The role of online visual feedback for the control of target-directed and allocentric hand movements

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1. Abstract

Studies that have investigated how sensory feedback about the moving hand is used to control hand movements have relied on paradigms such as pointing or reaching that require subjects to acquire target locations. In the context of these target-directed tasks, it has been found repeatedly that the human sensory-motor system relies heavily on visual feedback to control the ongoing movement. This finding has been formalized within the framework of statistical optimality according to which different sources of sensory feedback are combined such as to minimize variance in sensory information during movement control. Importantly, however, many hand movements that people perform every day are not target-directed, but based on allocentric (object-centered) visual information. Examples of allocentric movements are gesture imitation, drawing or copying. Here we tested if visual feedback about the moving hand is used in the same way to control target-directed and allocentric hand movements. The results show that visual feedback is used significantly more to reduce movement scatter in the target-directed as compared to the allocentric movement task. Furthermore, we found that differences in the use of visual feedback between target-directed and allocentric hand movements cannot be explained based on differences in uncertainty about the movement goal. We conclude that the role played by visual feedback for movement control is fundamentally different for target-directed and allocentric movements. The results suggest that current computational and neural models of sensorimotor control, which are based entirely on data derived from target-directed paradigms, have to be modified to accommodate performance in the allocentric tasks used in our experiments. As a consequence, the results cast doubt on the idea that models of sensorimotor control
developed exclusively from data obtained in target-directed paradigms are also valid in the context of allocentric tasks, such as drawing, copying or imitative gesturing, that characterize much of human behavior.

2. Introduction

People make literally thousands of visually guided hand movements every day, everything from picking up their morning cup of coffee to turning off the light switch at night. Studies that have investigated how visual feedback is used to control visually guided hand movements have relied on paradigms such as pointing or reaching tasks that require subjects to acquire target locations. In the context of these target-directed tasks, the programming and control of hand movements is dominated by visual as opposed to proprioceptive feedback (Pick et al. 1969; Rock, 1966; Warren, 1979; Welch and Warren, 1986). Not surprisingly perhaps, the use of visual feedback decreases when it becomes less reliable (Koerding and Wolpert, 2004; van Beers et al. 2002; 1999) or when the target is specified proprioceptively (e.g. McGuire and Sabes, 2009; Sarlegna and Sainburg, 2007; Sober and Sabes, 2005). These findings have been interpreted as evidence for the idea that the human sensorimotor system uses a statistically optimal sensory estimate of the current state of the system (e.g. the current position of the hand with respect to the movement target) to control the movement (Koerding and Wolpert, 2004, 2006; van Beers et al. 1999, 2002; McGuire and Sabes, 2009; Sarlegna and Sainburg, 2007; Sober and Sabes, 2005; Saunders and Knill, 2004; Smeets et al. 2006). The idea is that visual feedback is used in a way that minimizes the variability of the
sensory estimate of the state of the system and in this way reduces movement variability. Importantly, however, many movements that people perform every day are not target-directed, but are based on allocentric (object-centered) visual information. Examples of allocentric movements are imitating the gestures of others, making paintings or sketches of real-world objects or scenes, or simply copying drawings made by others. In these situations, the goal is to perform a movement, the spatial properties of which reflect certain spatial properties of the visual environment, but unlike in pointing or reaching, the movement is not target-directed. There is evidence that allocentric movements have different neural substrates than target-directed movements (Goodale and Milner, 1992; Schenk, 2006). This in turn may reflect differences in the way the sensorimotor system uses visual information during the control of these two types of movements. Remarkably, however, there have been no studies that have examined whether or not the rules of visual-feedback control that have been established for target-directed movements also apply for allocentric movements. Therefore, here we investigated how visual feedback of the moving hand is used to control both target-directed and allocentric movements.

Visual feedback during movement execution can be used to correct errors in the movement with respect to the goal. It cannot be used, however, to correct errors that might have arisen because of initial uncertainty about that movement goal (in our experiments, the location of the end-point of the required movement). In other words, control processes will be successful in getting the hand to its planned destination but will not correct for errors in the plan itself. As a consequence, initial uncertainty about the final position of the required movement will add to variability of movements. In previous experiments, we have shown that subjects are less variable in their selection of
the end-point of the movement in target-directed as compared to allocentric tasks (Thaler and Todd, 2009a; Thaler and Goodale, 2010). For this reason alone, one would expect to see differences in the variability of allocentric as compared to target-directed movements (i.e. differences that are not due to the control processes). Thus, to isolate the differences in the variability of target-directed and allocentric movements that were due to differences in visual feedback control from those that were due to differences in the uncertainty about where to move, we modeled this uncertainty for both the target-directed and the allocentric movements. This allowed us to focus on the variability due to the control processes themselves.

To summarize: The current experiments were designed to determine if visual feedback plays a different role in the control of allocentric as compared to target-directed movements. The experimental paradigm was designed such that, in principle, target-directed and allocentric tasks provided equal opportunities for movement control through visual feedback (see Methods). In addition, we developed a model of target uncertainty in order to separate differences in control from differences in the uncertainty about the movement goal (i.e. the required endpoint of the movement).

Our results show that visual feedback reduces movement scatter significantly more in the target-directed as compared to the allocentric task, particularly with respect to directional errors. In other words, the directional scatter of allocentric movements was largely unaffected by the availability of visual feedback. Importantly, we show that these differences in the use of visual feedback cannot be explained by differences in the uncertainty about the movement goal itself.
We conclude that the contribution of visual feedback to movement control is greatly reduced for allocentric as compared to target-directed movements. The results suggest that current computational and neural models of sensorimotor control, which are based entirely on data derived from target-directed paradigms, have to be modified to accommodate performance in the allocentric tasks used in our experiments. As a result, the results cast doubt on the idea that models of sensorimotor control developed exclusively from data obtained in target-directed paradigms are also valid in the context of allocentric tasks, such as drawing, copying or imitative gesturing, that characterize much of human behavior.

3. Methods and Materials

Overview of Experimental Paradigm

Subjects performed target-directed and allocentric hand movements either with or without online visual feedback about their moving hand (Fig.1). All stimuli were computer generated, projected onto a mirror located above the subject’s right arm, and appeared to be in the same plane as the subject’s hand. In the allocentric version of the task, subjects were presented with a black and a white dot and were asked to move their hand from the starting position to an imaginary target, whose relative position with respect to the starting point of the hand was the same as the position of the black dot with respect to the white dot. In the target-directed version of the task, subjects saw a black dot and were asked to move their hand from the starting position to the position indicated by the black dot. Targets were selected such that movements were biomechanically matched across tasks. The target dot(s) disappeared before movement onset, such that
they were never visible during the movement. That way, subjects could never compare
the position of the cursor directly to the visual target. On visual feedback trials, subjects
had visual feedback about their moving hand via a cursor that appeared to be
superimposed on the hand both in target-directed and allocentric tasks. The cursor was
absent during the no-visual feedback trials. It has been shown that the position of a target
on the retina as well as gaze direction affect pointing responses (Bock, 1986; Henriques
et al. 1998; Schlicht and Schrater, 2007). For that reason, in all conditions, subjects
directed their gaze at a fixation target, such that gaze direction and retinal eccentricities
of the targets and the cursor (when available) were matched across conditions. Thus, our
experimental design ensured that, in principle, target-directed and allocentric movements
provided equal opportunities for visual feedback control, when visual feedback was
available.

< Figure 1 >

Subjects

Fifteen right-handed subjects participated in the experiment. All subjects were
undergraduate students from the University of Western Ontario and participated for
course credit. Subjects had self-reported normal or corrected to normal vision and they
performed the experiment with their dominant right hand. All testing procedures were
approved by the ethics board at the University of Western Ontario, and participants gave
informed consent prior to testing.

Apparatus
Subjects were seated on an adjustable chair. Stimuli were displayed on a 17-inch CRT at a temporal and spatial resolution of 75 Hz and 1280(H) x 1024(V) pixels, respectively. The active display area subtended 335(H) x 268(V) mm. The monitor was mounted horizontally, facing downwards and subjects viewed stimuli in a half-silvered front-surface mirror that was mounted horizontally facing upwards, halfway between the monitor and a horizontally oriented touch panel (distance from the mirror to either surface was 30 cm). Subjects’ eyes were located ~ 460 mm above the touch panel. Displays were viewed binocularly in a darkened room and a combined chin/forehead rest was used avoid to changes in head position. During the experiment, the back of the half-silvered mirror was covered and subjects moved their hands below the mirror on the touch panel. Thus, subjects could not see their hand during the experiment. At the same time, the matched distances between monitor, mirror and touch panel made the mirror reflection of stimuli appear to be in the same plane as the touch panel.

Hand movements were recorded with a stylus on the touch panel (MagicTouch Add-On Touch Screen; Model: KTMT-1700-USB; Keytec, Garland, TX). Touch panel coordinates were calibrated to the display coordinates, i.e. pixels. Thus, the workspace on the touch panel was 335 x 268 mm and spatial resolution was 0.26 mm. Touch panel coordinates were sampled at 150 Hz. To ensure good correspondence between display and movement parameters, the apparatus was calibrated before each session. For calibration, display coordinates and touch panel coordinates were aligned using a 25-point calibration procedure. For calibration, the backing of the half-silvered mirror was removed to permit visual alignment between the physical stylus tip and the virtual image.
We monitored subjects’ eye movements with a webcam (Logitech Quickcam Pro9000). Due to the geometry of our apparatus and the mirror-based viewing, we could not use a standard eye tracker to monitor eye movements. A computer (Dell Optiplex 755 PC with an ATI Radeon HD 2400XT graphics card) was used to control stimulus presentation and data collection. Software was written in C/C++ using Windows API and OpenGL.

**Stimuli**

Target dots were 0.62 deg (5 mm) diameter circles and the center of the black and white target dots were white or black 0.31 deg (2.5 mm) diameter circles, respectively. The cursor starting position was a red 0.62 deg (5 mm) diameter circle with a white 0.31 deg (2.5 mm) diameter center. The cursor was a red 0.37 deg (3 mm) diameter circle. All stimuli were shown in front of a gray background.

In target-directed conditions, there were two positions of the black target dots with respect to the hand starting position (position 1: 20 mm to the right, 120 mm up; position 2: 60 mm to the right, 140 mm up). Only one of the two positions was shown on any given trial. In allocentric conditions, there were two equivalent positions of the black target dot with respect to the white target dot (i.e. position 1: 20 mm to the right, 120 mm up; position 2: 60 mm to the right, 140 mm up). Just as in target-directed conditions, only one of the two positions was shown on any given trial. The white target dot in allocentric conditions was located 150 mm to the left and 70 mm to the front of the starting point of the hand. For all subjects, the hand starting position was located 50 mm in front and 75 mm to the right of a subject’s sternum on the recording surface. We used two target positions in each task, because we wanted to keep the length of the experiment
reasonable for our participants, while at the same time being able to measure many
repetitions of movements to the same target to get precise and reliable estimates of
performance (see also ‘Procedure’).

Subjects were instructed to direct their gaze at a central fixation target (0.3 deg / 2.5 mm diameter circle) during a trial in all conditions. The fixation target was placed centrally on the computer screen in a position that ensured that average retinal eccentricity of visual stimuli and cursor was matched across target-directed and allocentric conditions. Average retinal eccentricity was ~12 degrees in all conditions.

From the design of our visual stimuli, it follows that visually specified hand movements (i.e. start and end position of the hand, direction and amplitude of movement) were the same in target-directed and allocentric conditions. Thus, the tasks had identical biomechanical requirements. In addition, the visual displays during the movement were the same in target-directed and allocentric conditions, and thus subjects had the same sensory information about the moving hand target-directed and allocentric conditions.

Furthermore, since the cursor (when visible) was always superimposed on the subject’s hand, the visual information about the subject’s hand position and movement was the same in target-directed and allocentric conditions.

**Procedure**

In the beginning of a trial subjects saw the fixation target, the target dot(s) and the cursor starting position. A trial was initiated when the cursor remained at least 1 s within the 5-mm dot indicating the starting position. Then a 100-ms beep would indicate the start of the trial. No instructions about movement speed were given, but it was emphasized to subjects that they should move in one smooth movement. The target dots
disappeared at movement onset. In visual feedback conditions, subjects could see the
screen cursor during a trial. In no visual feedback conditions, the cursor would disappear
as soon as the trial started. A trial was terminated when subjects had moved the cursor
less than 25 mm during the last 450 ms. Another 100-ms beep indicated the end of the
trial. The target dot(s) for the next trial (and in no-visual feedback condition also the
cursor) would only appear after subject moved at least 3 cm away from her final hand
position. Subjects were instructed to keep their gaze on the fixation target during a trial.
Eye movements were monitored on a separate monitor and trials were repeated if a
subject did not follow the instructions about eye movements. Conditions were
presented in pseudo-random order. Each target was presented 32 times in each condition,
such that subjects made 256 movements during the course of the experiment. Prior to the
experiment proper subjects participated in a short practice session in which they gave at
least 4 responses in each condition. The whole experiment took ~45 min.

Analysis of Movement Data

Kinematic Analyses

Movement trajectories were filtered using a Butterworth filter with a 7-Hz cutoff.
Movement start was defined as the first time movement speed exceeded 1 cm/s.
Movement end was defined as the first time movement speed fell below 1 cm/s.
Movement speed was obtained by numerical differentiation of smoothed movement
trajectories. To characterize movements kinematically, we computed the curvature of
movements in percent, by dividing the maximum absolute distance of any point on the
movement trajectory to the straight line joining movement start and endpoints by the
length of the line joining start and endpoints, and multiplying this quantity by 100
Atkeson and Hollerbach, 1985). A semicircular trajectory would have a value of 50%.

We also computed reaction time (movement onset time, measured from the time of the
onset of the 100 ms beep until movement start) and average and maximum movement
speed. To check in more detail if kinematics differed between target-directed and
allocentric conditions, we also computed average movement speed as a function of
average movement distance (mm) and as a function of movement path (%) in all
conditions (see Appendix for computational details). The %-based analysis also allowed
us to compute confidence intervals around the difference between speed curves in target-
directed and allocentric conditions, i.e. we could compute statistical curve-comparisons
(see Appendix). The mm-based analysis did not allow us to perform this kind of curve-
comparison, because average movement distances (mm) differed between subjects and
conditions. The statistical curve-comparison allowed us to detect whether or not
movement speed differed significantly between target-directed and allocentric curves at
any point during the movements. For example, if the onset of peak velocity or any other
kinematic parameter, such as skew or kurtosis, differed systematically between target-
directed and allocentric conditions then the 95% confidence interval of the difference
scores should no longer overlap both curves.

Spatial Analyses

We computed movement distance as the length of the straight line joining
movement start and endpoints and movement direction as the orientation of that line.
Movement direction errors were computed as the angular deviation between movement
direction and the physically indicated target direction. We computed averages and
variances of angular data using both linear and circular statistics (Fisher, 1993). The
results from the two methods were virtually identical. Here we report only linear statistics. To characterize spatial distributions of movement endpoints across subjects we fit minimum variance ellipses to the endpoints of all subjects’ hand movements for each target position and experimental condition (Gordon et al. 1994; van Beers et al. 2004). To remove any contribution of individual differences to this measure, we subtracted each subjects mean endpoint \((\bar{x}, \bar{y})\) for each target position and condition before computing the ellipse. Ellipses were determined by computing the eigenvalues \(\lambda\) and the eigenvectors of the 2 x 2 sample covariance matrix \(R\), whose elements are given by:

\[
R_{jk} = \frac{1}{n} \sum_{i=1}^{n} \delta_{ij} \delta_{ik}, \quad \text{[eq.1]}
\]

where the deviation \(\delta_i = \bar{p}_i - \bar{p}\) is the endpoint of movement \(i\) along one of two orthogonal axes (rows and columns \(j, k \in \{x, y\}\)) and \(\bar{p}\) is the mean position over \(n\) trials. The eigenvectors and eigenvalues determine orientation and shape of the ellipse, respectively. The variance of points in the plane, i.e. \(SD_{2D}^2\), can be computed either as the area of a minimum variance ellipse, or as the sum of the variances of the points measured in any two orthogonal directions. We chose the latter to compute the variance of points in the plane for each subject, target position and experimental condition.

The variance computations described so far were applied to the coordinates of movement endpoints. However, we also applied them to coordinates that were obtained from movement trajectories which had been truncated such that average movement distance was 90 mm for each target position, experimental condition and subject. We chose 90 mm average distance, because this is the furthest average distance shared across all subjects and conditions. We applied our variance computations to truncated movement
trajectories because we wanted to compare movement variances directly between visual feedback and no-visual feedback conditions and across tasks, and using a truncation ensured that movement variances were measured at the same average movement distance in all conditions. Importantly, even though average movement distance after truncation was 90 mm, the distance of individual movement traces was variable, such that variance of truncated movement traces contained variability of both distance and direction components (see next paragraph).

Movement trajectories were truncated and the variance at the point of truncation was computed as follows: First, we computed the average movement distance $d$ separately for each target position, experimental condition, and subject. Then, for each individual movement trajectory of length $l$ for each target position, experimental condition, and subject, we determined the point at which the distance traveled along that trajectory reached $d_i = l_i \times \frac{90}{d}$ and collected the $x$ and $y$ coordinates of that point. The computation of these coordinates was carried out separately for each trajectory, yielding 32 pairs of $x$ and $y$ coordinates for each subject, target position, and experimental condition. The 90 mm truncation point and 2D movement variance were then computed as the average of the 32 $x$ and $y$ coordinates, and the sum of the $x$ and $y$ variances, respectively, for each subject, target position and experimental condition. This means that the $x$ and $y$ coordinates were collected at a different distance ($d_i$) for each movement trajectory, even though the average distance of those points was, by definition, 90 mm. As a consequence, this analysis ensures that movement variance is a measure of $SD_{2D}^2$.

Our analysis of movement variance is sensitive to spatial aspects of movements, e.g. movement curvature, distance and direction. Our analysis, however, does not
consider temporal aspects of movements, e.g. movement speed. We limited our analysis of movement variance to spatial aspects of movements because we did not observe effects of our experimental manipulations on temporal aspects of the movements (see Results, subsection Kinematics).

Model of Target Uncertainty

We modeled uncertainty about the planned endpoint of the movement as the sum of variances in direction and distance of the visual target. Please note that even though direction and distance were used for the computations, this does not imply that these are the parameters that the brain uses to represent the position of the target (Thaler and Goodale, 2010).

Directional variance (azimuth) in the visual localization of a target located in a horizontal plane slanted away from the observer is between .2^2 and .46^2 degrees^2 of visual angle, when the computation of the directional variance is based on decomposition in terms of azimuth and angular elevation with respect to the cyclopean eye (van Beers et al. 1998, Table 2). If the computation of the directional variance is based on a decomposition in terms of azimuth and radius in the horizontal plane with respect to the cyclopean eye, however, it is between .32^2 and .58^2 degrees^2 of visual angle. The values were computed on the basis of data provided by van Beers et al. (1998; Fig.5 & 6, Table 1). The viewing conditions employed by van Beers et al. were similar to those in our target-directed task. Thus, for the target-directed task in our experiment, we assumed directional variance of 0.4^2 degrees^2 of visual angle measured from a subject’s cyclopean eye to the target in the horizontal plane. Variance in mm^2 was obtained by conversion from degrees visual angle. In the allocentric task in the current experiments, in which subjects not only saw the
target itself, but also had to consider the reference target, the directional variance was assumed to be the sum of the variances for the target itself and the reference target, i.e. $0.4^2 + 0.4^2$ degrees$^2$ of visual angle. In previous studies we had found that the variance of movement direction did not differ between target-directed and allocentric conditions, which would imply that the directional variability in the perception of target location is the same in target-directed and allocentric task (Thaler and Todd, 2009a; Thaler and Goodale, 2010). In those previous experiments, however, the movement direction in allocentric conditions was always explicitly marked with a visual ‘response’ line. Importantly, such a response line was not present in the current experiments. It was for this reason, therefore, that we assumed there was an increase in directional variance in target localization for the allocentric as compared to the target-directed task in the current experiments.

In previous studies, we measured the variability of perceived target distance (in mm) using a version of the method of adjustment (Thaler and Todd, 2009a; Thaler and Goodale, 2010). In those experiments, the relationship between the magnitude of the adjustment (bias) and the standard deviation (SD) of the adjustment were described as linear functions (obtained through simple linear regression) and we found that slopes and intercepts were higher in the allocentric as compared to the target-directed task. Furthermore, we also found that the bias in the adjustment was quantitatively matched to the bias in visually guided hand movements in the same conditions. Therefore, for the current experiments, we predicted the SD of target distance using a linear equation obtained by averaging the intercept and slope parameters from previous experiments (see Appendix for details) and applying this equation to the measured movement distances.
The variance of target distance was then computed as $SD^2$. In addition, to account for differences in global performance between previous and current experiments, we included a scale parameter $k$. The equations that predict variance of perceived distance for target-directed and allocentric conditions obtained this way were therefore

**Target-Directed:**

$$SD_{\text{Distance}}^2 = k(3.0 + 0.035x)^2 \quad [\text{eq.2}]$$

**Allocentric:**

$$SD_{\text{Distance}}^2 = k(4.2 + 0.057x)^2 \quad [\text{eq.3}]$$

Where $x$ was the movement distance (in mm) for each subject, target point, visual feedback and task, and $k = 0.449$. We chose $k$ such that the predicted distance variance in the target-directed task at 90 mm matched the average observed distance variance in the target-directed task at 90 mm, when visual feedback was available.

To summarize, the model predicts variance in the planned endpoint of the movement as the sum of directional and distance variance, the equations for which were based on previously published results. The total variance in the planned endpoint of the movement in any given condition is therefore $SD_{\text{Direction}}^2 + SD_{\text{Distance}}^2$. The only free parameter in the model is $k$, which applies only to the distance component, and which was kept constant across all experimental conditions and subjects.

For the computation of residual variance, i.e. variance in the actual endpoints of the movement that is independent from variance in the planned endpoint of the movement (as predicted by the model), we simply subtracted the amount of variance predicted from the model from the observed movement variance separately for each subject and experimental condition. To visualize the model prediction, we plotted ellipses
whose minor and major axis were chosen to be $SD_{\text{Direction}}$ and $SD_{\text{Distance}}$, respectively, computed across all subjects’ data, and that were oriented along the direction of movement and placed on the average movement endpoint. Since our variance analysis is based on the sum of the x and y variances, however, it is independent from ellipse shape and orientation.

4. Results

Spatial

Fig. 2 shows subjects’ movement endpoints (dots), observed minimum variance ellipses (thick curves) and model predictions (thin curves). Minimum variance ellipses and model predictions were computed from the data from all the subjects and these are plotted both at the endpoint of the movement and at the 90 mm truncation point. For better visibility, the latter curves have been enlarged in the insets. The movement endpoints that would have resulted from physically correct performance are shown as well (squares). The top and bottom panels show performance in no-visual feedback and visual feedback conditions, respectively.

With regard to constant errors, i.e. the difference between the physically correct movement endpoint and subjects’ average movement endpoint, it is evident from Fig. 2 that subjects were more accurate in the target-directed than in the allocentric task, because their movements tended to overshoot the target in the allocentric task. In addition, subjects appeared to become more accurate when visual feedback is available in
the target-directed, but not when such feedback is available in the allocentric task (see Table 1 for descriptive statistics). In agreement with this observation, a 2x2 repeated measures ANOVA applied to the constant errors averaged across target points and with task and feedback as factors reveals a significant main effects of task ($F(1,14)=16.2; p = .001$) and a significant interaction effect of task by feedback ($F(1,14)=5.287; p = .037$). No other effects were significant.

With regard to the variable errors, it is evident from Fig.2 that when no visual feedback about the moving hand was available (Fig.2, top panels) movement variability exceeded variability in the planned movement endpoint in both tasks, i.e. the thick ellipses are bigger than the thin ones. Furthermore, the residual variability, i.e. the difference between thick and thin curves, which signifies variance introduced by movement errors, appears to be similar in target-directed and allocentric task, when no visual feedback was available. Most interestingly, however, when visual feedback became available (Fig.2, bottom panels), it appears as if the residual variability in the allocentric task was larger than the residual variability in the target-directed task, i.e. the difference between thick and thin curves appears to be smaller in the target-directed as compared to the allocentric task, when visual feedback was available. This suggests that visual feedback was used more to correct movement errors in the target-directed as compared to the allocentric task. In the following paragraphs we will go over these results in more detail.

When no visual feedback was available (Fig.2, top panels), the residual variance averaged across target points at the 90 mm truncation point did not differ between allocentric and target-directed tasks (two-tailed paired t-test: $t(14) = 0.067; p = 0.948$ and
see Table 2 for descriptive statistics) and it was significantly different from zero in both tasks (target-directed: $t(14) = 2.86; p = 0.013$; allocentric: $t(14) = 3.78; p = 0.002$; and see Table 2 for descriptive statistics). In contrast, when we compared movement variability at 90 mm without taking into account differences in target uncertainty, variance in the allocentric task was significantly higher than in the target-directed task (two-tailed paired t-test: $t(14) = 2.55; p = 0.023$ and see Table 2 descriptive statistics). The same was true when we compared differences in residual and ‘raw’ movement variability at the movement endpoints, in which case the variance was always significantly larger in the allocentric as compared to the target-directed task (two-tailed paired t-test; residual variance no-visual feedback: $t(14) = 2.66; p = 0.019$; raw variance no-visual feedback: $t(14) = 4.47; p = 0.0005$; and see Table 2 for descriptive statistics). This finding suggests that, when no visual feedback was available (and when we compare variances at the same distance, i.e. 90 mm), our model of target uncertainty succeeds in explaining differences in movement variance between target-directed and allocentric tasks. However, when the movement distance in the allocentric task exceeded the movement distance in the target-directed task, differences in variance cannot be explained by the model. This presumably reflects the fact that response variance increases with an increase in response magnitude (i.e. Weber’s law or Fitt’s law), which would have also led to an increase in the residual variance at the movement endpoint in the allocentric task, because movement distances were generally larger in the allocentric task.

When visual feedback was available (bottom panels), the residual variance averaged across target points at the 90 mm truncation point was significantly larger in the
allocentric as compared to the target-directed task (two tailed paired t-test: \( t(14) = 2.93; p = 0.01 \); and Table 2 for descriptive statistics). Furthermore, the residual variance at the truncation point was not significantly different from zero for the target-directed task (compare also the almost perfect overlap between thin and thick ellipses in Fig. 2, bottom left panel), but it was significantly larger than zero for the allocentric task (target-directed: \( t(14) = 0.377; p = 0.712 \); allocentric: \( t(14) = 2.49; p = 0.0259 \); and see Table 2 for descriptive statistics). This finding suggests that subjects used visual feedback significantly more to control their movements in the target-directed as compared to the allocentric task. When we compared differences in residual and ‘raw’ movement variance at the movement endpoints, the variance was also significantly larger in the allocentric as compared to the target-directed task (residual variance: \( t(14) = 5.38; p = 0.000098 \); raw variance: \( t(14) = 7.15; p = 0.00005 \); and see Table 2 for descriptive statistics).

However, as stated above, this finding does not necessarily imply that visual feedback was used more in the target-directed task, but again could reflect the fact that response variance increases with response magnitude (i.e. Weber’s law or Fitt’s law), which would have also increased the residual variance at the movement endpoint in the allocentric task, because movement distances were generally larger in the allocentric task.

As evident from the previous paragraphs, the interpretation of differences between ‘raw’ variances across target-directed and allocentric task in terms of visual feedback control is ambiguous because differences between the tasks could have been due to uncertainty and/or bias in the planned endpoint of the movement (although in fairness, this is only an
issue for comparisons between movement endpoints, but not between truncated movements). This ambiguity is reduced when we compare residual variances at the 90 mm truncation point. Nevertheless, one might question the validity of this comparison because it is based on the assumption that our model of target uncertainty is true and on the assumption that the evaluation of variance at the 90 mm truncation point is legitimate. These two points are discussed below.

With respect to the model, one could argue that the results with regard to the residual variance are due to parameter $k$ and because $k$ is a free parameter the results are essentially meaningless. However, it is important to keep in mind (1) that $k$ is fixed across all subjects and experimental conditions and (2) that $k$ affects only the distance component. It follows, therefore, that parameter $k$ does not affect the predicted differences between the two tasks. Moreover, the amount of variance that our model of target uncertainty predicts is supported by previous data. Of course, this does not imply that the shape or orientation of the ellipses plotted in Fig.2 is correct. But as we pointed out in the methods section, our statistical analyses are independent of the shape and orientation of the ellipses.

It is important to emphasize that the method of truncation we used is valid only if movement variance is a strictly increasing function of average movement distance. To confirm this assumption, we analyzed movement variance as a function of average movement distance. The analysis of movement variance as a function of average movement distance was similar to the analysis of variance for truncation, but instead of applying the computation at a single average movement distance (i.e. 90 mm) we applied it at 101 equally spaced average movement distances, separately for each subject, target
position and experimental condition (see Appendix for computational details). The results of this analysis are shown in Fig.3. Please note that for ease of data visualization the ordinate in Fig.3 uses a non-linear scale (i.e. successive squares), whereas the abscissa uses a linear scale. It is evident that movement variance increased as a function of movement distance in all our experimental conditions.

It is important to realize that our analysis of movement variability will not always yield a strictly increasing function. For example, if movement trajectories first became less similar to one another and then converged onto a common target, then our analysis would yield a function that first increases and then decreases. Investigators who have used spatial analyses of movement variability similar to ours report such increasing-decreasing functions when subjects make target-directed movements under a number of conditions: when they can move their eyes freely, when visual feedback is available throughout the movement, and when the target is visible during the movement (e.g. Liu and Todorov, 2007; Fig.8; Todorov and Jordan, 2002, Fig.3). To confirm that our analysis of movement variability yields the same increasing-decreasing functions when applied to data obtained under similar conditions to the ones used by those researchers, we applied our analysis to data that had been collected in our lab for a different project. As expected, for those data our analysis yielded the expected increasing-decreasing function (see Suppl. Note). In contrast, for the current data we observed a strictly increasing function instead of an increasing-decreasing function, probably because the target was not visible during the movement and/or because subjects were required to direct their gaze at a fixation target. In summary, it is unlikely that our results are an artifact of the model or the truncation method.
Nevertheless, to analyze the data in a way that does not hinge on any assumptions about the model or the truncation method, we also compared raw movement variances at the movement endpoint within each task across visual feedback conditions. Since the response magnitudes within each task did not differ between visual feedback and no-visual feedback conditions (see Table 1), movement magnitude could not have been a confound and this comparison is therefore statistically sensible.

As expected, when we compared raw 2D variances within each task but across visual feedback conditions, we found a significant reduction from no-visual feedback to visual feedback condition in each task (two-tailed paired t-test; target-directed: \( t(14)=3.05 \); \( p = .0087 \); allocentric: \( t(14)= 2.81 \); \( p = .0139 \)). Thus, visual feedback was used to correct movement errors in each task. When we analyzed the variance in distance and direction separately, however, we found that in the target-directed task variance was reduced significantly both for amplitude (\( t(14) = 3.01; p = .009 \)) and for direction (\( t(14) = 2.98; p = .0099 \)). In contrast, in the allocentric task variance was reduced significantly only for amplitude (\( t(14)=2.31; p = .037 \)), but not for direction (\( t(14)=1.05; p = .31 \)). As expected, when the same analysis was applied to the SD’s in distance and direction (also shown in Table 2) the result was the same (target-directed - amplitude SD: \( t(14) = 4.76; p = .0003 \), target-directed - direction SD: \( t(14) = 4.12; p = .001 \); allocentric - amplitude SD: \( t(14) = 2.64; p = .019 \); allocentric - direction SD: \( t(14) = 1.17; p = .26 \)). This suggests that subjects did not use visual feedback to control movement direction in the allocentric task. This result supports the conclusion drawn from the analysis of residual variance, namely, that visual feedback was used less to control movements in the allocentric as compared to
the target-directed task. The results also appear to be consistent with Fig.2, in which the availability of visual feedback in allocentric conditions appears to reduce movement-scatter more in the direction parallel to the direction of movement than in the direction orthogonal to the direction of movement.

Kinematics

Repeated-measures ANOVA with task and visual feedback as factors applied to average and maximum movement speed and movement curvature averaged across target positions, revealed no significant differences between the experimental conditions (see Table 1 for descriptive statistics). This suggests that movements were really quite similar with regard to their biomechanics in all conditions. However, the same statistical analysis applied to movement onset time showed a significant main effect of task (F(1,4)=13.4; p = .003) and a significant main effect of visual feedback (F(91,14)=7.1; p = .018). On average, onset times were 58 ms faster for the target-directed task and 48 ms faster when visual feedback was available.

Fig.4 shows average movement speed plotted as a function of average movement distance (mm) in all conditions (see Appendix for computational details). The groups of curves look very similar across target directed and allocentric tasks for both the further and the closer target.

Fig.5 shows average movement speed plotted as a function of movement path (%) and the results of our statistical curve comparison (see Appendix for computational
Left and right columns show data for a target position 1 and 2, respectively, and top and bottom rows show data for no-visual feedback and visual feedback conditions, respectively. Dashed and solid lines show the average speed curve across subjects in allocentric and target-directed tasks, respectively and gray areas denote 95% confidence intervals around the difference between allocentric and target-directed curves for each target position and feedback condition. Because confidence intervals were computed based on the difference between target-directed and allocentric curves, they could be placed on either curve. We chose to place them on the allocentric curve. It is evident that the 95% confidence intervals overlap both curves for all target positions and visual feedback conditions. This shows that there was no difference between the shape of movement speed curves in target-directed and allocentric tasks.

Results Summary

Our analysis of residual variance suggests that visual feedback reduces movement variance significantly more in the target-directed as compared to the allocentric tasks and that differences between the tasks cannot be explained based on differences in uncertainty about the planned endpoint of the movement. The analysis of raw variance at the movement endpoint supports this interpretation of the data and also suggests that the directional scatter of allocentric movements in particular is unaffected by visual feedback. Furthermore, visual feedback improved accuracy more in the target-directed as compared to the allocentric task. Thus, both constant and variable errors suggest that visual feedback was used more in the target-directed than in the allocentric task. Finally,
our analysis of movement kinematics suggests that the differences we observed in the use of visual feedback between allocentric and target-directed tasks cannot be explained by differences in movement speed or curvature.

5. Discussion

The current experiments were designed to determine if the contribution of visual feedback to online control differs between target-directed and allocentric movements. The experiments were designed such that, in principle, target-directed and allocentric movements provided the exact same opportunities for visual feedback control. Yet, the results show unequivocally that visual feedback is used more to control movements in the target-directed as compared to the allocentric task.

Ruling out Target Uncertainty as a Potential Explanation of our Results

Due to our experimental paradigm, in which the visual target(s) disappeared as soon as subjects started moving, movements on each trial can be divided into a planning and a control stage (see also Faisal and Wolpert, 2008). During planning, target-directed or allocentric visual spatial information was used to determine the desired movement endpoint. During control, sensory feedback was used to bring the hand to the desired movement endpoint. As stated in the Introduction, the nature of the visual spatial information used for movement planning (i.e. target-directed vs. allocentric) is confounded with uncertainty about the location of the targets (i.e. uncertainty is higher in allocentric conditions). Our model of target uncertainty takes care of this. One could argue however, that target uncertainty is not only an additive component during
movement planning (as is the case in our model), but it also affects movement control.

According to this argument, the differences in feedback control that we observed between target-directed and allocentric movements were not due to differences between target-directed and allocentric movements *per se*, but to the differences in target uncertainty between the two tasks. Below we explain why this argument does not provide a satisfying account of our data.

First, the effect of visual target uncertainty on movement control, as it is conceptualized in models of optimal feedback control, does not predict the interaction between task and different types of sensory feedback that we observed (Liu and Todorov, 2007; Izawa and Shadmehr, 2008). Specifically, based on those models, we would expect a main effect of visual target uncertainty (which in our experiment would be the main effect of ‘task’) on movement variance in both visual feedback and no-visual feedback conditions, because the state estimate that these models use for movement control is based on any source of sensory feedback. In our experiments, however, we obtained an interaction between task and sensory feedback condition, i.e. we found that while visual feedback reduced movement variance more in target-directed as compared to the allocentric task, there was no such effect when only proprioceptive feedback was available. This interaction would not have been predicted by current models (Liu and Todorov, 2007; Izawa and Shadmehr, 2008). For completeness, we should point out that these models have been tested only in tasks where the target was visible throughout the movement, where subjects always had both visual and proprioceptive feedback about their hand, and where the target changed position during the movement. But even though our experimental paradigm was quite different, the conceptual argument still applies.
Second, if higher target uncertainty during movement planning led to higher uncertainty during movement control in allocentric conditions in our experiment, we would have expected to see lower movement speed in those conditions. This prediction follows from both behavioral data reported in the literature (e.g. see Loftus et al., 2004, and the literature reviewed in this report) and from models of optimal control, which predict a decrease in movement speed as control becomes less ‘certain’ (e.g. movement speed decreases when the movement target increases its blurriness during a movement; Izawa and Shadmehr, 2008). In short, if subjects were less certain during movement control in allocentric as compared to target-directed conditions in our experiment, then movement speed should have been lower in those conditions. This was clearly not the case (see Table 1, Fig.4 and 5).

In summary, the pattern of results we observed cannot be explained by appealing to target uncertainty.

Implications for Models of Sensory Integration for Movement Control

The finding that the relative magnitude of visual control can change with the task demands is consistent with previous results and lends further support to the idea that the sensory-motor system is highly flexible in the way it uses different sources of sensory information for movement control (McGuire and Sabes, 2009; Sarlegna and Sainburg, 2007; Sober and Sabes, 2005; van Beers et al. 1999, 2002). Importantly, however, our results are the first to demonstrate a reduction in the use of visual feedback for the control of allocentric as compared to target-directed movements. The only difference between the two movement tasks that we used was with respect to how the visual target was spatially
encoded prior to movement onset, i.e. whether it was coded in a target-directed or
allocentric fashion. Thus, our results strongly suggest that models of sensory integration
for sensorimotor control have to take into consideration how a visual target is spatially
encoded.

As laid out in the Introduction, models that argue for a statistically optimal
integration of different sources of sensory information for movement control have been
based entirely on data obtained from target-directed paradigms (Koerding and Wolpert,
2004, 2006; van Beers et al. 1999, 2002; McGuire and Sabes, 2009; Sarlegna and
Sainburg, 2007; Sober and Sabes, 2005; Saunders and Knill, 2004; Smeets et al. 2006).
Yet our experiments clearly show that allocentric movements rely less on visual
information about the moving hand than do target-directed movements. To reconcile
these findings with models derived entirely from target-directed movements, one could
either suggest that the principle of statistical optimality does not apply for the integration
of sensory information for the control of allocentric movements or one could suggest a
Bayesian framework that uses different priors for the weighting of visual information
about the moving hand in target-directed and allocentric tasks. Future research is needed
to test these and other possibilities.

Recently, Byrne and Crawford (2010) have shown that egocentric and allocentric
cues can make different contributions to the localization of a target in a reaching task –
and that the relative weighting of their contributions cannot be captured by statistical
optimality alone. It is important to emphasize, however, that all the movements in Byrne
and Crawford’s experiments were target-directed – and they did not compare, as we did,
target-directed movements to allocentric movements. Moreover, because the movements
in their experiments were always visual open-loop, they could not evaluate the contribution of visual feedback about the hand movement in their different conditions. If we take the idea that the influence of visual feedback is lower in the allocentric as compared to the target-directed task and combine it with recent modeling results relating the magnitude of visuo-kinesthetic drift (Smeets et al. 2006) and speed of visuomotor learning (Burge et al. 2008) to the relative weighting of visual and proprioceptive feedback for the control of hand movements, we can make new predictions about these two variables in allocentric and target-directed tasks. Specifically, based on the idea that the influence of visual feedback is reduced in the allocentric task, we would predict that magnitude of visuo-kinesthetic drift and speed of visuo-motor learning should be smaller in the allocentric than in the target-directed task. In a previous visuo-motor adaptation experiment we found results that are consistent with the latter prediction (Thaler and Todd, 2010). Further research is needed to test these predictions more systematically.

The finding that the influence of visual feedback differs between target-directed and allocentric tasks leads to additional predictions what might happen when visual-feedback mechanisms are disrupted. For example, based on our interpretation, we would expect that such disruptions would impair performance more in the target-directed than in the allocentric task.

Finally, it is important to keep in mind that the current experiments focused on the processing of visual feedback as it was acquired during movement execution. More research is needed to test how the differences between target-directed and allocentric tasks that we found here generalize to paradigms that manipulate visual feedback about
hand position prior to movement onset (e.g. Sarlegna and Sainburg, 2007; Sober and Sabes, 2005).

Implications for Models of Optimal Feedback Control

Current models of optimal feedback control use sensory estimates to derive state estimates that are then used to control the movement (Todorov and Jordan, 2002; Todorov, 2004). It is important to realize that the word ‘optimal’ in the context of models of optimal feedback control does not refer to the way sensory information is integrated, but to the way the control law is chosen, e.g. if the movement should be controlled by minimizing jerk, torque change, endpoint variance, etc. It follows then that the idea of optimal sensory integration is different from the idea of optimal control, and in fact, these two topics are studied separately from one another in the literature. Importantly, however, even though these topics are studied separately, current models of optimal feedback control nevertheless assume that the sensory information that is used for control is used in a statistically optimal fashion (for review see Diedrichsen et al. 2010). Given that this is the case, current models of optimal feedback control do not predict the interaction between task and type of sensory feedback that we observed in our experiments (see also our discussion of the issue of target uncertainty).

In the context of optimal control models, an anonymous reviewer suggested that it would be natural to model a subject’s performance in an allocentric task, such as figure copying, using a ‘via-point task’ like the one used by Todorov and Jordan (2002). Whether or not this is an appropriate model remains to be tested in future research. Based on our current results, however, we would predict that performance in a via-point task
would differ from performance in a matched figure-drawing task. In the via-point task used by Todorov and Jordan (2002), the visual information is target-directed (i.e. the finger moves through visual targets in a sequence), whereas in a figure-copying task, the visual information would be allocentric (i.e. the finger would move through a trajectory whose shape is based on the spatial layout of the targets, but the finger would never actually pass through any of the targets). As a consequence, we would predict that subjects should exert more visual control in a via-point task than in a figure-copying task. Again, we want to emphasize that we do not argue that copying a figure cannot in principle be modeled within the framework of optimal control. We would argue, however, that current models of optimal feedback control would not predict (and cannot account for) our results.

Relationship to Research about Vector and Endpoint Coding of Hand Movements

One of the questions that has been studied extensively over the years concerns the issue of whether the human motor system codes movements in terms of the displacement vector of the hand or in terms of the final position of the hand (for reviews, see Desmurget et al. 1998; De Grave et al. 2004). Several researchers have proposed that the human motor system may employ not just one, but two mechanisms for issuing motor commands: one dealing with the vector displacement, and the other with the final position of the hand (Brown et al. 2003; De Grave et al., 2004; DiZio and Lackner, 1995; Ghez et al. 2007; Gottlieb, 1996; Hirayama et al. 1993; Lackner and DiZio, 1994; 1998; Sainburg et al. 1999; Sainburg and Wang, 2002; Scheidt and Ghez, 2007). In our opinion, the distinction between allocentric and target-directed movements that we are proposing
might be related to the distinction between vector and endpoint coding. For example, the allocentric task could be considered a task in which subjects use predominantly vector coding because the visual instruction given to them specifies the movement vector, that is, movement distance and direction, whereas the target-directed task could be considered a task in which subjects rely more on endpoint coding. In fact, we have shown evidence for this idea in previous work (Thaler and Todd, 2009b). If we assume that subjects rely more on vector coding in the allocentric task and more on endpoint coding in the target-directed task, then the reduction that we observe in the use of visual feedback in allocentric as compared to target-directed tasks could be taken as evidence for the idea that there is a reduction in the use of visual feedback in updating the vector component of movement commands. We have put forth such a hypothesis in previous work (Thaler and Todd, 2009b; p.595, end of first paragraph). In summary, we believe that our results are not only consistent with previous findings about vector and endpoint coding of movements but they also extend them in new directions.

Neural Correlates

It has been suggested that allocentric movements of the kind used in our study make use of visual information processed in the ventral stream, whereas target-directed movements make use of visual information processed in the dorsal stream (Milner and Goodale, 2008; Schenk, 2006). In our experiments, we observed an increase in reaction times of 58 ms for allocentric as compared to target-directed movements. This delay in manual reaction time is consistent with delays in reaction time that have been reported when visual information used for movement programming is switched from ventral to
dorsal (e.g. Veerman et al. 2008). This result is consistent with the conjecture that allocentric and target-directed movements might potentially be mediated by the ventral and dorsal stream, respectively.

Interestingly, performance in a target-directed task, particularly when vision is being used to control the movement, has been linked to neural activity in the posterior parietal cortex, the terminus of the dorsal visual stream (Filimon et al. 2009; Ogawa et al. 2006). It has even been suggested that the posterior parietal cortex is the neural substrate of a ‘visual autopilot’ that monitors and adjusts ongoing movements based on visual information (Pisella et al. 2000). Our behavioral findings provide indirect support for this idea in that the performance on the target-directed task we used was associated with a strong reliance on online visual control. It might be the case, however, that the visual autopilot works more efficiently during target-directed movements where the visuomotor circuitry in the dorsal stream is engaged. The putative autopilot in the dorsal stream might not operate as efficiently in allocentric tasks. This idea can be easily tested.

**Beyond the phenomenon**

The question arises as to why our sensorimotor system should be predisposed to use visual feedback more for the control of target-directed than allocentric movements. One possible explanation might be that target-directed movements are typically performed more often under visual control than are allocentric movements. In other words, the architecture of our sensorimotor system might simply reflect how often visual feedback has been used to control these different kinds of movements in the past (either ontogenetically or phylogenetically, or both). As stated above, from a computational
perspective, this could be modeled within a Bayesian framework by using different priors for the weighting of visual information in the target-directed and allocentric tasks. Another possible explanation, which could be related, is that the spatial representations that underlie performance in allocentric tasks cannot be updated as rapidly by online visual information as can the representations that underlie the performance of target-directed tasks. We have argued elsewhere that target-directed and allocentric hand movements are based on different kinds of spatial representations and that the representations that can be used in target-directed tasks can be computed faster and more reliably (Thaler and Goodale, 2010; Thaler and Todd, 2009a). Again, future research is needed in order to answer these questions.

**Implications for Everyday Behavior**

The tasks used in the current paper were designed to equate target-directed and allocentric tasks in as many aspects as possible. As in most experimental settings, even though this strengthens the validity of the experimental comparison, it also potentially reduces the degree to which the findings generalize to everyday behavior. But given that our tasks were designed to minimize the differences between target-directed and allocentric tasks, we would argue that the results of our experiments capture real differences between everyday target-directed movements, such as picking a coffee cup or pressing an elevator button, and everyday allocentric movements, such as sketching a building, copying a diagram, or even imitating a gesture.

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References


Appendix

Equations for Distance Variance in Model of Target Uncertainty

In Thaler and Todd (2009a), the relationship between the SD (in mm) and magnitude of a probe dot adjustment (in mm) in target-directed conditions was described as $y = 1.9 + 0.01x$. In allocentric conditions the relationship was described as $y = 2.9 + 0.044x$ and $y = 1.5 + 0.054x$, when the adjustment direction was parallel or rotated with respect to the direction of the allocentric target configuration, respectively. Thaler and Goodale (2010) measured the relationship between the SD and magnitude of a probe dot adjustment in target-directed and allocentric conditions as $y = 7.3 + 0.03x$ and $y = 13 + 0.019x$, respectively. In that study, the data showed a non-linear trend. The non-linear trend was strongly reduced when the data obtained in response to the farthest target distance (220 mm) was omitted. In that case the equations are $4.1 + 0.06x$ and $6.2 + 0.065x$, respectively.

Since the current experiments did not employ distances beyond 152 mm we used the second set of equations for the current experiments. For completeness, however, we confirmed that the results with regard to the analysis of residual variances hold when we compute the model using equations that include data from trials with the farthest target distance. The numerical differences between equations from Thaler and Todd and Thaler and Goodale are due to differences in eye movements. In particular, in Thaler and Todd (2009a) subjects moved their eye freely, but in Thaler and Goodale (2010), they directed their gaze at a central fixation target which changed position between target presentation and adjustment. To obtain equations for the current study, we first averaged coefficients across the two different allocentric conditions in Thaler and Todd. Then, we averaged coefficients across studies separately for target-directed and allocentric conditions.
Computation of Movement Variance as Function of Average Movement Distance (mm)

First, we computed average movement distance $d$ separately for each subject, target position, and experimental condition. Then, for each individual movement trajectory of length $l_i$ for each target position, experimental condition, and subject, where average movement distance is $d$, we collected the x and y coordinates at 101 points. These 101 points were defined as the sequential points along the trajectory where the distance traveled reached $d_i = l_i \cdot \frac{n^*}{100}$, with $n$ going from 0 to 100. The computation of those coordinates was carried out for all 32 movement trajectories separately for each subject, target position, and experimental condition, yielding 101 bins, each bin containing 32 pairs of x and y coordinates, for each subject, target position and experimental condition. Movement variance was then computed as the sum of the x and y variances for each bin, i.e. $s_n^2 = s_{x_n}^2 + s_{y_n}^2$, where $n$ denotes the $n^{th}$ bin, which corresponds to the $n^{th}$ portion of the average movement distance. A function that expresses movement variance as a function of average movement distance (mm) was obtained by plotting movement variance obtained this way against the corresponding average movement distance. The results of this procedure are shown in Fig.3 and in the Suppl. Note.

Computation of Average Movement Speed as Function of Average Movement Distance (mm) and Movement Path (%)

The computation of movement speed as a function of movement distance was the same as the computation of movement variance with the only difference that instead of collecting the x and y coordinates at $d_i$ we measured speed at $d_i$. This speed measurement
was carried out separately for all 32 movement trajectories for each subject, target position, and experimental condition, yielding 101 bins, each bin containing 32 speed values, for each subject, target position, and experimental condition. Average movement speed was then computed for each bin. A function that expressed average movement speed as a function of average movement distance (mm) was then obtained by plotting average movement speed obtained this way against the corresponding average movement distance. The results of this procedure are shown in Fig.4. A function that expressed average movement speed as a function of movement path (%) was obtained by plotting average movement speed against bin number. The results of this procedure are shown in Fig.5.

Statistical Comparison of Speed Curves

To determine if there was a difference in the way movement speed changes as a function of movement path (%) between target and allocentric conditions, we computed the difference between average speed values at corresponding parts of the movement path (%) in allocentric and target-directed conditions, separately for each subject, target position and visual feedback condition. Thus, for each target position and feedback condition and for each of the 101 parts of the movement path, we obtained 14 difference-values. Based on these values we then computed 95% confidence intervals around the difference for each of the 101 parts of the movement path, separately for each target position and visual feedback condition. To be liberal in our statistical criterion, we did not perform a Bonferroni correction, but computed each confidence interval using alpha p=.05. The confidence intervals obtained this way are shown in Fig.5.
Figure Captions

Figure 1
Illustration of the two movement tasks and visual feedback conditions. The hand is drawn for illustration but was never visible during the experiment. Before movement onset, the visual display differed between the allocentric and target-directed movements. During movement execution, the visual display was the same in allocentric and target-directed movements, and differed only between visual feedback and no-visual feedback conditions. Subjects had to maintain their gaze on the fixation spot in all conditions. Please see text for details about the visual stimuli.

Figure 2
Thin curves: Minimum variance ellipses expected based on variability in visual target localization. Thick curves: Minimum variance ellipses that were computed based on all subjects (n=15) movement endpoints after each subject’s mean was subtracted. Curves are plotted at the end of the average movement trace and at a 90 mm cutoff-point. For better visibility the latter curves have been enlarged in the insets. Ellipse axes denote two SDs. Dots: Subjects movement endpoints. The thick and thin curves overlap almost perfectly for the target-directed task at 90 mm when visual feedback is available (bottom left panel). In all other conditions, the thick ellipses are bigger than the thin ones.

Figure 3
Movement variance (mm²) plotted as a function of average movement distance (mm). Each curve denotes the data for one individual subject. For ease of data display, the ordinate uses a non-linear scale (i.e. successive squares), whereas the abscissa uses a linear scale. Vertical lines denote the 90mm truncation point.

Figure 4
Average movement speed plotted as a function of average movement distance (mm). Each curve denotes the data for one individual subject. Vertical lines denote the 90mm truncation point.

Figure 5
Average movement speed plotted as a function of movement path (%). Each curve denotes the data averaged across subjects. Gray areas denote 95% confidence intervals around the difference between target-directed and allocentric curves. Because confidence intervals were computed based on the difference between target-directed and allocentric curves they could be placed on either curve. We chose to place them on the allocentric curves.
Visual Display Before Movement Onset

Target Directed

Allocentric

Visual Display During Movement Execution

No Visual Feedback

Visual Feedback

- Visual Feedback Cursor
- Fixation Target
- Hand Starting Point
- Target Dot
- Reference Target Dot (Allocentric Task Only)
Target Directed

No Visual Feedback

Target Uncertainty (Model)

Movement Variability (Data)

Average Movement Trace

Individual Movement Endpoint

Allocentric

Visual Feedback

Target Directed Allocentric No Visual Feedback

Target Uncertainty (Model)

Movement Variability (Data)

Average Movement Trace

Individual Movement Endpoint
Target Point 1

Target-Directed

Allocentric

Average Movement Speed (mm/s)

No Visual Feedback

Visual Feedback

Average Movement Distance (mm)

Target Point 2

Target-Directed

Allocentric

Average Movement Speed (mm/s)

No Visual Feedback

Visual Feedback

Average Movement Distance (mm)
Target Point 1

Target Point 2

No Visual Feedback

Visual Feedback

Average Movement Speed (mm/s)

Movement Path (%)
<table>
<thead>
<tr>
<th>Target-directed</th>
<th>Allocentric</th>
</tr>
</thead>
<tbody>
<tr>
<td>Physically correct Movement Distance (mm)</td>
<td>Target point 1</td>
</tr>
<tr>
<td></td>
<td>122</td>
</tr>
<tr>
<td>Movement Distance (mm)</td>
<td>123 (14)</td>
</tr>
<tr>
<td>Movement Direction Error (Degrees)</td>
<td>Target point 1</td>
</tr>
<tr>
<td></td>
<td>-2.5 (3.2)</td>
</tr>
<tr>
<td>Endpoint Error (mm)</td>
<td>14.7 (7.7)</td>
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<tr>
<td>Curvature (%)</td>
<td>2.7 (1.7)</td>
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<tr>
<td>Average Movement Speed (mm/s)</td>
<td>133 (26)</td>
</tr>
<tr>
<td>Maximum Movement Speed (mm/s)</td>
<td>233 (53)</td>
</tr>
<tr>
<td>Movement Onset Time (ms)</td>
<td>402 (186)</td>
</tr>
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</table>

Table 1 – Averages and sample standard deviations (in parenthesis) of constant errors and movement kinematics. Standard deviations were computed across subjects.
<table>
<thead>
<tr>
<th></th>
<th>Target-directed</th>
<th>Allocentric</th>
</tr>
</thead>
<tbody>
<tr>
<td>Raw Movement Variance at Endpoint (mm²)</td>
<td>181 (149)</td>
<td>61 (33)</td>
</tr>
<tr>
<td>Residual Movement Variance at Endpoint (mm²)</td>
<td>141 (150)</td>
<td>21 (33)</td>
</tr>
<tr>
<td>Raw Movement Variance at 90 mm (mm²)</td>
<td>84 (73)</td>
<td>30 (13)</td>
</tr>
<tr>
<td>Residual Movement Variance at 90 mm (mm²)</td>
<td>56 (73)</td>
<td>1 (13)</td>
</tr>
<tr>
<td>(SD^2) Movement Distance (mm²)</td>
<td>134 (117)</td>
<td>40 (27)</td>
</tr>
<tr>
<td>(SD) Movement Distance (mm)</td>
<td>10.9 (3.7)</td>
<td>6 (1.8)</td>
</tr>
<tr>
<td>(SD^2) Movement Direction (Degrees²)</td>
<td>8.4 (6.3)</td>
<td>3.7 (1.6)</td>
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<td>(SD) Movement Direction (Degrees)</td>
<td>2.7 (0.9)</td>
<td>1.9 (0.5)</td>
</tr>
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</table>

**Table 2** – Averages and sample standard deviations (in parenthesis) of variable errors. Standard deviations were computed between subjects after averaging across the two different target points.