Neuropsychologia 47 (2009) 1227–1244

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

The use of head/eye-centered, hand-centered and allocentric representations for visually guided hand movements and perceptual judgments

Lore Thaler*, James T. Todd

Department of Psychology, The Ohio State University, Columbus, OH, USA

ARTICLE INFO

Article history:
Received 1 April 2008
Received in revised form 27 November 2008
Accepted 3 December 2008
Available online 7 February 2009

Keywords:
Visually guided movement
Visual perception
Motor control
Hand movement
Egocentric
Allocentric
Coordinate system
Representation

ABSTRACT

Two experiments are reported that were designed to measure the accuracy and reliability of both visually guided hand movements (Exp. 1) and perceptual matching judgments (Exp. 2). The specific procedure for informing subjects of the required response on each trial was manipulated so that some tasks could only be performed using an allocentric representation of the visual target; others could be performed using either an allocentric or hand-centered representation; still others could be performed based on an allocentric, hand-centered or head/eye-centered representation. Both head/eye and hand centered representations are egocentric because they specify visual coordinates with respect to the subject. The results reveal that accuracy and reliability of both motor and perceptual responses are highest when subjects direct their response towards a visible target location, which allows them to rely on a representation of the target in head/eye-centered coordinates. Systematic changes in averages and standard deviations of responses are observed when subjects cannot direct their response towards a visible target location, but have to represent target distance and direction in either hand-centered or allocentric visual coordinates instead. Subjects' motor and perceptual performance agree quantitatively well. These results strongly suggest that subjects process head/eye-centered representations differently from hand-centered or allocentric representations, but that they process visual information for motor actions and perceptual judgments together.

1. Introduction

One of the most common actions performed by humans is to reach out and grab or touch visible objects in the environment. The ability to perform these actions is generally taken for granted in our day-to-day activities. However, from a scientific perspective, our understanding of the basic mechanisms of visually guided reaching behavior is far from complete (for reviews see Desmurget & Grafton, 2000; Desmurget, Pelisson, Rossetti, & Prablanc, 1998; Lacquaniti & Caminiti, 1998; Todorov, 2004).

In order to successfully move one's finger to precisely touch a visible target it is necessary to have corresponding representations of both visual and haptic/motor space. One possibility, for example, is that each of these spaces has a full blown metric structure, such that it is possible to determine the distance and orientation between any pair of locations. In order to move one's finger from point A to point B using this type of allocentric representation, it would first be necessary to visually determine the distance and orientation between those points, and then use those parameters to program an appropriate limb movement.

An alternative possibility is to employ an egocentric hand-centered representation, in which the position of a point in space is defined relative to the subject's hand. In order to move one's finger to a visible target using an hand-centered representation, it would first be necessary to visually determine the position of the target relative to the subject's hand, and then use that information to position the finger in haptic space. In the literature, it has been suggested that the position of the target with respect to the hand is represented in terms of the distance and direction of the vector pointing from the hand to the target, and that movement parameters will be selected that will move the hand over the visually perceived hand-target vector (i.e. Bock & Eckmiller, 1986; Vindras & Viviani, 1998). It is important to note that, by definition, distance and direction of the hand-target vector always match distance and direction of the desired movement vector.

A third possibility is to employ an egocentric head or eye-centered representation, in which the position of a point in space is defined relative to the subject's head or eye. In order to move one's finger to a visible target using an head/eye-centered representation, it would first be necessary to visually determine the position of the target relative to the subject's head/eye, and then use that information to position the finger in haptic space. In the literature, it has been suggested that the position of the target with respect to the head or eye is represented in terms of the distance and direction of the vector pointing from the head/eye to the tar-

* Corresponding author at: Department of Psychology, The University of Western Ontario, Social Science Building, Room 6237, London, Ontario, N6A 5C2, Canada.
E-mail address: lthaler2@uwo.ca (L. Thaler).

0028-3932/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2008.12.039

get, and that movement parameters will be selected that will move the hand towards the visually perceived position of the target (i.e. Bizzi, Accornero, Chapple, & Hogan, 1984; Desmurget & Prablanc, 1997; Feldman, 1966; Flanders, Helms-Tillery, & Soechting, 1992; McIntyre, Stratta, & Lacquaniti, 1997; Polit & Bizzi, 1979; Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995; Vetter, Goodbody, & Wolpert, 1999). It is important to note that target position in head/eye-centered coordinates will not match distance and direction of the desired movement vector—unless the movement originates at the head/eye. Thus, if subjects relied on a head/eye-centered representation to guide their hand, they effectively guide their hand towards desired endpoints whose coordinates are stable, even when the hand-target vector changes from one movement to the next.

In the literature, models that use head/eye-centered visual coordinates for the selection of the goal state of the limb ('Endpoint Coding Models') are distinguished from those that use hand-centered coordinates ('Vector Coding Models') (De Grave, Brenner, & Smeets, 2004; van den Dobbelsteen, Brenner, & Smeets, 2001; Vindras, Desmurget, & Viviani, 2005). It is important to note that Endpoint Coding Models differ to the degree that they consider current hand position in the selection of the motor commands that will bring the hand into the desired goal state. For example, whereas some assume that motor commands are selected by interpolating from the current to the desired posture (Desmurget & Prablanc, 1997; Rosenbaum et al., 1995), others assume that they result from the motor apparatus being 'pulled' into a desired equilibrium state (i.e. Feldman, 1966; Polit & Bizzi, 1979). Despite differences regarding the selection of motor commands, all Endpoint Coding Models initially determine the goal state of the limb based on a visual representation of the target that is independent from current hand position.

There is considerable body of evidence to suggest that the representations of visual and haptic space employed by humans may vary in different contexts or tasks or for different aspects of a single action (Brenner & Smeets, 1996; Carey, 2001; Franz, 2001; Jeannerod, Paulignan, Mackenzie, & Marteniuk, 1992; Smeets, Brenner, DeGrave, & Cuijpers, 2002). A particularly influential paper on this topic was reported by Goodale, Milner, Jakobson, and Carey (1991). They examined a patient (DF) with bilateral damage to the ventral visual stream, using a variety of tasks. When DF was asked to provide a perceptual report on the orientation of a visible slot, by turning a hand held card until its orientation matched that of the visible slot, her performance was barely above chance. However, when she was asked to simply insert the card into the slot, her performance was quite similar to that of normal controls. Although these tasks may appear at first blush to be quite similar, they are obviously quite different with respect to the visual-motor capabilities of DF. In order to explain these findings, as well as several others, Goodale and Milner (1992) and Milner and Goodale (2008) argue that perceptual judgments and motor actions involve functionally and neurologically distinct processing streams.

An alternative explanation proposed by Schenk (2006) is that the insertion task could be achieved using a hand centered egocentric representation of visual and haptic space, but that the matching task requires an allocentric representation. According to this idea, allocentric and hand centered egocentric visual spatial information is computed in independent processing streams and DF's cortical lesions impaired her ability to use allocentric information, while leaving her ability to perform tasks based on a hand-centered egocentric representation intact.

Yet other researchers have suggested that various differences that have been observed between visuo-motor and perceptual performance can be explained by the fact that visuo-motor tasks permitted subjects to move their hand towards endpoints in head/eye-centered coordinates, whereas perceptual tasks required subjects to compute distances and directions in either hand centered or allocentric coordinates (Smeets et al., 2002).

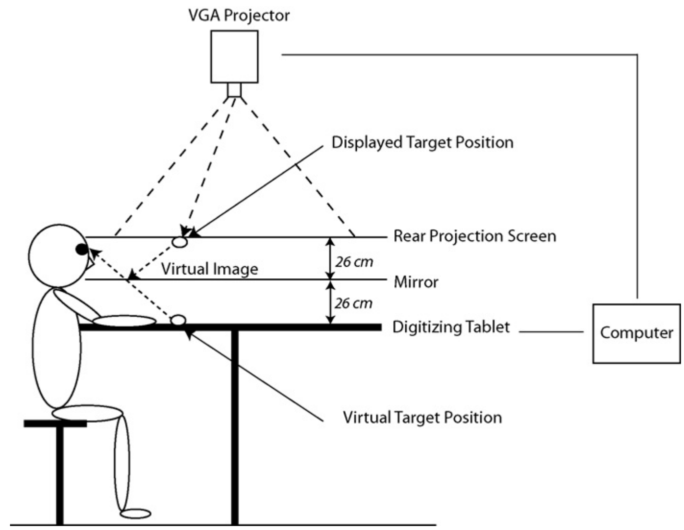

Fig. 1. Sketch of the experimental apparatus.

The research described in the present article was designed to assess the relative importance of egocentric hand centered, egocentric head/eye-centered and allocentric representations for visuo-motor and perceptual performance. In order to achieve this goal we compared performance on tasks that could potentially be performed using head/eye-centered coordinates relative to those that require hand centered or allocentric coordinates. In addition, we compared performance for tasks involving visually guided reaching movements (in Exp. 1) with those that involved perceptual matching judgments (in Exp. 2) that did not require any motions of the arm or hand.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

Eight subjects (five males, three females), including the authors, participated in the experiment. Prior to the experiment subjects were asked if they were right or left-handed and with which hand they would prefer to perform the task. Two male and one female subject reported to be left-handed and chose to perform the task with their left hand. The other subjects reported to be right-handed and chose to perform the task with their right hand. Subjects gave informed consent before the experiment and were paid for their participation. All subjects had self-reported normal or corrected to normal vision.

2.1.2. Apparatus

A sketch of the experimental apparatus is provided in Fig. 1. Subjects were seated on a height adjustable chair. Stimuli were displayed on a rear projection screen and viewed by subjects in a front-surface mirror that was mounted halfway between the rear projection screen and a digitizing tablet. Subjects moved their hands on the digitizing tablet. Thus, the mirror prevented subjects from seeing their hand during the experiment. At the same time, the matched distances between mirror surface and screen and mirror surface and tablet made the mirror reflection of stimuli appear to be in the same plane as the digitizing tablet.

Hand movements were recorded with a stylus on the digitizing tablet (AccuGrid, Model A90; Numonics Corporation, Montgomeryville, PA; 1200(H) × 900(V) mm, accuracy 0.254 mm) at a temporal and spatial resolution of 200 Hz and 40 lines/mm, respectively. Stimuli were projected on the rear projection screen with a VGA projector (Casio XJ-360) at a temporal and spatial resolution of 60 Hz and 1024(H) × 768(V) pixels, respectively. The active display area subtended 863(H) × 647(V) mm. Displays were viewed binocularly in a darkened room and a chin rest was used avoid changes in head position. Subjects' eyes were located ∼460 mm above the tablet. A computer (Dell Dimension 8300 PC with an ATI Radeon 9700 PRO graphics card) was used to control stimulus presentation and data collection. In order to calibrate the apparatus, changes in lens position that could occur between sessions were corrected by optically aligning a projected 17-point grid with a corresponding grid on the rear projection surface before each session.

2.1.3. Stimuli and task

The experiment involved four tasks outlined schematically in Fig. 2a. In all tasks, the subject's hand is initially located at a visible starting point. Visual feedback is provided in between trials to help subjects move their hand towards the starting point. However, during experimental trials, visual feedback is not available and the hand is unseen. Along with the visible starting point, there are two visible lines, one of which indicates target direction, the other target distance. The task on each trial is to move the hand in the visually specified target direction, over the visually specified target distance. In the 'Endpoint – Head/Eye Centered' task (top row in Fig. 2a), the two lines that specify target direction and distance originate at the starting point of the hand and have the same orientation. Therefore, the endpoint of the line segment that signifies target distance creates a visible target location towards which subjects can move their unseen hand. Note that actions in the 'Endpoint – Head/Eye Centered' task could therefore be achieved using any of the three possible representations (head/eye-centered, hand centered, allocentric) described above. In the 'Rotated – Hand Centered' task (second row in Fig. 2a), the two visible lines that specify target direction and distance also originate at the starting point of the hand, but they differ 45° in orientation. Therefore, subjects cannot move their hand towards the endpoint of the line segment that specifies target distance but an explicit computation of distance with respect to the hand required. In the 'Allocentric' tasks employed in the current experiments (third and bottom row in Fig. 2a), only the line that specifies target direction emanates at the starting point of the hand, whereas the line that specifies target distance does not. Just as in 'Endpoint – Head/Eye Centered' and 'Rotated – Hand Centered' tasks, the task on each trial is to move the hand along the visually specified target direction, over the visually specified target distance. However, because visually specified target distance in this case is not defined relative to the subject, this task can only be performed using an allocentric representation. We used two different allocentric tasks. In 'Translated - Allocentric' tasks, target distances were indicated by line segments that had been translated with respect to the starting position of the hand (target direction 90°: 70 mm right, 130 mm up; target direction 45°: 40 mm right, 140 mm up). In 'Translated and Rotated - Allocentric' tasks target distances were indicated by line segments that had been translated (target direction 90°: 70 mm right, 130 mm up; target direction 45°: 70 mm left) and rotated 45° with respect to the starting position of the hand. We used the rotated version of the allocentric task for the following reason. In the 'Rotated – Hand Centered' task, the target distance segment is rotated with respect to the target direction. In contrast, in the 'Translated - Allocentric' task the target distance segment is parallel to the target direction. Including 'Allocentric' conditions in which the orientation of the target distance segment and target direction differ in the same way as in 'Rotated – Hand Centered' conditions, will enable us to determine if the difference in orientation between the target distance segment and the target direction introduces systematic errors, irrespective of the representation being egocentric or allocentric.

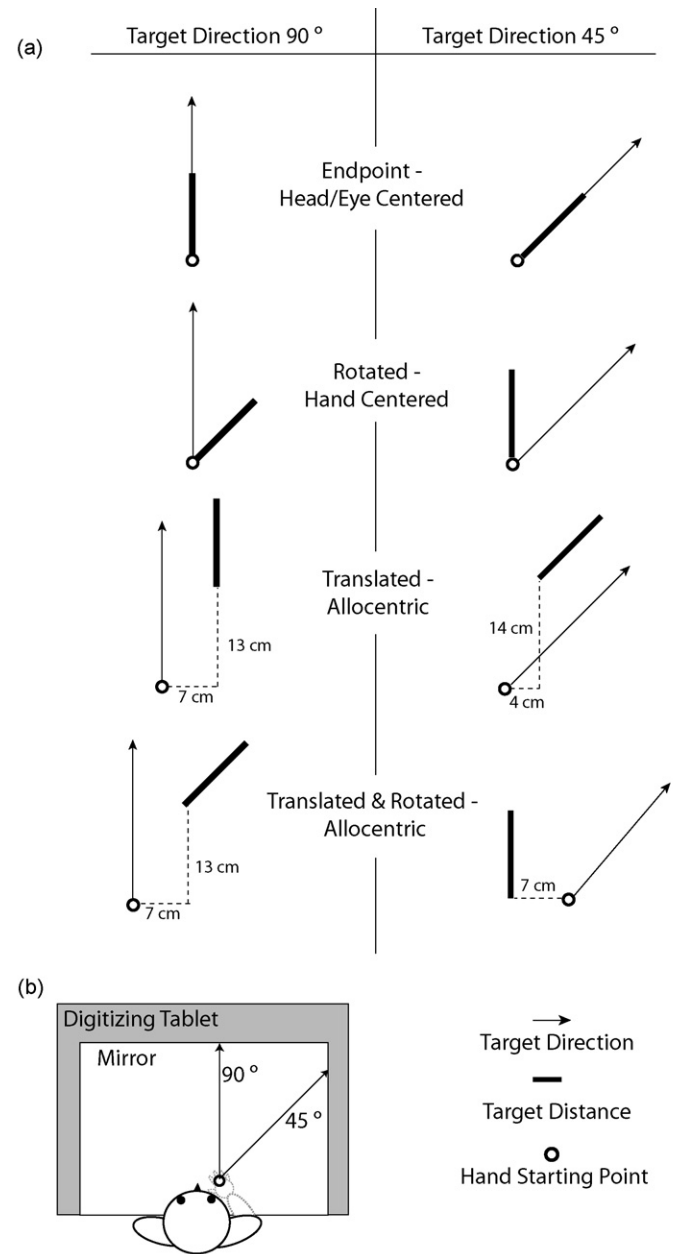

Fig. 2. (a) Illustration of the four tasks used in the experiment. Only one target distance is illustrated for each condition. Setup for left-handed subjects was mirror symmetric. Please see text for details. (b) Bird's eye view of the (virtual) movement area (not drawn to scale).

In all conditions, subjects were asked to move their hand in one of two target directions (90° or 45°) over five different target distances (60, 100, 140, 180, 220 mm). Hand starting position was fixed over the course of the experiment and located on the recording surface 460 mm below, 89 mm right and 55 mm to the front of subjects' eyes. A red circular area (5 mm diameter) projected on the virtual movement area indicated hand starting position throughout the experiment and black lines (width 2 mm) that emanated from the visible starting position and that extended over the whole movement area indicated target direction. Blue line segments (width 2 mm) indicated target distances. A bird's eye view of the (virtual) movement area is illustrated in Fig. 2b. The setup for left-handed subjects was mirror symmetric. All Stimuli were presented in front of a light gray background covered with 2500 small, randomly positioned points. Random positions were recomputed on every trial.

Two aspects of our experimental design need to be highlighted. First, our experimental manipulation only affects the way target distance is visually specified, since target direction was visually specified in the same way in all conditions. Thus, we might expect larger effects of our manipulations on movement distance than movement direction. Second, in 'Rotated – Hand centered' 45° and 90° conditions subjects respond to the same visual target distance segments as in 'Endpoint – Head/Eye centered' 90° and 45° conditions, respectively. Therefore, if subjects used a hand-centered representation of target distance to perform in 'Endpoint – Head/Eye centered' conditions, we would expect that their performance in 'Endpoint – Head/Eye centered' 90° and 45° conditions matches their performance in 'Rotated – Hand centered' 45° and 90° conditions, respectively.

2.1.4. Procedure

Each trial began with the display of the target direction and hand starting position. To initiate a trial subjects moved their hand to the starting position. During this phase subjects received online feedback on hand position via a green cursor dot (4 mm diameter) projected on their real hand position. This feedback facilitated the move to the starting position and provided subjects with visual information on their hand position without giving feedback relevant to the experimental task. Short periods of visual feedback on hand position prevent systematic shifts of hand position over time (Wann & Ibrahim, 1992; Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006). These shifts are referred to in the literature as visuo-kinesthetic drift (Wann & Ibrahim, 1992), but they can also be explained as a shift from a combined visual/proprioceptive towards a more proprioceptive estimate of hand position (Smeets et al., 2006). Once subjects had remained within the 5 mm diameter circle around the starting position for at least 1.8 s, a beep would indicate begin of a trial. Synchronous with the beep the target distance segment would appear and online hand feedback would disappear. Target direction and hand starting point would remain visible during a trial. Subjects were instructed to move over the target distance along the target direction in one smooth movement. Subjects were told that there was no time pressure and that they should move as accurately as possible.

A trial was terminated either if subjects had not started to move after 2.5 s or if the hand would move less than 1 mm during the last 300 ms. A beep signaled the end of a trial. The target distance segment would disappear and target direction and starting position for the next trial would appear. After subjects had moved at least 30 mm away from their final hand position online feedback was restored. Movement traces for individual trials were stored on disk for off-line analysis. Stimulus presentation was blocked with respect to the two target directions and four tasks ('Endpoint – Head/Eye Centered', 'Rotated – Hand Centered', 'Translated - Allocentric', 'Translated and Rotated - Allocentric'), yielding eight blocks. Within a block, each of the five target distances was presented four times in random order. Each subject participated in two ~40 min sessions on separate days. Each session contained two sets of eight blocks. Thus, every subject gave 16 responses to every stimulus. In the beginning of each session, subjects were made familiar with task and set-up by giving a short practice phase, during which they gave at least four responses in each of the four tasks (at least 16 practice trials total before each session). Practice trials were not recorded.

2.1.5. Kinematic analysis

Movement trajectories were smoothed using a Butterworth filter with 7 Hz cut off. Movement velocities were obtained by numerical differentiation. Trajectories with velocity profiles containing more than one peak or with duration above 2.5 s were rejected (2.1%). The first coordinate of each trace at which velocity exceeded 1 cm/s was considered the start point of a trajectory. The first coordinate of each trace at which velocity fell below 1 cm/s was considered the endpoint of a trajectory.

2.1.6. Data analysis

For each movement the equation for a straight line joining start and endpoints was computed. *Movement Distance* was computed as the length of that line and movement direction as its angular orientation. For each movement we could then compute the *Movement Direction Error* as angular deviation between the target direction and movement direction. To assess systematic deviations from the visually specified target distance and direction, we computed *constant errors* as average movement distance and average movement direction error. To assess reliability of subjects' performance, we computed *variable errors* as standard deviations (S.D.s) of subjects' movement distance and movement direction error. To characterize distributions of movement endpoints we fitted minimum variance ellipses to endpoints of all subjects hand movements for each target distance, direction and task (Gordon, Ghilardi, & Ghez, 1994; van Beers, Haggard, & Wolpert, 2004). To avoid that individual differences would affect distributions of movement endpoints we subtracted each subjects mean endpoint $(\bar{x}, \bar{y})$ for that target distance, direction and task before computing the ellipse. Ellipses were determined by computing the normalized eigenvectors v and eigenvalues d of the 2×2 sample covariance matrix R, whose elements are given by

$$R_{jk} = \frac{1}{n}\sum_{i=1}^{n} \delta_{ij}\delta_{ik},$$

where the deviation $\delta_i = \vec{p}_i - \bar{\vec{p}}$ is the endpoint of movement i along one of two orthogonal axes (rows and columns j, $k \subset \{x, y\}$) and $\bar{\vec{p}}$ is the mean position over n trials. The square root of the eigenvalues corresponds to the standard deviation of movements along each axis specified by the associated eigenvectors. The shape or aspect ratio of the ellipse is determined by the ratio of the square roots of the eigenvalues, i.e. $\sqrt{d1}/\sqrt{d2}$. Ellipse size, i.e. area, is determined by the absolute magnitude of the eigenvalues and orientation by the orientation of the eigenvectors.

Errors in movement direction and distance and therefore the distribution of movement endpoints are affected by *Kinematic Parameters* such as movement velocity and trajectory shape (van Beers et al., 2004). To determine if shape of movement trajectories differed across conditions, we determined movement curvedness by computing the absolute distance of any point on a movement trajectory to the straight line connecting trajectory start and endpoints, and by dividing the maximum absolute distance by the length of the straight line (Atkeson & Hollerbach, 1985). To represent curvedness values in percent, we multiplied this ratio by 100. Movement Curvedness of 0% corresponds to a straight-line trajectory, whereas Movement Curvedness of 50% could correspond to a half-circular trajectory. Average movement velocity, peak movement velocity and movement duration were computed based on smoothed movement trajectories. In order to base our analyses on representative samples of movements, we excluded movements whose distance, orientation error, curvedness or x and y coordinate exceeded the $25\% - 1.5 \times$ iqr or 75%tile + $1.5 \times$ iqr (iqr = inter quartile range). Using this method, which is robust in the presence of outliers, 13% of movements were rejected.

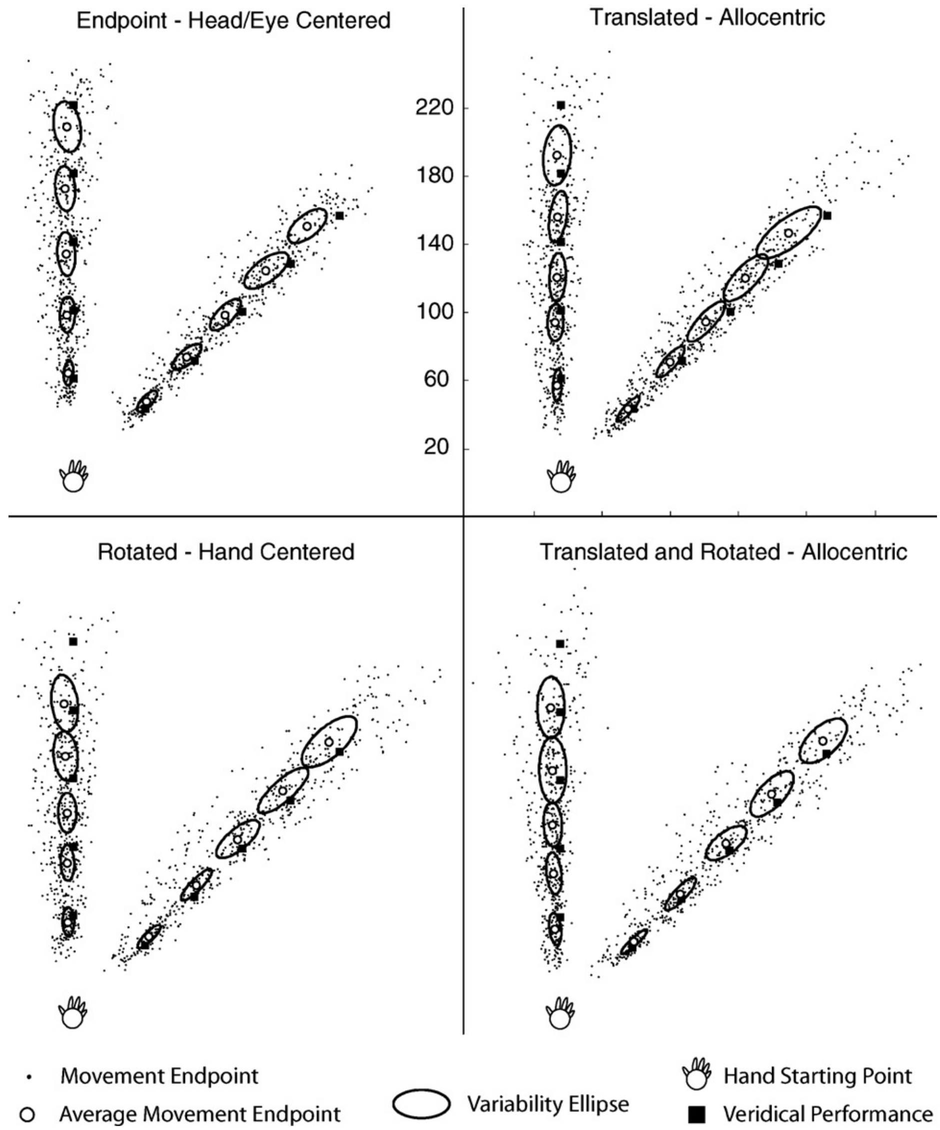

Fig. 3. Distributions of movement endpoints and variability ellipses for the different experimental conditions in Exp. 1. Ellipse axes denote two S.D. around the mean. Ellipses were computed based on all subjects' responses after subtracting each subject's mean. Ellipses are positioned on the average movement endpoint across all subjects. Black squares mark the endpoint that would have resulted from a movement executed veridical along the target direction over the target distance.

2.2. Results

There were no systematic differences among naïve subjects and authors. Furthermore, the data from left-handed subjects did not differ systematically from those of the right-handed subjects in our experiment. Proprioceptive biases for the perceived position of the hand are known to be mirror symmetric for the right and left arm (Haggard, Newman, Blundell, & Andrew, 2000). Thus, we mirrored the data of the three left-handed subjects for our analyses and analyzed them together with the right-handed subjects. For completeness, statistical results are reported for the whole group and for right-handed subjects only.[1] We report statistical results with degrees of freedom corrected according to Huynh and Feldt (1976) where the sphericity assumption is rejected ($p < .05$).

Fig. 3 shows subjects' movement endpoints in the four different tasks. The average movement endpoint across all subjects is

[1] It has been reported that reliability of perceived position of the hand in space is higher for the right than for the left hand, for both right and left-handed subjects (van Beers, Sittig, & Denier van der Gon, 1998). If this difference were due to a true right-left hand asymmetry, left-hander performing with their left hand are expected to have a disadvantage in our 'Endpoint' task, which might question the generalizability of our findings to the population of left-handed subjects. However, there are various reasons why we consider our results to hold for both right and left-handed subjects. First, inferior performance of the left hand for both left and right handed subjects in van Beers et al.'s (1998) study is well explained by the fact that the left hand was moved in an unnatural posture below a table top whereas the right hand moved in a natural posture above the table top (van Beers et al., 1998, p. 373). Second, across a wide array of visuo-motor tasks left-handed subjects perform equivalent to right handed subjects when they use their preferred hand (Henkel et al., 2001; Peters & Servos, 1989; Wang & Sainburg, 2006). Our own data is consistent with these findings, because left-handers perform with their left hand just like right-handers with their right hand and statistical results hold even when left-handers are excluded from analysis (see subsequent paragraphs). Third, both left and right-handed subjects perform very similar in the visuo-motor and the perceptual task in our experiments (compare Table 4). Thus, it appears that the visual spatial representations that are used for both the perceptual and visuo-motor task determine performance, irrespective of the subjects being right or left handed. In summary, even though many studies cannot exclude the possibility that there is a true left-right hand difference, because they exclude left-handers from analysis (i.e. Sainburg & Kalakanis, 2000; Sainburg & Wang, 2002), we believe that handedness does not affect the generality of our results.

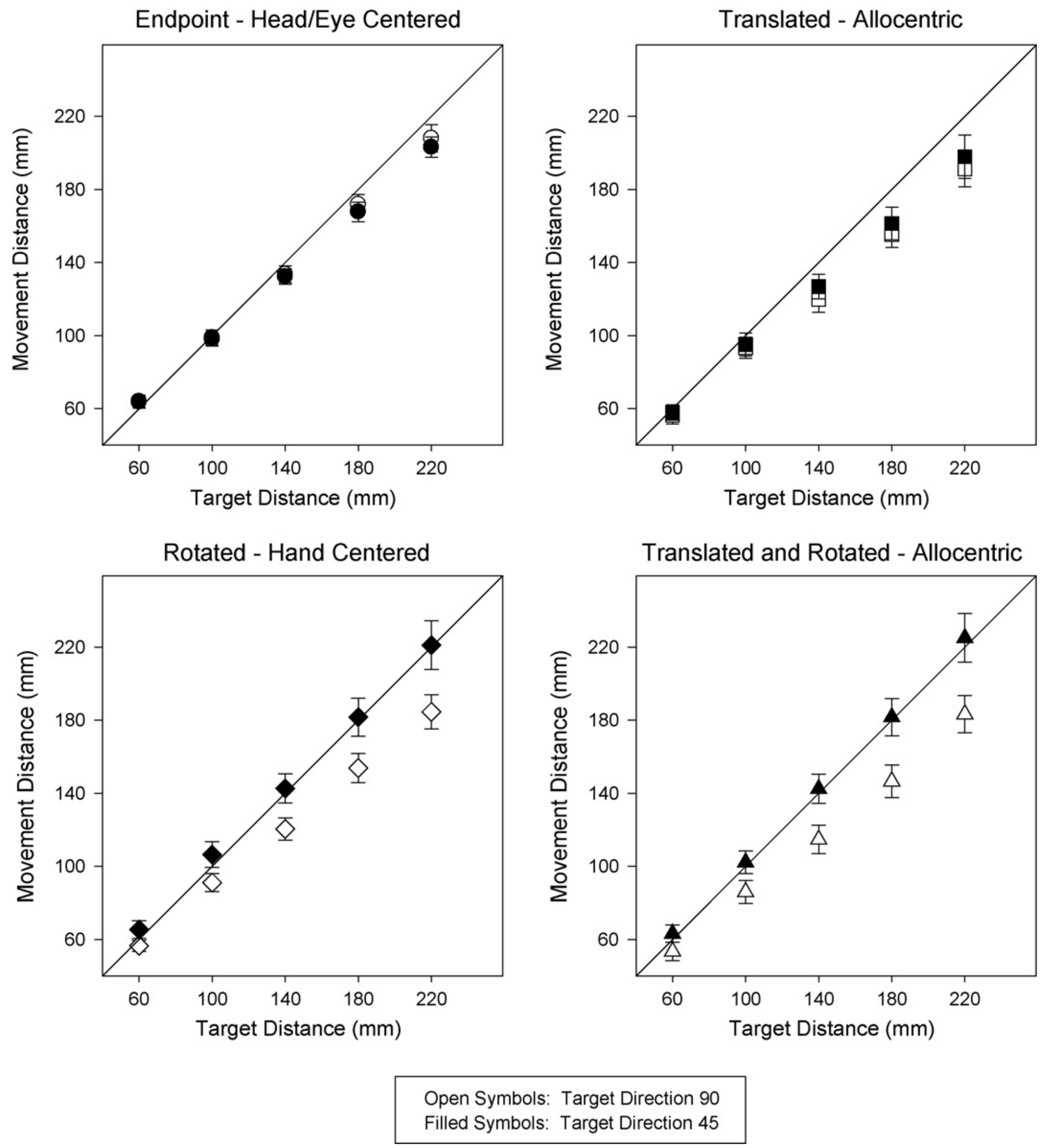

Fig. 4. Average movement distances for the different experimental conditions in Exp. 1. Error bars denote standard errors of the mean between subjects. Diagonal lines indicate veridical performance.

shown as well (white circles). Ellipses in Fig. 3 represent variability ellipses computed based on all subjects' responses after subtracting each subject's mean. Axes of each ellipse denote two standard deviations around the mean. Black squares mark the endpoint that would have resulted from a movement executed veridical along the target direction over the target distance.

It is evident from Fig. 3 that variability ellipses are smallest in the 'Endpoint – Head/Eye Centered' conditions and that ellipses are more elongated in 'Rotated – Hand Centered', 'Translated - Allocentric' and 'Translated and Rotated - Allocentric' conditions. The increased elongation of ellipses is due to increased major axis length, which is caused by increased scatter of movement endpoints along the direction of movement in those conditions. Angular scatter around the movement direction appears to be similar across all tasks. Not only scatter, but also average movement endpoints change systematically in the different tasks. Changes appear to affect average movement distance rather than average movement orientation. In all conditions, ellipse centers are located slightly to the left, and thus towards the body center.

2.2.1. *Movement distance—constant errors*

Fig. 4 shows subjects' average movement distances for the different conditions. Diagonal lines indicate veridical performance. It is evident that movement distance varies linearly with physical target distance in all conditions, but that the slope of linear functions differs systematically across tasks and target directions. Variability between subjects is smallest and overall accuracy with respect to physical target distance highest in 'Endpoint – Head/Eye Centered' conditions. Compared to 'Endpoint – Head/Eye Centered' conditions, subjects reach shorter in 'Translated - Allocentric' conditions. The differences between 'Translated - Allocentric' and 'Endpoint – Head/Eye Centered' conditions are larger at larger target distances. When the target distance segment is rotated with respect to the target direction ('Rotated – Hand Centered' and 'Translated and Rotated - Allocentric'), subjects reach either shorter or farther compared to 'Endpoint – Head/Eye Centered' conditions, depending on the orientation of the target distance segment with respect to the target direction. When the target distance segment is oriented 45°, but target direction is 90°, subjects reach shorter than in 'Endpoint – Head/Eye Centered' conditions. When the target distance segment

Table 1
Results of statistical analysis of constant errors in movement distance in Exp. 1 for right and left-handed subjects combined and right-handed subjects only (RH). Input to each analysis was the difference in movement distance of a condition to the 'Endpoint – Head/Eye Centered' condition. Repeated measures ANOVA with target distance and target direction was computed for each task separately, because an initial analysis revealed a significant interaction between target distance, target direction and task (see text for details). HF: value was obtained using Huynh–Feldt adjustment of degrees of freedom.

	Rotated – Hand Centered	Translated - Allocentric	Translated and Rotated - Allocentric
Target direction	$F(1,7) = 43.45$; $p = .0001$, RH: $F(1,4) = 14.67$; $p = .019$	$F(1,7) = 10.19$; $p = .015$, RH: $F(1,4) = 4.73$; $p = .095$	$F(1,7) = 26.7$; $p = .001$, RH: $F(1,4) = 9.78$; $p = .035$
Target distance	$F_{HF}(1.3,9.3) = .35$; $p = .631$, RH: $F_{HF}(1.2,4.9) = 1.072$; $p = .368$	$F_{HF}(1.6,11.2) = 1.23$; $p = .319$, RH: $F_{HF}(2.3,9.1) = 2.52$; $p = .14$	$F_{HF}(1.7,11.8) = .51$; $p = .581$, RH: $F(4,16) = .363$; $p = .831$
Target distance × target direction	$F_{HF}(2.1,14.6) = 14.06$; $p = .0001$, RH: $F(4,16) = 4.1$; $p = .018$	F(4,28) = 3.67; $p = .016$, RH: $F(4,16) = 1.62$; $p = .219$	$F_{HF}(1.7,11.9) = 16.12$; $p = .001$, RH: $F(4,16) = 5.61$; $p = .005$

is oriented 90° but target direction is 45°, subjects reach farther than in 'Endpoint – Head/Eye Centered' conditions. Differences to the 'Endpoint – Head/Eye Centered' condition are larger at larger target distances and they are unaffected by an additional translation, i.e. differences to the 'Endpoint – Head/Eye Centered' condition are almost identical in 'Rotated – Hand Centered' and 'Translated and Rotated - Allocentric' conditions.

To summarize, on average subjects are most accurate with respect to physical target distance in 'Endpoint – Head/Eye Centered' conditions, i.e. when they can reach towards a visible target location and therefore, when they can rely on a representation of target location in eye/head centered coordinates. We observe systematic changes in movement distance when subjects have to rely on either hand-centered or allocentric representations. Average movement distance appears to change most when the target distance segment is specified in a direction other than the target direction, but there appear to be no differences between hand centered and allocentric conditions.

To confirm the reliability of these effects we computed the difference of each condition to the 'Endpoint – Head/Eye Centered' condition and applied repeated measures ANOVA to the differences, with target distance, target direction and task as within-subjects factors. The initial analysis revealed a significant interaction between target distance, target direction and task ($F_{HF}(7.6,52.9) = 7.11$; $p = .0001$; *right-handers:* $F(8,32) = 2.49$; $p = .032$). This interaction corresponds well to our observation from Fig. 4 that differences in movement distance to the 'Endpoint – Head/Eye Centered' condition depend on the specific task employed, as well as on specific combinations of target distance and direction. Therefore, we subsequently analyzed effects of target distance and direction for each task separately. Table 1 summarizes the results.

The statistical results from Table 1 agree well with our observations from Fig. 4. Specifically, significant interactions between target distance and direction for all conditions (except when left-handed subjects are excluded from 'Translated - Allocentric' conditions[2]) indicates that differences to the 'Endpoint – Head/Eye Centered' task are small at short target distances, and that they grow at different rates for target direction 45° and 90° for all conditions. The significant main effect of target direction for all conditions (except when left-handed subjects are excluded from 'Translated - Allocentric' conditions) indicates that differences to the 'Endpoint – Head/Eye Centered' task are different for the two target directions, even when we collapse across the various target distances. As mentioned in the description of our stimuli, we can compute two meaningful comparisons between performance in 'Rotated – Hand Centered' and 'Endpoint – Head/Eye Centered' tasks. The first comparison regards distances of movements performed along the same target direction as in the 'Endpoint – Head/Eye Centered' task but in response to mirror-symmetric visual target distance segments. This comparison is shown in Table 1, first column. The second comparison regards distances of movements performed in response to visually identical target distance segments as in 'Endpoint – Head/Eye Centered' conditions, but in mirror symmetric target directions. The latter comparison is a more direct test of the head/eye-centered vs. hand-centered representation, because it is expected that movement distance in these conditions is the same if subjects use a hand-centered representation to perform in 'Endpoint – Head/Eye Centered' conditions. The statistical results of the latter comparison reveal that subjects' movement distances between 'Endpoint – Head/Eye Centered' and 'Egocentric' conditions differ, even when they are performed in response to the same target distance segment (*target direction:* $F(1,7) = 15.736$; $p = .005$ [RH: $F(1,4) = 8.56$; $p = .043$]; *target distance*: $F_{HF}(1.3,9.3) = .346$; $p = .631$ [RH: $F_{HF}(1.2,4.9) = 1.07$; $p = .368$]; *target direction × target distance*: $F(4,28) = 3.457$; $p = .02$ [RH: $F(4,16) = .572$; $p = .687$]).

2.2.2. Movement distance—variable errors

Fig. 5 shows subjects' average S.D. of movement distance plotted against subjects' average movement distance for the different target directions and tasks. Lines in each plot show the best linear fit to the data using the least squares method. Resulting equations and fit statistics are shown in the top left corner of each plot.

It is obvious from Fig. 5 that S.D. of movement distance increases proportional to movement distance in all conditions and that linear functions that express S.D. of movement distance as a function of movement distance capture the relationship well (compare Messier & Kalaska, 1997).[3] Both slopes and intercepts of linear regression lines differ between conditions. Most notably, slope is much lower in 'Endpoint – Head/Eye Centered' than the other conditions, indicating that S.D. of movement distance increases at a lower rate in that condition. This finding is in agreement with the observation from Fig. 3 that ellipse major axes are shorter in 'Endpoint – Head/Eye Centered', compared to the other conditions.

When average movement distance increases, S.D.s increase as well. Thus, variables errors depend to some degree on constant

[2] Upon numerical exploration of the data, we saw that neither differences between means nor standard deviations changed considerably when left-handed subjects were excluded from analysis. Fig. 4 reveals that differences in means between 'Endpoint' and 'Translated – Allocentric' conditions are generally small, for both 90° and 45° target directions. Since exclusion of subjects reduces statistical power due to smaller sample size, the interaction effect in 'Translated – Allocentric' conditions is not significant when left-handers are excluded, because statistical power is too low to detect the generally small effect.

[3] When we express S.D. of movement distance as a linear function of physical target distance instead of movement distance the linear fit is lower, especially for 'Rotated – Hand Centered' and 'Translated and Rotated - Allocentric' conditions. The reason is that for those conditions S.D. of movement distance at target direction 90 is lower than S.D. of movement distance at target direction 45, especially at larger physical target distances. Therefore, when we express movement S.D. as function of physical target distance in those conditions, slope of target direction 45 is higher than slope of target direction 90. This in turn results in an overall worse fit based on physical target distance.

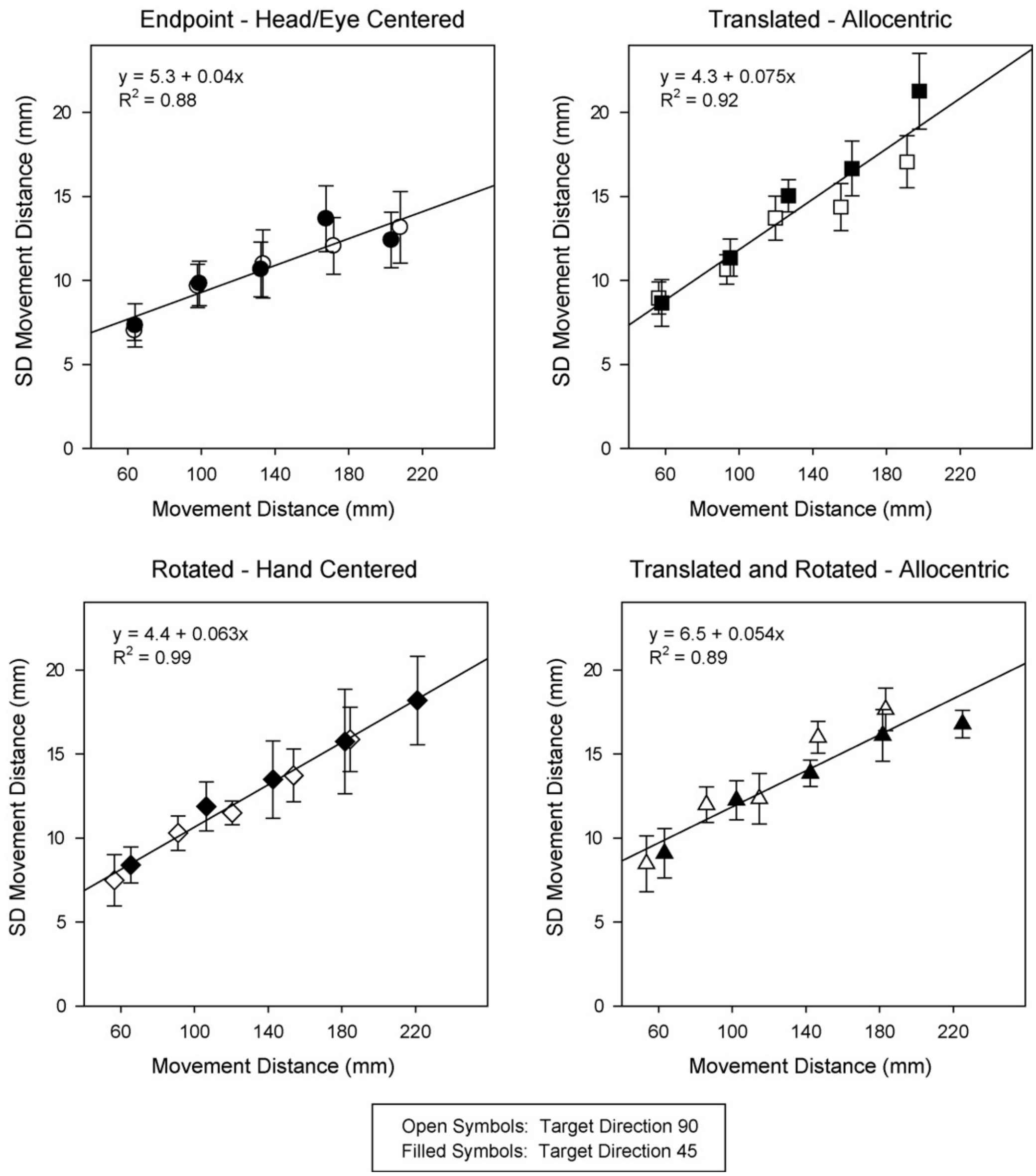

Fig. 5. Average S.D. of movement distances for the different experimental conditions in Exp. 1. Error bars denote standard errors of the mean between subjects. Lines in each plot show the best linear fit to the data. Resulting equations and least square fit statistic are shown in the top left corner of each plot.

errors in movement distance. We used linear regression to obtain a measure of variable errors that is independent from linear effects of average movement distance. First, we computed the linear regression equation that predicts S.D. of movement distance from average movement distance across all experimental conditions for each subject. The residual S.D., i.e. the difference between predicted and actually observed S.D., represents variable errors in movement distance that are independent from linear effects of average movement distance.

The average residuals in S.D. of movement distance for the four tasks (in mm) are −2.27 [RH: −2.52] (Endpoint – Head/Eye Centered), 0 [RH: −1.0] (Rotated – Hand Centered) and 1.37 [RH: 2.1] (Translated - Allocentric) and 0.87 [RH: 1.4] (Translated and Rotated - Allocentric). We used *t*-test for paired samples to determine which residuals differ significantly from each other. Residuals in the 'Endpoint – Head/Eye Centered' condition differ significantly from those in all other conditions for the whole group and when left-handed subjects are excluded from analysis (Rotated – Hand Centered: $t(7) = 3.81$, $p = .007$ [RH: $t(4) = 2.8$, $p = .05$], Translated - Allocentric: $t(7) = 3.13$, $p = .017$ [RH: $t(4) = 3.0$, $p = .04$], Translated and Rotated - Allocentric: $t(7) = 3.8$, $p = .007$ [RH: $t(4) = 5.0$, $p = .007$]). For the whole group no other comparisons were significant. However, when left-handed subjects are excluded from analysis, comparisons between hand centered and allocentric conditions were significant as well (Rotated – Hand Centered vs. Translated - Allocentric: $t(4) = 2.8$, $p = .05$; Rotated – Hand Centered vs. Translated and Rotated - Allocentric: $t(4) = 4.5$, $p = .01$). The results suggest that performance is most reliable when subjects move their hands towards a visible target, more (but not necessarily significantly more) reliable when they have to rely on hand-centered distance information, and least reliable when they have to rely on allocentric distance information.

2.2.3. Movement direction—constant and variable errors

We computed both arithmetic and circular statistics (Fisher, 1993) of directional data. The differences were negligible (maximum absolute difference .002). For this reason, and because all statistical analyses revealed equivalent results, we report arithmetic measures only. There were no systematic effects of task on either constant (averages) or variable (standard deviations) move-

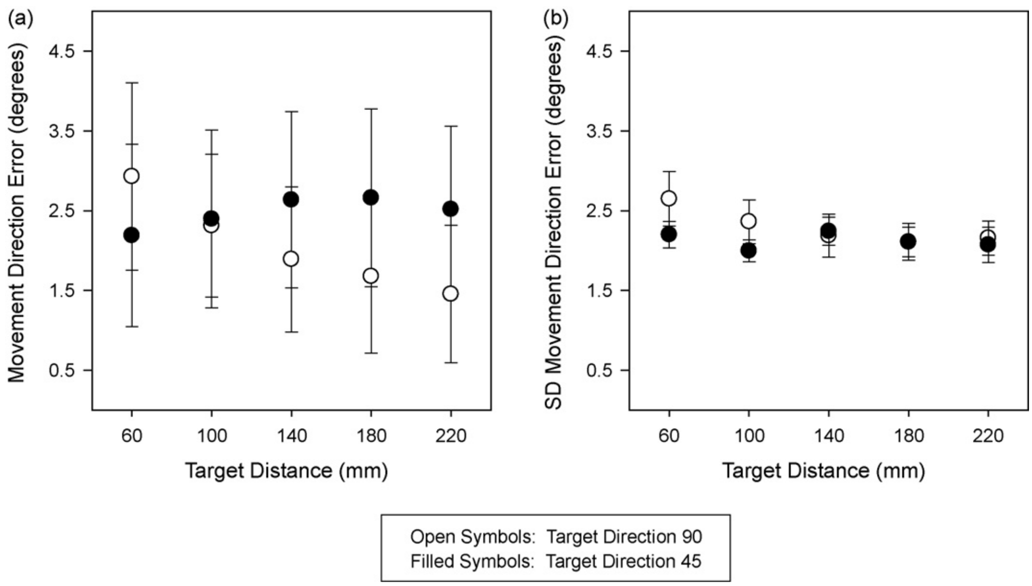

Fig. 6. (a) Average direction errors (in degrees) averaged across tasks in Exp. 1. Positive errors indicate errors towards the sagittal body midline. (b) S.D. of direction errors (in degrees) averaged across tasks in Exp. 1. Error bars denote standard errors of the mean between subjects.

ment direction errors. Thus, Fig. 6a and b shows constant and variable movement direction errors averaged across tasks. Error bars denote standard errors of the mean between subjects in both plots. The hand was slightly offset to the right or left from the sagittal body midline for right and left-handed subjects, respectively. We thus decided to indicate movement shifts towards the sagittal body midline as positive direction errors, and shifts away from the sagittal body midline as negative direction errors. It is evident from Fig. 6a that subjects' have an overall tendency to shift the endpoints of their movements slightly (~2°) towards their body midline and that this tendency decreases with increasing target distance for target direction 90°, but increases for target direction 45. The reliability of this effect was confirmed applying a repeated measures ANOVA with target distance, target direction and task as within-subjects factors. The analysis revealed a significant interaction between target distance and direction ($F_{HF}(2,14.1) = 7.21$, $p = .007$ [RH: $F(4,16) = 3.6$, $p = .029$]). No other effects were significant. Fig. 6b shows that S.D.s of direction errors decrease with increasing target distance (compare Gordon et al., 1994; Messier & Kalaska, 1997) and that this tendency is stronger for target direction 90°. The overall effect is small (~0.5°). The reliability of this effect was confirmed applying a repeated measures ANOVA with target distance, target direction and task as within-subjects factors. For right and left-handed subjects combined the analysis revealed a significant main effect of target distance ($F(4,28) = 3.21$, $p = .027$), qualified by a significant interaction between target distance and direction ($F(4,28) = 3.52$, $p = .019$) and no other effects were significant. For right-handed subjects only, none of the effects were significant (target distance: $F(4,16) = 2.3$, $p = .106$; target distance × target direction interaction: $F(4,16) = 1.3$, $p < .301$). In summary, subjects movement direction errors were unaffected by changes in the presentation of the target distance segment. As outlined in the method section, this was expected since the target direction was specified in the same way across all tasks.

2.2.4. Kinematic parameters

Table 2 shows statistics on kinematic parameters computed across target distances and directions for the different tasks. Statistical significance of average movement velocity, peak velocity and movement duration was determined computing paired samples *t*-tests (two tailed) between the different tasks. Significant differences in means are indicated with asterisks.

It is evident from Table 2 that movement velocity, duration and curvedness are very similar across conditions. Nevertheless, average and peak movement velocity is significantly lower in 'Translated - Allocentric' than the other conditions. Movement Curvedness is very low (1.6%) for all experimental conditions, indicating that movement traces are almost perfectly straight. The movement curvedness observed in our experiment is in reasonably good agreement with curvedness values that have been reported elsewhere (Brenner, Smeets, & Remijnse-Tamerius, 2002, Figs. 3 and 5; Desmurget, Jordan, Prablanc, & Jeannerod, 1997). To test if curvedness is larger or smaller for different target distances and directions we applied repeated measure ANOVA with target distance, target direction and task as within-subjects factors. The analysis did not reveal any significant effects for all subjects combined or right-handed subjects only. In summary, changes in movement kinematics do not correspond to changes in movement reliability and accuracy observed in our experiment.

2.3. Discussion Exp. 1

Only in 'Endpoint – Head/Eye Centered' conditions can subjects move their hands towards a visible target location. Therefore, only in those conditions could subjects in principle perform their movement based on a representation of target location in head/eye-centered coordinates. In all other conditions, no visible target is available, and subjects, at least in a first step, have to represent target distance in either hand-centered or allocentric coordinates.

Our results show that subjects' movements are most reliable and accurate in 'Endpoint – Head/Eye Centered' conditions. Variable and constant errors in movement distance increase when subjects are forced to represent distance in either hand-centered or allocentric format. Constant errors in movement distance are highest when target distances differ in orientation from the target direction, but they are equivalent in 'Rotated – Hand Centered' and 'Translated and Rotated - Allocentric' conditions. Thus, constant errors in movement distance depend on the orientation of the target distance segment with respect to the target direction, but not on the specification of the visual information in a

Table 2
Statistics on movement kinematics and trajectory shape (curvedness) from Exp. 1. Numbers in each cell correspond to: mean (standard deviation), median, min, max (in that order), computed across subjects, target distances and target directions. *a-t = significant difference in means ($p < .05$) to 'Translated - Allocentric' condition. **a-t = significant difference in means ($p < .01$) to 'Translated - Allocentric' condition.

	Endpoint – Head/Eye Centered	Rotated – Hand Centered	Translated - Allocentric	Translated and Rotated – Allocentric
Mean velocity (cm/s)	18.5*a-t (8.4), 16.4, 5.3, 50.3	17.8**a-t (8), 16, 5.1, 52.8	16.4 (7.5), 14.7, 4.1, 43.2	17.1*a-t (8), 15.6, 4.7, 49.3
Peak velocity (cm/s)	31*a-t (15.3), 26.7, 8.9, 101.8	29.6**a-t (14.2), 26.1, 8.6, 106.2	27.4 (13.1), 23.7, 6.5, 80.7	28.5*a-t (13.6), 25.1, 6.7, 90.2
Duration (s)	0.81 (0.39), 0.73, 0.21, 1.52	0.81 (0.37), 0.73, 0.24, 1.62	0.84 (0.37), 0.77, 0.2, 1.55	0.83 (0.4), 0.74, 0.25, 1.8
Curvedness	1.6 (1), 1.4, 0.2, 6.4	1.6 (0.8), 1.4, 0.2, 5.7	1.6 (0.9), 1.4, 0.2, 5.1	1.6 (0.9), 1.4, 0.2, 5

hand-centered or allocentric format. Variable errors in movement distance increase slightly more for allocentric than for hand-centered conditions, but the difference between allocentric and hand-centered conditions is only significant when left-handed subjects are excluded from statistical analysis. The non-significant effect when left-handed subjects are included is due to the fact that one left-handed subject had a comparably large residual variability in 'Rotated – Hand Centered' conditions (compare Table 4, subject 5).

While we did find changes in errors in movement distance with respect to the task, we did not find changes in either constant or variable errors in movement direction. This was expected, since target direction was specified in exactly the same way in the four experimental tasks. Furthermore, the finding that errors in movement distance change while errors in movement direction do not is in agreement with previous studies that showed that errors in movement distance and direction can be manipulated independently from each other (Messier & Kalaska, 1997; Gordon et al., 1994).

Although we did observe statistically significant differences in average and peak movement velocity between 'Translated - Allocentric' and the other tasks, these differences do not correspond to systematic changes in constant and variable errors in movement distance. Movement duration and trajectory shape did not differ across tasks. Thus, changes in movement velocity, duration or trajectory shape are most likely not accountable for the observed systematic changes in movement distance. The reader might find it confusing that movement velocity, but not movement duration changed, since these two measures appear to be each other's inverse. For example, higher movement duration results in lower movement velocity and vice versa. However, inversion only holds when movement distance is constant. This is not the case in our experiment, because distances of subjects' hand movements were not the same, even though physically specified target distances were.

In summary, movement accuracy and reliability is highest when subjects move their hands towards a visible target location which permits them to use a representation of visual space in head/eye-centered coordinates. Movement reliability and accuracy decrease as we go from conditions that permit the use of head/eye-centered representations to conditions that permit the use of hand-centered representations to conditions that permit the use of allocentric representations only. The results are consistent with the idea that to perform a movement subjects represent information on target location with respect to the head/eye qualitatively differently from information in either hand-centered or allocentric distance and direction.

The question arises, if the observed systematic differences are limited to motor behavior, or if they are a general principle of human processing of visual information. In order to address this question Exp. 2 measured subjects' visual perception of target distance. Exp. 2 used the same stimuli and setup as Exp. 1 and the same subjects participated in Exp. 2. The only difference between Exp. 1 and Exp. 2 was that instead of moving their hand, subjects reported perceived target distance by adjusting a probe stimulus using a computer keyboard.

3. Experiment 2

3.1. Methods

3.1.1. Subjects and apparatus

The same subjects as in Exp. 1 also participated in Exp. 2 and the experiment was performed using the same apparatus as in Exp. 1. However, the digitizing tablet was switched off and a keyboard that was used by subjects to produce their response was placed on the recording surface in front of subjects' sternum. The keyboard was placed such that the location of the hand coincided with the adjustment starting position. The adjustment starting position in Exp. 2 was thereby the same as the starting position of the hand in Exp. 1. Just as in the motor task, left and right-handed subjects used their preferred left and right hand respectively, to generate their response. To ensure that visual stimuli were equivalent in Exp. 2 and 1, the apparatus was calibrated before each session the same way it had been calibrated in Exp. 1.

3.1.2. Stimuli and task

The stimuli in Exp. 2 were the same as those used in Exp. 1. Subjects were instructed to adjust a probe line segment such as to match the distance of the target distance segment. The probe distance segment (green line, 2 mm width) was displayed on top of the 45° or 90° target direction line such that orientation of the probe line segment always matched target direction. Probe distance was adjusted in 1 mm steps using up- and down-arrow keys on the computer keyboard. The start point of the probe distance segment coincided with hand starting point from Exp. 1. The base setting of probe distance was zero, such that the circle indicating the starting position was the only visible part of the probe figure at the beginning of each trial. Please note that we could also have asked subjects to position a dot along the target direction line to indicate target distance. However, adjusting the probe line segment in our experiment is equivalent to adjusting the position of the boundary between the probe line and the target direction line. Thus, we believe that adjusting the probe line is equivalent to positioning a dot in our experiment.

3.1.3. Procedure

Each trial began with the display of the 90° or 45° target direction, the adjustment start position and the target distance segment. In 'Endpoint – Head/Eye Centered' Conditions, the start position was horizontally offset with respect to the target direction line. The offset location was randomly chosen between 2 and 8 mm to the left or right from the target direction line. In all other conditions, the start position was located directly on the line. To initiate a trial in 'Endpoint – Head/Eye Centered' conditions subjects used the left or right arrow keys to align the start point horizontally with the target direction line. Once they had aligned the start position, they could use the up-arrow key to adjust the distance of the probe figure. Once subjects pressed any of the arrow keys, the target distance segment disappeared from view. The horizontal alignment task in 'Endpoint – Head/Eye Centered' conditions was used to force subjects to shift their gaze shortly away from the target endpoint before starting the adjustment task to prevent them from

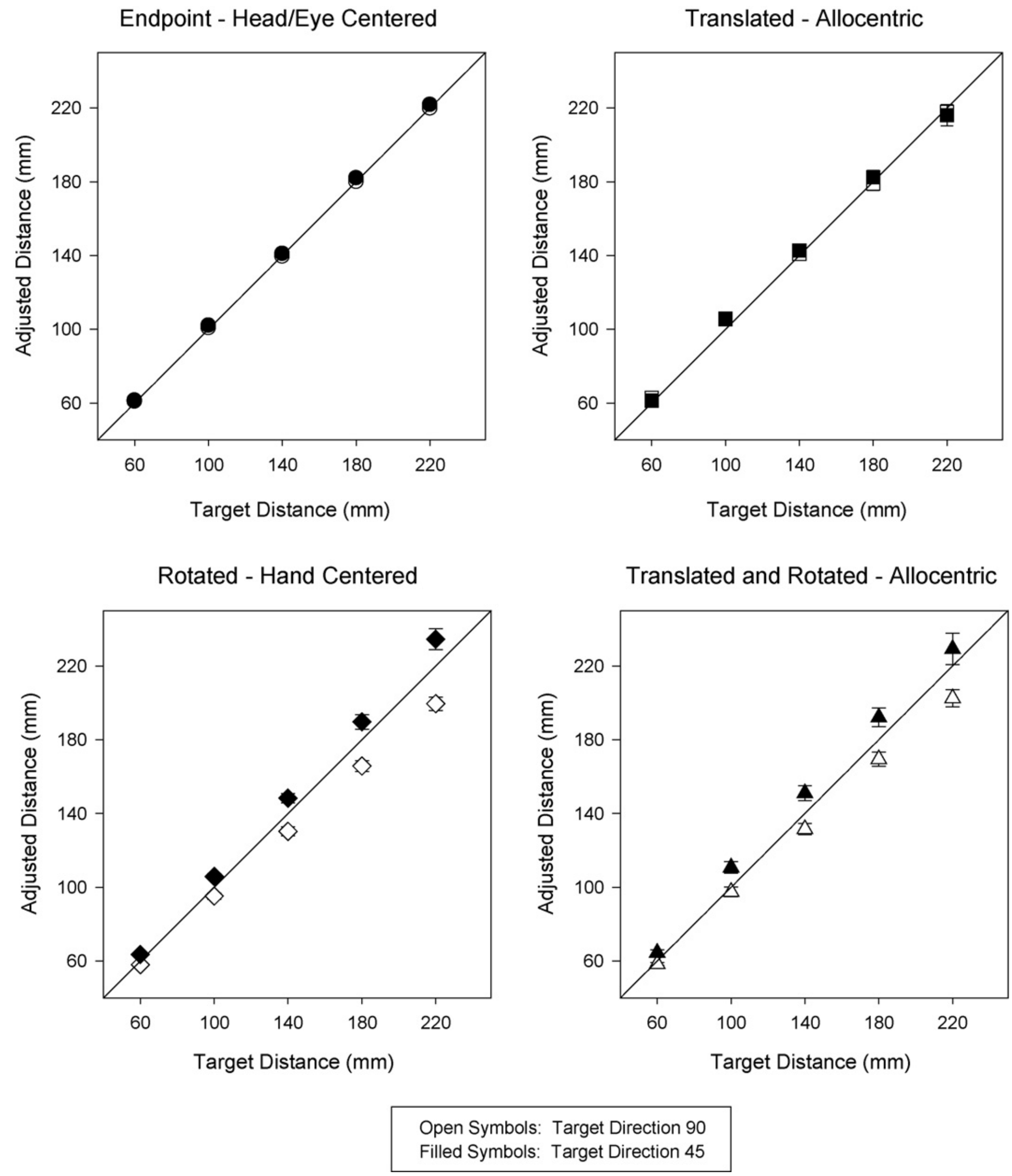

Fig. 7. Average adjusted distance for the different experimental conditions in Exp. 2. Error bars denote standard errors of the mean across subjects. Diagonal lines indicate veridical performance.

giving their response based on retinal matching. In all other conditions, subjects could use the up-arrow key to adjust probe distance right from the beginning. Since the target distance segment disappeared as soon as any arrow key was pressed, subjects never saw the target distance and probe distance segment together. This created similar viewing conditions as in Exp. 1, in which subjects never saw their hand and the target distance segment together. To prevent subjects from using visual 'landmarks' to make their response, the location of the gray dots covering the background shifted randomly as soon as subjects pressed any of the arrow keys.

Stimulus presentation was blocked with respect to the two target directions and four tasks, yielding eight blocks. Within a block, each of the five target distances was presented four times in random order. Each subject participated in one ~40 min session that contained three sets of eight blocks. Thus, every subject gave 12 responses to every stimulus. In the beginning of the session, subjects were made familiar with task and set-up by giving a short practice phase, during which they gave two responses in each of the four tasks (eight practice trials total). Practice trials were not recorded.

3.1.4. Data analysis

Perceived Distance was computed as the distance of the adjusted probe segment. To assess systematic deviations from the visually specified target distance we computed average perceived distance. To assess the reliability of subjects' perceptual judgments we computed S.D. of perceived distance. In order to base our analyses on representative samples, we excluded responses whose distance exceeded the 25%tile − 1.5 × iqr or 75%tile + 1.5 × iqr (iqr = inter quartile range). 3.57% of responses were rejected.

3.2. Results

There were no systematic differences among naïve subjects and authors. Since the response did not require any significant motor response and since there were no differences between left and right-handed subjects, we mirrored the data of the three left-

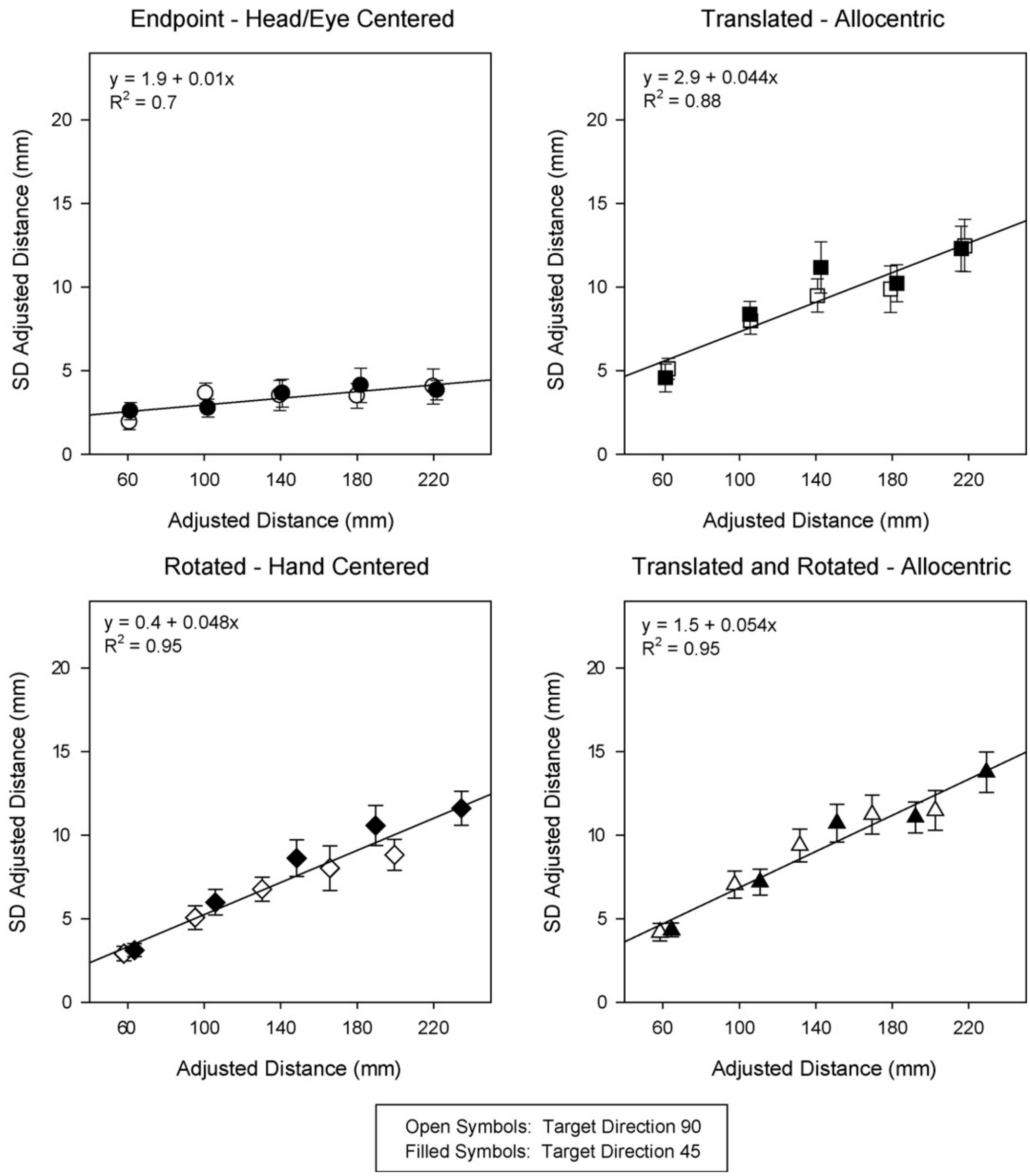

Fig. 8. Average S.D. of adjusted distances for the different experimental conditions in Exp. 2. Error bars denote standard errors of the mean across subjects. Lines show linear regression lines. Equations and fit statistics are shown in the top left corner of each plot.

handed subjects for our analyses and analyzed them together with the right-handed subjects. We report statistical results for the whole group only and with degrees of freedom corrected according to Huynh and Feldt (1976) where the sphericity assumption is rejected ($p < .05$).

Fig. 7 shows subjects' average adjusted distances for the different conditions. Diagonal lines indicate veridical performance. Fig. 8 shows S.D. of adjusted distance. Lines indicate the best fitting linear line to the group data using a least squares criterion. Equations and fit statistics are given in the top left corner of each plot. In both plots, error bars denote standard errors of the mean between subjects.

It is evident from both plots, that subjects' performance in the perceptual adjustment task is very similar to their performance in the motor task, except that S.D.s are about 50% smaller in the perceptual task. Just as average movement distance in Exp. 1, average adjusted distance varies linearly with target distance in all conditions, but slopes of linear functions vary. When the target distance segment is rotated with respect to the target direction ('Rotated – Hand Centered' and 'Translated and Rotated - Allocentric'), subjects perceive target distances as shorter or farther compared to 'Endpoint – Head/Eye Centered' conditions, depending on the orientation of the target distance segment with respect to the target direction. When the target distance segment is oriented 45°, but target direction is 90°, subjects perceive target distance as shorter than in 'Endpoint – Head/Eye Centered' conditions. When the target distance segment is oriented 90° but target direction is 45°, subjects perceive target distance as farther than in 'Endpoint – Head/Eye Centered' conditions. Differences to the 'Endpoint – Head/Eye Centered' condition are larger at larger target distances and they are unaffected by an additional translation, i.e. differences to the 'Endpoint – Head/Eye Centered' condition are almost identical in allocentric and hand-centered conditions. Adjustment distance does not change compared to the 'Endpoint – Head/Eye Centered' conditions in the 'Translated - Allocentric' condition and is most veridical in those conditions. Variability between subjects is smallest in 'Endpoint – Head/Eye Centered' conditions, which suggests that subjects are most accurate with respect to physical target distance when they respond to a visible target location. To confirm the reliability of these effects we computed the difference of each condition to the 'Endpoint – Head/Eye Centered' condition

Table 3
Results of statistical analysis of constant errors in adjusted distance in Exp. 2. Input to each analysis was the difference in adjusted distance of a condition to the 'Endpoint – Head/Eye Centered' condition. Repeated measures ANOVA with target distance and target direction was computed for each task separately, because an initial analysis revealed a significant interaction between target distance, target direction and task (see text for details). HF: value was obtained using Huynh–Feldt adjustment of degrees of freedom.

	Rotated – Hand Centered	Translated - Allocentric	Translated and Rotated - Allocentric
Target direction	$F(1,7) = 25.49$; $p = .001$	$F(1,7) = .84$; $p = .39$	$F(1,7) = 11.74$; $p = .011$
Target distance	$F_{HF}(1.6,11.1) = 1.41$; $p = .279$	$F_{HF}(1.6,10.8) = 1.64$; $p = .236$	$F_{HF}(1.9,13.3) = 1.7$; $p = .22$
Target distance × target direction	$F_{HF}(1.5,10.3) = 17.25$; $p = .001$	$F(4,28) = .88$; $p = .486$	$F_{HF}(1.3,9.1) = 6.59$; $p = .024$

and applied repeated measures ANOVA to the differences, with target distance, target direction and task as within-subjects factors. Just as in Exp. 1, the initial analysis revealed a significant interaction between target distance, direction and task ($F(4.5,31.4) = 11.76$; $p = .0001$). Thus, we subsequently assessed the effects of target distance and direction for each task separately. Table 3 summarizes the results of the statistical analysis. It is evident that the results are equivalent to those from Exp. 1.

Just as in the visuo-motor task from Exp. 1 we can compute two comparisons between 'Rotated – Hand Centered' and 'Endpoint – Head/Eye Centered' tasks. The first comparison examines adjusted distances along the same target direction as in the 'Endpoint – Head/Eye Centered' task but in response to mirror symmetric visual target distance segments (first column in Table 3). The second comparison regards adjustment distances performed in response to the same visual target distance segment as in 'Endpoint – Head/Eye Centered' conditions, but in mirror symmetric target directions. Just as in Exp. 1, statistical results of the latter comparison are equivalent to those of the first (*target direction:* $F(1,7) = 46.36$; $p = .0001$; *target distance*: $F_{HF}(1.6,11.1) = 1.4$; $p = .279$; *target direction* × *target distance*: $F_{HF}(1.6,11.4) = 29.94$; $p = .0001$).

Adjustment S.D. increases proportional to adjusted distance and, just as in Exp. 1, the relationship is captured well by linear regression. As in Exp. 1, the slopes and intercepts of the regression lines differ between tasks. Slopes are much lower in 'Endpoint – Head/Eye Centered' compared to the other conditions. To obtain a measure of adjustment reliability that is independent from average adjusted distance, we used linear regression to remove linear effects of average adjusted distance on standard deviations as in Exp. 1. The average residuals in the different tasks are (in mm) −3.82 [RH: −4.1] (Endpoint – Head/Eye Centered), 0.07 [RH: −0.17] (Rotated – Hand Centered), 1.89 [RH: 2.28] (Translated - Allocentric) and 2 [RH: 2.2] (Translated and Rotated - Allocentric). We used *t*-test for paired samples to determine which residuals differed significantly from each other. The 'Endpoint – Head/Eye Centered' condition has significantly lower residuals than the other conditions (Rotated – Hand Centered: $t(7) = 7$, $p = .0002$, Translated - Allocentric: $t(7) = 6.22$, $p = .0004$, Translated and Rotated - Allocentric: $t(7) = 8.19$, $p = .0001$). In addition, residuals in the 'Rotated – Hand Centered' condition are significantly lower than in 'Translated - Allocentric' ($t(7) = 2.77$, $p = .028$) and 'Translated and Rotated - Allocentric' conditions ($t(7) = 5.07$, $p = .001$), both of which do not differ significantly from each other. Thus, reliability of subjects adjustments is highest when they respond to a visible target location, lower when they respond to visual information of distance in hand-centered coordinates, and lowest when they respond to visual information in allocentric coordinates. These results are very similar to the those obtained in Exp. 1.

3.3. Direct comparison of results from Exp. 1 and Exp. 2

Based on our experimental design we can directly compare subjects' average movement distances to their average adjusted distances, and subjects' S.D. of movement distance to their S.D. in adjusted distance. Fig. 9a shows average movement distances for each condition and subject plotted against average adjusted distances. The diagonal line indicates the line with slope one and intercept zero, such that data should fall on this line if perceptual and motor performance were perfect matches. It is evident that there is very high agreement between performances in the two tasks, such that subjects' moved distance follows closely their perceived distance ($r = .95$, $t(318) = 54.3$, $p = .0001$), or that subjects moved their hands over the distance they perceived, respectively. Despite high agreement, data points for the 'Endpoint – Head/Eye Centered' condition (black symbols) seem to be slightly vertically offset, suggesting that for a given perceived distance, subjects have a tendency to produce longer movements in the 'Endpoint – Head/Eye Centered' compared to the other conditions.

High correlation between adjusted and moved distance is expected simply on the basis that both responses correlate highly with physical target distance. In order to investigate the relationship between perceptual and motor responses independently from linear effects of physical target distance we used linear regression to remove effects of physical target distance from both movement and adjusted distance. We first made predictions on movement distance and adjusted distance based on their linear relationship to physical target distance. Then, we computed residual movement and residual adjusted distance, i.e. differences between predicted and observed values. Fig. 9b shows the plot of residuals for all subjects. The diagonal line is the line with slope one and intercept zero. Regression equations and residuals were computed for each subject and task (motor and perceptual) separately. It is evident that there is still very high agreement between perceptual and motor responses ($r = .71$, $t(318) = 18$, $p = .0001$), indicating that subjects' deviations from their average movement distance tracks their deviations from their average adjusted distance. In addition, we can see that the slope of the residuals is larger than one, indicating that subjects' deviations from their average movement distance, as predicted from physical target distance, are larger in the motor task, than in the perceptual task. Correlations for distances and residual distances for individual subjects (Table 4, first and second row) are in good agreement with the group data. Only one residual correlation (subject 7) is very low. Inspection of data for that subject showed that residuals in the perceptual task for that subject were small and at most half magnitude that of any other subject (average absolute value of perceptual residual for subject 7 is 3 mm).

Fig. 9c shows subjects' S.D. of movement distance plotted against S.D. of adjusted distances. Diagonal lines have slope one and intercept zero, such that values should fall on this line if perceptual and motor performance were perfect matches. It is evident that S.D.s are about twice as high and increase at a faster rate in the motor

Table 4
Correlations between measures of motor and perceptual performance from Exp. 1 and Exp. 2 for individual subjects and all subjects together (group). Subjects 2, 5 and 6 are left-handed.

	Subject								Group
	1	2	3	4	5	6	7	8	
Distance	0.97	0.98	0.99	0.99	0.99	0.99	0.97	0.97	0.95
Residual distance	0.78	0.73	0.86	0.51	0.89	0.81	0.03	0.52	0.71
S.D.	0.7	0.51	0.59	0.81	0.52	0.53	0.4	0.57	0.5
Residual S.D.	0.46	0.4	0.49	0.72	−0.09	0.44	0.29	0.6	0.41
Average residual S.D.	0.75	0.9	0.96	0.97	−0.23	0.9	0.6	0.92	0.73

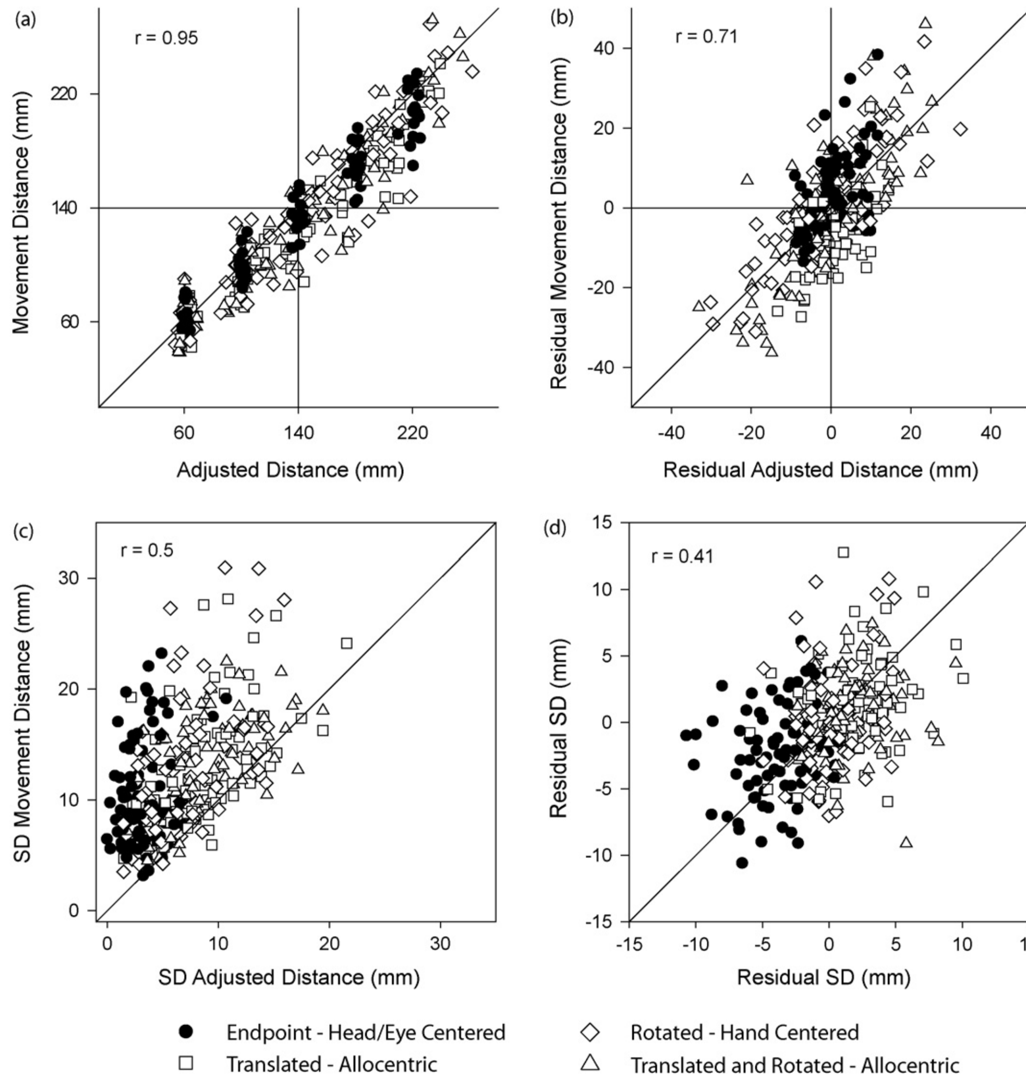

Fig. 9. Indicators of motor and perceptual performance obtained in Exp. 1 and Exp. 2 plotted against each other. In each plot, perceptual performance is plotted on the *x*-axis and motor performance on the *y*-axis. Diagonal lines have slope one and intercept zero. Residual values were obtained using linear regression. Please see text for details.

than in the perceptual task, but that overall S.D.s in the motor task track those in the perceptual task ($r = .5$, ($t(318) = 10.3$, $p = .0001$). Fig. 9d shows subjects' residuals plotted against each other. Again, residuals are in relatively good correspondence between the motor and perceptual task ($r = .41$, $t(318) = 8$, $p = .0001$). Individual subject's correlations for standard deviations and their residuals are shown in Table 4 third and fourth row. In addition Table 4 (fifth row) also shows correlations for average residuals. Average residuals are not plotted, but their correlation on group level is comparably high ($r = .73$, $t(30) = 5.9$, $p = .0001$). Correlations obtained for individual subjects are higher than those obtained on group level for most subjects. Only one subject (subject 5) shows low, and even negative, correlation. Inspection of the data for that subject showed that this is caused by comparably large residuals in movement S.D. in 'Rotated – Hand Centered' conditions.

3.4. Discussion Exp. 2

Subjects' perceptual performance in Exp. 2 agrees not only qualitatively, but also quantitatively well with their motor performance in Exp. 1. Thus, there appears to be a shared computational resource that governs both perceptual and motor performance. Adjustment accuracy and reliability is highest when subjects perform a perceptual judgment in response to a visible target location, which permits them to rely on a representation of space in head/eye-centered coordinates. Adjustment reliability and accuracy decrease as we go from conditions that permit the use of head/eye-centered representations to conditions that permit the use of hand-centered representations to conditions that permit the use of allocentric representations only. Major differences between data obtained in the motor task and the perceptual task are that standard deviations in the perceptual task are smaller and that accuracy in 'Endpoint – Head/Eye Centered' conditions is higher in the perceptual task. The overall finding that subjects show similar error patterns in perceptual and motor responses is consistent with previous results (i.e. De Graaf, Sittig, & Denier van der Gon, 1991; Gegenfurtner & Franz, 2007). However, the current experiments extend previous studies in that they reveal that error patterns depend systematically on the spatial representation that is needed to perform a task, for both perceptual and motor responses. Our results are strong evidence for the idea that perceptual and motor performance are based on the same visual representation, but that there is additional noise in the motor system (De Graaf et al., 1991; Franz, Fahle, Buelthoff, & Gegenfurtner, 2001; Gegenfurtner & Franz, 2007). In summary, our results are consistent with the idea, that, to perform a perceptual judgment subjects represent information on target location qualitatively differently from information on either hand-centered- or allocentric distance and direction. In addition, the high agreement between motor and perceptual performance suggests that this difference in processing is a general principle of human processing of visual information that determines performance in motor as well as perceptual tasks.

4. General discussion

When subjects reach out and touch a visible target location, the question arises, which representation of visual and haptic space they use to guide their hand. As pointed out in Section 1, subjects could rely on a representation of the target in head/eye, hand or allocentric coordinates. Both head/eye and hand centered coordinates are egocentric because they define the location of the target with respect to the subject. The role played by these three different representations for both visually guided hand movements and perceptual judgments has not been systematically studied. The experiments reported here were designed to remedy this situation. For both visually guided reaching and perceptual judgments, we compared performance on tasks that could potentially be performed using a representation of the target in head/eye-centered, hand centered or allocentric coordinates.

We found that reliability and accuracy of hand movements and perceptual judgments was highest when subjects could reach towards or make a judgment on target location, which permitted the use of a representation of visual and haptic space with respect to the subject's head/eye. Reliability was lower when distance and direction were defined with respect to the subject's hand. Reliability was lowest when subjects had to represent target distance in an allocentric format, at least in a first step. Accuracy of movement distance and adjustment distance decreased with respect to the physical target distance when the response direction differed from the orientation of the target distance segment and the effects were almost identical in hand-centered and allocentric conditions. Taken together, our findings strongly suggest that subjects represent information on target location differently from information on target distance in either hand-centered or allocentric coordinates for both motor actions and perceptual judgments.

As mentioned in Section 1, models that determine the goal state of the limb based on a target representation that is independent from hand starting position in head/eye-centered coordinates are referred to as Endpoint Coding models, whereas models that determine the goal state based on representation of the target in hand-centered coordinates are referred to as Vector Coding models. In our experiment only 'Endpoint – Head/Eye Centered' conditions presented subjects with a visible target location towards they could move their hand, whereas the other conditions required subjects to compute distance and direction either in hand-centered or allocentric coordinates. The possibility arises that subjects employ Endpoint Coding in 'Endpoint – Head/Eye Centered' conditions, but Vector Coding otherwise. This hypothesis implies that subjects use inherently different mechanisms to plan and control their movement in 'Endpoint – Head/Eye Centered' compared to the other conditions, and consequently, that visual information alone might affect how movements are planned and controlled. Alternatively, it is also possible that movements are planned and controlled in the same way in all conditions and that only the initial perceptual transformation differs. For example, it is possible that subjects mentally transform the visual information in 'Rotated – Hand Centered' or 'Allocentric' conditions into a 'virtual' target location and then use Endpoint Coding to determine the goal state of the limb.[4]

The exact nature of the processes that transform visual input into motor commands as well as the parameters that are controlled by the motor system in the planning and control of movements are an area of active research (for reviews see: Desmurget & Grafton, 2000; Desmurget et al., 1998; Lacquaniti & Caminiti, 1998; Todorov, 2004). Furthermore, the idea that planning and control of movements may depend on task demands has been suggested previously in the context of external constraints imposed on the movement effector by recoding devices (Desmurget et al., 1998) and in the context of the choice of control laws that minimize error in task relevant dimensions (Todorov & Jordan, 2002; Liu & Todorov, 2007). Based on the current results it appears possible that the type of visual information alone can affect how movements are planned and controlled. Yet, this hypothesis remains to be tested in future experiments.

Our experiments clearly emphasize the special role played by visible target locations in guiding the hand and for generating perceptual responses. Yet, they are inconclusive with regard to the question how target location is represented. The currently dominant theory is that target location is represented in a metric format, i.e. as the distance and direction of the target with respect to the subjects head or eye. However, in principle it is also possible that target location is represented in some other format, for example in the form of a topology. The main difference between metric and topological geometries is that a topology does not permit computation of distances and directions. However, just as a metric representation a topology uniquely defines locations of points in space as well as neighborhood relationships. We currently investigate if target location is represented in the form of a topology or in terms of its distance and direction with respect to the subjects head or eye.

Eye and hand movements are tightly coupled and the question arises if differences in eye movements can explain our results. The most likely difference between eye movements in 'Endpoint – Head/Eye Centered' and the other conditions would be that subjects anchored their gaze to the visible target in 'Endpoint – Head/Eye Centered' conditions, but they did not consistently anchor their gaze in the other conditions, since those did not provide a visible target. If gaze anchoring leads to better performance under conditions such as those studied in the current experiment and if subjects anchor their gaze in 'Endpoint – Head/Eye Centered' but not the other conditions, it would be expected that motor performance is better in 'Endpoint – Head/Eye Centered' compared to the other conditions. Since we did not record eye movement in our experiment, we cannot quantitatively analyze subjects' gaze position as a potential covariate. However, other results in the literature strongly suggest that better performance in our 'Endpoint – Head/Eye Centered' conditions cannot be explained based on differences in eye movements. Two of the major points to consider in this context are that (a) subject performed open-loop pointing movements (i.e. no online visual feedback during trials) and (b) that the visual scene was visible all the time, so that there were no rapid visual stimulus onsets or sudden changes in the visual stimulus. Under these conditions eye movements do not affect variability of hand movements and they affect average hand movement distances in a way that is inconsistent with our current results (Abrams, Meyer, & Kornblum, 1990, Exp. 2 and 3). Thus, we believe that eye movements are not responsible for improved performance in 'Endpoint – Head/Eye

[4] It is interesting to note in this context that an increase in movement reliability and accuracy is also observed when subjects are asked to reproduce kinesthetically perceived movement endpoints, compared to when they are asked to reproduce kinesthetically perceived movement distances (Marteniuk & Roy, 1972). Thus, a distinction into movement endpoint and movement distance and direction appears to apply not only in the context of visually guided movements in our experiment, but also in the context of kinesthetically based movement reproduction. Furthermore, it has been found that when subjects are temporarily deprived of proprioceptive feedback of the joints and skin, their reproduction of movement distances suffers, whereas their reproduction of movement endpoints does not (Kelso, 1977). This finding is consistent with the idea that there might separate control mechanisms for the production of movement endpoints and movement distance and direction.

Centered' conditions in our experiments. Nevertheless, we think that it should be investigated in future experiments how eye movements contribute to performance in the different tasks, when these are performed under eye movement sensitive conditions (i.e. visual feedback is available, sudden changes in target position).

Why does response reliability decrease from 'Endpoint – Head/Eye Centered', to 'Rotated – Hand Centered' to 'Allocentric' tasks? The observed ordering of performance reliability could in principle be explained assuming that subjects can use combinations of head/eye-centered, hand centered and allocentric representations where possible and that each representation provides its own source of information. Used in combination, the different representations would provide the benefit of information redundancy and therefore increase response reliability. In our experiment, subjects could rely on all three representations in the 'Endpoint – Head/Eye Centered' task, only on hand centered and allocentric information in the 'Rotated – Hand Centered' task and only on allocentric information in 'Allocentric' tasks. Therefore, based on information redundancy we would predict the observed ordering of performance reliability. Alternatively, it is also possible that the ordering of reliability is observed because a head/eye-centered representation of space is inherently more reliable than a hand centered representation, which in turn might be inherently more reliable than an allocentric representation. Based on this explanation, differences in reliability are not due to combined used of multiple representation but due to an independent use of representations that differ in reliability. It is important to note that the number of geometrical transformations that has been applied to the target distance segment, i.e. rotation and translation, does not correspond to the observed differences in reliability in our experiment. For example, based on the number of transformations we would expect that reliability in 'Endpoint – Head/Eye Centered' conditions (zero transformations) is higher than in 'Rotated – Hand Centered' and 'Translated - Allocentric' conditions (one transformation), which in turn should be higher than in 'Translated and Rotated - Allocentric' conditions (two transformations). Yet, in our experiment, we observe an ordering that distinguishes between head/eye-centered, hand centered and allocentric representations, regardless of the number of transformations, for both perception and visually guided hand movements.

Why does response accuracy decrease when target direction does not match the orientation of the target distance segment? In both Exp. 1 and Exp. 2 vertically oriented target segments are perceived as longer than target segments oriented at 45° and this result is in agreement with other reports on orientation dependent perception of length (Howe & Purves, 2002). A popular example of this effect is the horizontal–vertical illusion, where vertically oriented lines appear longer then their horizontally oriented counterparts (Avery & Day, 1969; Cormack & Cormack, 1974). Our finding that the effect disappears in conditions where the target direction matches the orientation of the target distance segment replicates findings by Teghtsoonian (1972) who used a perceptual length-matching task. A possible explanation of variations in average movement and adjusted distance in our experiment involves two lines of evidence. First, perceived space is not Euclidean (Todd & Norman, 2003). Thus, when subjects are required to compute target distance, they are not expected to compute the same distance estimate in different directions. Second, the specific non-Euclidean 'bias' to perceive more vertically oriented lines as longer than more horizontally oriented lines has been attributed to the fact that projected lines that are oriented more vertically typically correspond to longer lines in the physical world than more horizontally oriented lines (Howe & Purves, 2002). Thus, decreased response accuracy when the target direction does not match the direction of the target distance segment can possibly be explained based on a combination of non-Euclidean space perception and bias. The absence of a distortion in 'Endpoint – Head/Eye Centered' and 'Translated - Allocentric' conditions can be explained by the fact that target direction matches the orientation of the target distance segment in which case bias does not come into play.

A non-veridical response to the target distance segment is only observed in conditions that require subjects to compute distance in a direction other than their response direction. It follows that if we had compared subject's average motor performance in 'Endpoint – Head/Eye Centered' or 'Translated - Allocentric' conditions with their average perceptual performance in either 'Rotated – Hand Centered' or 'Translated and Rotated - Allocentric' conditions, we might have concluded that perceptual performance is affected by illusions of length or size, whereas motor performance is not. This conclusion has been drawn in several studies (Aglioti, DeSouza, & Goodale, 1995; Haffenden, Schiff, & Goodale, 2001; Loomis, DaSilva, Fujita, & Fukusima, 1992) and has been taken as support for the idea that visual processing for perception and action is independent (Goodale & Milner, 1992). This interpretation of the data has been criticized based on the argument that perceptual and motor performance might have been compared across tasks that require the processing of different spatial attributes (Smeets et al., 2002; Post & Welch, 1996) and our results provide indirect support for this criticism. In a related argument it has also been suggested that subjects employ two different types of perception, that are mediated by either one (absolute perception) or more than one (relative perception) display elements and that illusions of size only affect relative perception (Vishton, Rea, Cutting, & Nunez, 1999). According to Vishton et al.'s (1999) distinction into absolute and relative perception, an ambiguity exists regarding the classification of our experimental conditions. For example, all our conditions could be considered absolute perception, because subjects always respond to the distance of a single target distance segment. Alternatively, it could be argued that only 'Endpoint – Head/Eye Centered' conditions require absolute perception, because in all other conditions subjects compute the distance of the target distance segment with respect to the line indicating the response direction. Most importantly, irrespective of the classification of our experimental conditions, there is no clear correspondence between changes in average movement or adjusted distance observed in the current experiments and the distinction into absolute and relative perception suggested by Vishton et al. (1999). Therefore, Vishton et al.'s (1999) distinction into absolute and relative perception cannot explain the results obtained in the current experiments and it appears that a classification into the different types of spatial representations is better.

A recent study (Schenk, 2006) varied response mode (motor vs. perception) and visual information (allocentric vs. egocentric) independently from each other and found that a patient (DF) with bilateral damage to ventral regions showed impaired performance for both perceptual and motor tasks when they required the use of allocentric information. To explain the results Schenk (2006) suggested that allocentric and egocentric hand-centered visual spatial information might be computed in independent processing streams and that DF's cortical lesions impaired her ability to use allocentric information, while leaving her ability to perform tasks based on an egocentric hand-centered representation intact. In general, our results are consistent with this interpretation. However, the results obtained in the current experiments also suggest that it might not only be necessary to distinguish between hand-centered egocentric and allocentric, but also between head/eye and hand-centered egocentric representations. In this context, it is interesting to note that Schenk's (2006) egocentric perceptual task required subjects to judge which of two points was closer to their finger, which requires the use of a hand centered egocentric representation. DF's performance in this task was worse than the average performance of normal subjects, but not significantly so (Schenk, 2006, p. 1370:

$t(9) = 1.68$, $p = .063$). In contrast, DFs performance in the egocentric visuo-motor task which required pointing to visible target locations matched average performance of control subjects (Schenk, 2006, p. 1370: $t(9) = 0.52$ $p = .284$). Please note that the latter task could be performed based on both hand and head/eye-centered representations.

The difference in performance between allocentric and egocentric conditions for DF clearly highlights the distinction between egocentric and allocentric processing. At the same time, the slight asymmetry between her performances in the head/eye vs. hand-centered conditions might suggest that she might employ different types of egocentric representations in those two tasks. Alternatively, it has also been suggested that DF's performance in the egocentric perceptual task is worse because she employs a visuo-motor help-strategy, i.e. imagined hand movements, to perform (Milner & Goodale, 2008). The question arises if the behavioral dissociations observed in the current experiments have a neurological correspondence and if dissociations between egocentric head/eye-centered and hand-centered and allocentric representations can explain performance dissociations observed in DF.

5. Conclusion

We found that visual information on target location in head/eye-centered coordinates is crucial to guide the hand towards visible locations in space, but that hand-centered and allocentric representation can be used as well. We found that perceptual and visuo-motor results agree quantitatively well, which suggests that a common computational principle underlies performance in both perceptual and visuo-motor tasks (i.e. De Graaf et al., 1991; Gegenfurtner & Franz, 2007; Post & Welch, 1996; Smeets et al., 2002; Smeets & Brenner, 1995). Our results emphasize that a meaningful comparison between perceptual and visuo-motor responses can only be drawn when tasks are matched with respect to the spatial representation that is needed to perform. Future investigations will determine if target location in head/eye-centered coordinates is represented in terms of distance and direction with respect to the observers head or eye, or if it is represented in another format, i.e. a topology.

Acknowledgements

The authors thank Jeroen Smeets, Eli Brenner, Gavin Buckingham and one anonymous reviewer for helpful comments on a previous version of this manuscript.

References

Abrams, R. A., Meyer, D. E., & Kornblum, S. (1990). Eye-hand coordination: Oculomotor control in rapid aimed limb movements. *Journal of Experimental Psychology: Human Perception & Performance*, *16*, 248–267.

Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679–685.

Atkeson, C. G., & Hollerbach, J. M. (1985). Kinematic features of unrestrained vertical arm movements. *The Journal of Neuroscience*, *5*, 2318–2330.

Avery, G. H., & Day, R. H. (1969). Basis of the horizontal–vertical illusion. *Journal of Experimental Psychology*, *81*(2), 376–380.

Bizzi, E., Accornero, N., Chapple, W., & Hogan, N. (1984). Posture control and trajectory formation during arm movement. *Journal of Neuroscience*, *4*, 2738–2744.

Bock, O., & Eckmiller, R. (1986). Goal-directed arm movements in absence of visual guidance: Evidence for amplitude rather than position control. *Experimental Brain Research*, *62*(3), 451–458.

Brenner, E., & Smeets, J. B. J. (1996). Size illusion influences how we lift but not how we grasp an object. *Experimental Brain Research*, *111*, 473–476.

Brenner, E., Smeets, J. B. J., & Remijnse-Tamerius, H. C. (2002). Curvature in hand movements as a result of visual misjudgements of direction. *Spatial Vision*, *15*, 393–414.

Carey, D. P. (2001). Do action systems resist visual illusions? *Trends in Cognitive Sciences*, *5*(3), 109–113.

Cormack, E. O., & Cormack, R. H. (1974). Stimulus configuration and line orientation in the horizontal vertical illusion. *Perception and Psychophysics*, *16*, 208–212.

De Grave, D. D., Brenner, E., & Smeets, J. B. (2004). Illusions as a tool to study the coding of pointing movements. Experimental. *Brain Research*, *155*, 56–62.

De Graaf, J. B., Sittig, A. C., & Denier van der Gon, J. J. (1991). Misdirections in slow goal-directed arm movements and pointer setting tasks. *Experimental Brain Research*, *84*, 434–438.

Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, *4*, 423–431.

Desmurget, M., Jordan, M., Prablanc, C., & Jeannerod, M. (1997). Constrained and unconstrained movements involve different control strategies. *Journal of Neurophysiology*, *77*, 1644–1650.

Desmurget, M., Pelisson, D., Rossetti, Y., & Prablanc, C. (1998). From eye to hand: Planning goal-directed movements. *Neuroscience and Biobehavioral Reviews*, *22*, 761–788.

Desmurget, M., & Prablanc, C. (1997). Postural control of three dimensional prehension movements. *Journal of Neurophysiology*, *77*, 452–464.

Feldman, A. G. (1966). Functional tuning of the nervous system during control of movement or maintenance of a steady posture. III. Mechanographic analysis of the execution by man of the simplest motor tasks. *Biophysics*, *11*, 766–775.

Fisher, N. I. (1993). *Statistical analysis of circular data*. New York, NY: Cambridge University Press.

Flanders, M., Helms Tillery, S. I., & Soechting, J. F. (1992). Early stages in a sensorimotor transformation. *Behavioral and Brain Sciences*, *15*, 309–362.

Franz, V. H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences*, *5*(11), 457–459.

Franz, V. H., Fahle, M., Buelthoff, H. H., & Gegenfurtner, K. R. (2001). Effects of visual illusions on grasping. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 1124–1144.

Gegenfurtner, K. R., & Franz, V. H. (2007). A comparison of localization judgments and pointing precision. *Journal of Vision*, *7*(5), 11, 1–12.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20–25.

Goodale, M. A., Milner, D. A., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*, 154–156.

Gordon, J., Ghilardi, M. F., & Ghez, C. (1994). Accuracy of planar reaching movements. I. Independence of direction and extent variability. *Experimental Brain Research*, *99*, 97–111.

Haffenden, A. M., Schiff, K. C., & Goodale, M. A. (2001). The dissociation between perception and action in the Ebbinghaus illusion Nonillusory effects of pictorial cues on grasp. *Current Biology*, *11*(3), 177–181.

Haggard, P., Newman, C., Blundell, J., & Andrew, H. (2000). The perceived position of the hand in space. *Perception & Psychophysics*, *62*(2), 363–377.

Henkel, V., Mergl, R., Juckel, G., Rujescu, D., Mavrogiorgou, P., Giegling, I., et al. (2001). Assessment of handedness using a digitizing tablet: A new method. *Neuropsychologia*, *39*(11), 1158–1166.

Howe, C. Q., & Purves, D. (2002). Range image statistics can explain the anomalous perception of length. *Proceedings of the National Academy of Sciences*, *99*, 13184–13188.

Huynh, H., & Feldt, L. S. (1976). Estimation of the box correction for degrees of freedom from sample data in randomized block and split-plot designs. *Journal of Educational and Behavioral Statistics*, *1*(1), 69–82.

Jeannerod, M., Paulignan, Y., Mackenzie, C., & Marteniuk, R. M. (1992). Parallel visuomotor processing in human prehension movements. In R. Caminiti, P. B> Johnson, & Y. Burnod (Eds.), *Control of arm movement in space: neurophysiological and computational approaches* (pp. 27–44). Berlin: Springer.

Kelso, J. A. (1977). Motor control mechanisms underlying human movement reproduction. *Journal of Experimental Psychology: Human Perception and Performance*, *3*(4), 529–543.

Lacquaniti, F., & Caminiti, R. (1998). Visuo-motor transformations for arm reaching. *European Journal of Neuroscience*, *10*, 195–203.

Liu, D., & Todorov, E. (2007). Evidence for the flexible sensorimotor strategies predicted by optimal feedback control. *Journal of Neuroscience*, *27*(35), 9354–9368.

Loomis, J. M., Da Silva, J. A., Fujita, N., & Fukusima, S. S. (1992). Visual space perception and visually directed action. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 906–921.

Marteniuk, R. G., & Roy, E. A. (1972). The codability of kinesthetic location and distance information. *Acta Psychologica*, *36*, 471–479.

McIntyre, J., Stratta, F., & Lacquaniti, F. (1997). Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space. *Journal of Neurophysiology*, *78*, 1601–1618.

Messier, J., & Kalaska, J. F. (1997). Differential effect of task conditions on errors of direction and extent of reaching movements. *Experimental Brain Research*, *115*, 469–478.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*(3), 774–785.

Peters, M., & Servos, P. (1989). Performance of subgroups of left-handers and right-handers. *Canadian Journal of Psychology*, *43*, 341–358.

Polit, A., & Bizzi, E. (1979). Characteristics of motor programs underlying arm movements in monkeys. *Journal of Neurophysiology*, *42*, 183–194.

Post, R. B., & Welch, R. B. (1996). Is there dissociation of perceptual and motor responses to figural illusions? *Perception*, *25*, 569–581.

Rosenbaum, D. A., Loukopoulos, L. D., Meulenbroek, R. G., Vaughan, J., & Engelbrecht, S. E. (1995). Planning reaches by evaluating stored postures. *Psychological Review*, *102*, 28–67.

Sainburg, R. L., & Kalakanis, D. (2000). Differences in control of limb dynamics during dominant and nondominant arm reaching. *Journal Neurophysiology*, *83*, 2661–2675.

Sainburg, R. L., & Wang, J. (2002). Interlimb transfer of visuomotor rotations: Independence of direction and final position information. *Experimental Brain Research*, *145*, 437–447.

Schenk, T. (2006). An allocentric rather than perceptual deficit in patient D.F. *Nature Neuroscience*, *9*, 1369–1370.

Smeets, J. B. J., & Brenner, E. (1995). Perception and action are based on the same visual information: Distinction between position and velocity. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 19–31.

Smeets, J. B. J., Brenner, E., de Grave, D. D. J., & Cuijpers, R. H. (2002). Illusions in action: Consequences of inconsistent processing of spatial attributes. *Experimental Brain Research*, *147*, 135–144.

Smeets, J. B. J., van den Dobbelsteen, J. J., de Grave, D. D. J., van Beers, R. J., & Brenner, E. (2006). Sensory integration does not lead to sensory calibration. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(49), 18781–18786.

Teghtsoonian, M. (1972). Apparent length as a function of tilt does not depend on orientation of the standard. *Journal of Experimental Psychology*, *94*, 191–197.

Todd, J. T., & Norman, J. F. (2003). The visual perception of 3-D shape from multiple cues: are observers capable of perceiving metric structure? *Perception and Psychophysics*, *65*, 31–47.

Todorov, E., & Jordan, M. I. (2002). Optimal feedback control as a theory for motor coordination. *Nature Neuroscience*, *5*, 1226–1235.

Todorov, E. (2004). Optimality principles in sensorimotor control (review). *Nature Neuroscience*, *7*(9), 907–915.

van Beers, R. J., Haggard, P., & Wolpert, D. M. (2004). The role of execution noise in movement variability. *Journal of Neurophysiology*, *91*, 1050–1063.

van Beers, R. J., Sittig, A. C., & Denier van der Gon, J. J. (1998). The precision of proprioceptive position sense. *Experimental Brain Research*, *122*, 367–377.

van den Dobbelsteen, J. J., Brenner, E., & Smeets, J. B. J. (2001). Endpoints of arm movements to visual targets. *Experimental Brain Research*, *138*, 279–287.

Vetter, P., Goodbody, S. J., & Wolpert, D. M. (1999). Evidence for an eye-centered spherical representation of the visuomotor map. *Journal of Neurophysiology*, *81*, 935–939.

Vindras, P., & Viviani, P. (1998). Frames of reference and control parameters in visuomanual pointing. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(2), 569–591.

Vindras, P., Desmurget, M., & Viviani, P. (2005). Error parsing in visuomotor pointing reveals independent processing of amplitude and direction. *Journal of Neurophysiology*, *94*, 1212–1224.

Vishton, P. M., Rea, J. G., Cutting, J. E., & Nunez, L. N. (1999). Comparing effects of the horizontal–vertical illusion on grip scaling and judgment: Relative versus absolute, not perception versus action. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(6), 1659–1672.

Wang, J., & Sainburg, R. L. (2006). Interlimb transfer of visuomotor rotations depends on handedness. *Experimental Brain Research*, *175*, 223–230.

Wann, J. P., & Ibrahim, S. F. (1992). Does limb proprioception drift? *Experimental Brain Research*, *91*, 162–166.