. The shape and size of these ellipsoids show the variability in the settings. The length of each axis of the ellipsoids is equal to twice the standard deviation along that axis. Lines represent projections of a 20-cm line aligned with the longest axis of each endpoint ellipsoid. The filled circle is the point for which the summed distance from all (extrapolated) lines is minimal. Dots are the projections of movement endpoints of individual movements relative to the overall mean for one movement configuration (i.e. corrected for individual biases by subtracting each subject's mean endpoint for that movement configuration).*
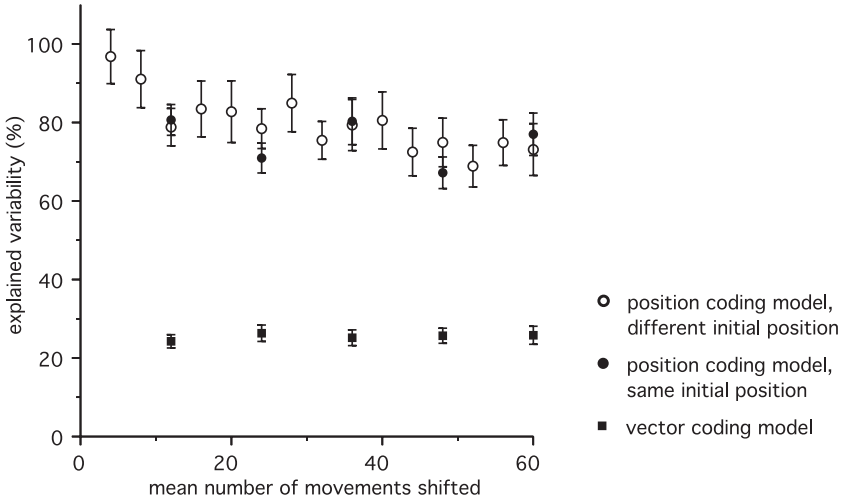

Figure 2.4 *The percentage variability explained by combining components of pairs of movements as a function of the time difference between the movements. For the position coding model the observed starting positions were combined with endpoints of movements that occurred a number of movements later. For the vector coding model the observed starting positions were combined with vectorial displacements a number of movements later. When only movements with the same initial position were considered the average shifts were multiples of 12 movements (filled symbols). Otherwise it was 4 (open circles). The error bars show the standard errors in the explained variability across subjects and movement configurations.*

To evaluate whether only the positions are relevant (position coding) we generated fictional displacements using new combinations of observed initial positions and observed endpoints. According to the hypothesis, variability in the vectorial displacements emerges from variability in encoding of the endpoint, independent of the initial position. As can be seen in figure 2.4 (filled circles), the variability in observed displacements is almost as large as for fictional displacements, suggesting that our data can best be explained by the hypothesis of position coding. However, the explained variability is below 100% indicating that additional sources of variability must have affected the displacements. The percentage tends to decrease with increasing time shifts. One possible factor could therefore be drift, because we combined endpoints with initial positions that occurred earlier in time. We did an additional analysis to see whether the deviation from the predicted value of 100% can be attributed to drift or whether it is related to the starting position of the movement.

In the former analysis, we only combined initial and final positions that were recorded within the same movement configuration. However, if movements are encoded according to the principles of position coding the initial positions are irrelevant, so we can also use combinations of initial and final positions from different movement configurations. Thus, we also generated new vectorial displacements for all 12 movement configurations using the endpoints recorded for each target, instead of the endpoints recorded for each movement configuration. This allowed us to determine the ratio of observed and constructed displacements for trials separated (on average) by multiples of 4 rather than 12. Differences between the results of the latter analysis and the results based on positions recorded within movement configurations would be attributed to the influence of starting position. As shown in figure 2.4, the results are the same whether we used initial and final positions derived from the same movement configuration (filled circles), or combined initial positions with final positions derived from all movement configurations that were directed toward the same target (open circles). Thus, the starting points have no influence on the endpoints. The deviation from 100% explained variability can presumably be attributed to drift. A simple linear regression analysis of the effect of time shifts on explained variability reveals a slight negative slope (-0.34% per number of movements shifted, p=0.004). In table 2.1 we show that explained variability for the position coding model is higher than for the vector coding model for all subjects. Thus, these results also hold at the individual level.

Orientation matching

If one would orient the cube randomly, the chances to make any particular orientation error are asymmetrically distributed. Therefore, interpreting the 3D error in orientation can be difficult. For instance, it is meaningless to simply calculate the
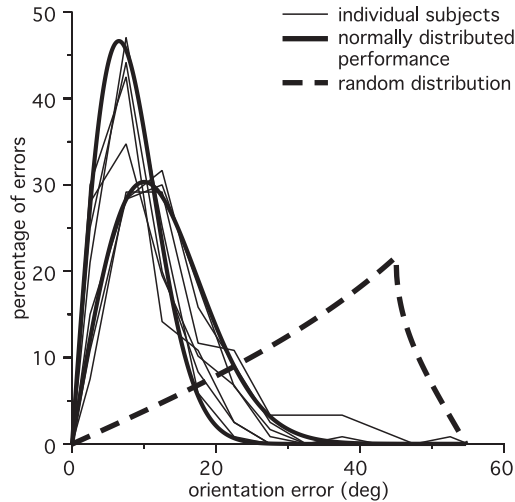
Figure 2.5 *Errors in the alignment of orientation. Due to the symmetry of the cube the orientation errors could not exceed 54°. The dashed line shows how the distribution of errors would look for random performance. This distribution is not flat, due to the unequal probability of obtaining each angular error. Thin lines represent the distributions of errors for individual subjects. The thick bell shaped curves show normally distributed performance with a standard deviation of 12.3° and 14.4°, obtained by multiplying these normal distributions with the distribution for random performance. Performance of individual subjects lies within this range.*

standard deviation of the error. We therefore compared the measured distribution of errors with normal distributions that were multiplied with this asymmetric random distribution. Distributions of orientation errors are plotted for each subject in figure 2.5. This analysis shows that subjects varied the orientation of their hand in accordance with variations in the orientation of the simulated cube.

Discussion

In the present experiment we attempted to assess the way the nervous system controls the endpoint in natural reaching movements to a visual target. Our subjects aligned a cube that they held in their unseen hand with a visual simulation of such a cube. Analysis of the distribution of movement endpoints revealed anisotropic patterns of variable errors. Endpoints were mainly scattered along the line of sight. The origin of the lines of highest variability was shifted a few cm to the lower right of the eyes, in the direction of the effector arm. Thus, visual localisation affected endpoint variability to a higher degree than kinaesthetic localisation. These results are in line with previous studies, which have shown that the accuracy of visual depth perception is particularly low for isolated objects in the dark (Brenner and Smeets

2000, Brenner and Van Damme 1999, Foley 1980, Gogel 1969). However, body-centered distributions of errors have also been found (Carrozzo et al. 1999, McIntyre et al. 1998, 1997, Soechting et al. 1990)

The directions of highest variability were slightly different for the various movement configurations but not related to the direction of movement. This is in contrast with previous reports of spatial dispersions of endpoints that suggest larger variations in movement amplitude than in movement direction (Vindras and Vivianni 1998, Messier and Kalaska 1999, 1997, Gordon et al. 1994). Such findings have been interpreted as evidence for vector coding. However, they can be reconciled with control of final position. Forces that arise when moving against a constraining surface are not necessarily accounted for by a position control system. External forces could induce distortions in the execution of movements (Desmurget et al. 1997a) resulting in a mismatch between the desired state and the actual movement endpoint. Thus, the effects of starting point manipulations do not necessarily relate to variability in coding of a displacement but could be due to non-conservative forces, which add variability in the direction of movement. In our study, the arm movements were unconstrained and we imposed large variations in hand and arm orientation by asking subjects to align the orientation of the cubes. Forcing the subjects to vary limb orientation changes the configuration of the arm and thus gravitational torques and muscle lengths on each setting. Furthermore, it ensures that for each setting subjects produce a hand position and do not reproduce a remembered posture. This presumably gets rid of systematic influences of external forces and anatomical constraints on the subject's settings, although it may increase total variability.

Implications for movement control

Our results show that the motor system uses only intended final position to control these simple movements. Other studies showed that vision of the hand prior to movement onset improves endpoint accuracy (Desmurget et al. 1997b, Rossetti et al. 1995, 1994), and that errors in the kinaesthetic estimation of the initial arm position are correlated with endpoint errors (Vindras et al. 1998), suggesting that information about the initial position is important too. Such observations imply that the accuracy of targeted movements does not only depend on the goal of the effector, but also on knowledge about its initial state and the starting point. However, we argue that these results do not contradict the idea of position coding. Our reasoning is that the nervous system may use afferent kinaesthetic signals to adjust the motor plan (Smeets 1992). Occlusion of the arm almost instantaneously produces a drift between visual and kinaesthetic information (Wann and Ibrahim 1992). If afference is involved in specifying final positions, correlations between errors in the estimation of initial positions and final positions emerge as a result of lack of correspondence between the visual and kinaesthetic modality. Vision of the hand before movement

will improve endpoint accuracy since it enables alignment of the afferent visual and kinaesthetic information.

The same argument holds for the observation that successive errors in pointing at sequentially presented targets tend to accumulate (Bock and Arnold 1993, Bock and Eckmiller 1986). After each pointing movement vision and kinaesthesia are perceptually aligned, even though there is a lack of correspondence (as shown by the presence of pointing errors). The perceptual correspondence may prevent correction of the mismatch between vision and kinaesthesia. If kinaesthesia is calibrated by vision or vice versa, then this should yield error accumulation so that pointing errors are related to initial errors. This idea is supported by a study of Vetter et al. (1999). They showed that introducing a mismatch between visual and kinaesthetic feedback for pointing movements toward a single target induced a corresponding bias in pointing toward other targets. Thus, drift, whether it is induced or spontaneous, will bias endpoint error in sequential pointing movements. Moreover, in that case corresponding errors for starting points and endpoints will leave the movement vectors between the targets unaffected.

Our method enabled us to delineate the effects of drift and starting position on endpoint settings. The results we obtained for the position coding model showed that the subjects' settings were slightly affected by an additional variability factor that developed in time, but did not depend on the starting position. A simple linear regression analysis of the data showed a significant negative slope between the explained variability we obtained for the position coding model and increasing time shifts, which indicates the presence of drift (Wann and Ibrahim 1992). The explained variability for the vector coding model remained unaffected throughout the experiment. Together these findings suggest that the small error accumulation in the subjects' endpoint settings is a result of drift between vision and kinaesthesia. It should be noted here that our method relies on the quantitative comparison of the volumes of observed ellipsoids and fictional ellipsoids and not directly on the comparison of orientations of the ellipsoids. The orientations of observed and fictional ellipsoids could have been used to test the position coding model. However, the orientation of an ellipsoid can only be characterised reliably if one eigenvalue is significantly different from the other two. We tested whether this was so for all ellipsoids using a χ^2 test described by Morrison (1990, p.336) and McIntyre et al. (1997). For 14 of the 84 ellipsoids (16.7%) the largest eigenvalue was significantly different from the other two. For 13 of the 84 ellipsoids (15.5%) one of the eigenvalues was significantly shorter than the others. Thus, two-third of all distributions is isotropic and cannot be evaluated in terms of orientation. We therefore relied on the increased volume that is expected instead.

Abrams et al. (1994, 1990) reported evidence for a hybrid model. They showed that the type of eye movement (pursuit or saccade) toward the target affected the initial phase but not the end of the arm movement (Abrams et al. 1990). Accordingly, they proposed that different parts of the movement involve different types of specification. Distance and direction of the required movement vector may be used for planning the initial phase, while the final phase may be based on a specification of the desired endpoint. The latter phase compensates for variability in the first part and exhibits properties corresponding to the tendency to correct errors that was described by Bock and Arnold (1993) for sequential pointing. In our experiment, subjects made slow, self-paced movements toward the target positions, which gave them ample time to make corrections. Therefore, an alternative explanation of our findings is that error correction based on endpoint compensated for errors related to the direction of movement. If this is so, preventing subjects from making corrective movements by increasing the required movement speed should affect the final endpoints. Adamovich et al. (1994) investigated the effect of movement speed on pointing toward remembered visually defined targets. They found that neither constant nor variable pointing errors increased with higher arm velocity. However, this could mean that subjects make no corrections for movements toward remembered targets, while they do for continuously visual targets, or that they still had enough time to make corrections (Adamovich et al. 1999, 1994).

Studies on the cortical representations of arm movements also show a variety of frames of reference. Several brain areas are involved in the initiation and control of reaching. Electrophysiological recordings in the motor cortex of the behaving monkey reveal correlations between a population vector formed by many neurons and the movement of the arm (Georgopoulos et al. 1988, 1983); the direction of movement corresponds to a vector, coded by a population of cells on the basis of the preferred direction and the change of activity of individual cells. However, vectorial coding by a neural population implies that patterns of neural activity should be the same for movements of equal length along parallel directions but from different initial positions. Caminiti et al. (1990) studied the effects of workspace on directional tuning for reaching movements and showed that neural activity differs for similar movements but different starting points. This may indicate that the movements were encoded relative to the body rather than relative to the starting position of the hand. Further, the activity of many cells in various areas of the visuomotor pathways that are involved in reaching is modulated by the orientation of the eye, head and gaze (Stuphorn et al. 2000, Boussaoud and Bremmer 1999, Andersen et al. 1995) and could be devoted to the coding of endpoints in egocentric coordinates.

In summary, the simplest explanation of our findings is that intended final positions rather than intended displacements guide natural movements toward visual targets.

The effects of (information on) initial position on endpoint accuracy that have been reported can be explained by either drift or non-conservative external forces.

Appendix

The analysis we presented in this article to evaluate the vector and position coding model is a refined version of the following analysis. Given a population of vectors formed by the sum or difference of pairs of vectors drawn from two independent populations, the standard deviation of the sum or difference is equal to the root of the summed squared standard deviations of the two component populations. We can test whether this is so for both models by comparing the following variables: SD_i = 3D variability of initial positions, SD_f = 3D variability of final positions, SD_d = 3D variability of displacements. If the initial position and displacement are controlled independently, then $SD_f = \sqrt{SD_i^2 + SD_d^2}$ and therefore $SD_f > SD_d$. Conversely, if the initial position and final position are controlled independently, then $SD_d = \sqrt{SD_i^2 + SD_f^2}$ and therefore $SD_d > SD_f$. In table 2.1 we show the mean values (averaged over movement configuration) for the 3D variability of final positions and displacements for each subject. SD_d is higher than SD_f for all subjects in agreement with the results we obtained with our initial analysis.

subject	1	2	3	4	5	6	7
vector coding model (%)	30.2	15.1	27.2	29.7	25.6	19.7	28.8
position coding model, same initial position (%)	57.9	134.2	50.3	99.4	60.1	91.0	69.3
position coding model, different initial position (%)	47.7	104.3	56.4	128.3	58.1	87.2	73.5
3D variability of final positions (cm^3)	0.9	2.8	1.2	0.5	2.3	2.7	0.3
3D variability of displacements (cm^3)	1.5	7.8	2.3	1.2	3.9	7.5	0.6

Table 2.1 *Individual measures for various variables. The percentages of explained variability were calculated for a shift of 36 movements. The 3D variability was computed as the volume of the variability ellipsoid, and averaged over movement configuration.*