Evidence From Visuomotor Adaptation for Two Partially Independent Visuomotor Systems

Lore Thaler and James T. Todd
The Ohio State University

Visual information can specify spatial layout with respect to the observer (egocentric) or with respect to an external frame of reference (allocentric). People can use both of these types of visual spatial information to guide their hands. The question arises if movements based on egocentric and movements based on allocentric visual information comprise 2 independent visuomotor systems. In the experiments reported here, we used visuomotor adaptation to address this question. In an adaptation phase, subjects received distorted-visual feedback about their hand movements (17° rotation and 110% amplitude stretch). In a testing phase (no-visual feedback), we measured how behavior changes in response to the distorted-visual feedback. During adaptation and testing, we used 2 tasks that required processing of either egocentric or allocentric visual information. The results show that behavioral changes are significantly larger when the same task is used during testing and adaptation, compared to when the task is switched. The findings suggest that the human brain employs 2 partially independent visuomotor systems that rely on different types of visual spatial information.

Keywords: visually guided hand movements, visuomotor adaptation, visuomotor transformation, egocentric, allocentric

There are various ways to represent the spatial structure of the physical world surrounding us. In the literature, we traditionally distinguish between *egocentric* representations that code spatial information with respect to the observer or the observer's body parts (eye, head, shoulder, hand) and *allocentric* representations that code spatial information with respect to an external frame of reference. There are several behavioral studies that investigate the effects of egocentric and allocentric spatial information on perceptual judgments (Bridgeman, Peery & Anand, 1997; Neggers, Scholvinck, van der Lubbe & Postma, 2005; Schenk, 2006; Thaler & Todd, 2009b) as well as on visually guided pointing movements (Bridgeman et al., 1997; Schenk, 2006; Thaler & Todd, 2009a, 2009b). In recent years, there have also been various neuroimaging studies that investigated neural correlates of egocentric and allocentric perceptual judgments (Committeri et al., 2004; Galati et al., 2000; Neggers, van der Lubbe, Ramsey, & Postma, 2006; Vallar et al., 1999; Zaehle et al., 2007). Behavioral studies have shown that allocentric and egocentric visual information lead to different performance characteristics, suggesting that these two types of spatial information might be processed separately from one another (Neggers et al, 2005; Thaler & Todd, 2009a, 2009b). Con-

sistent with these findings, neuroimaging studies revealed that allocentric and egocentric perceptual judgments engage different brain circuitry. Specifically, it appears that ventral visual stream areas and hippocampus are more active during allocentric perceptual judgments, whereas dorsal visual stream areas and parietal cortex are more active during egocentric spatial judgments (Committeri et al., 2004; Galati et al, 2000; Neggers et al., 2006; Vallar et al., 1999; Zaehle et al., 2007). Hitherto, neuroimaging studies that investigated egocentric and allocentric visual processing only considered spatial judgments. Yet, it is known from other neuroimaging and neurophysiological research that visually guided pointing and grasping movements toward visible target objects invoke a parietal cortical network (for reviews, see Andersen, Snyder, Bradley & Xing, 1997; Culham, Cavina-Pratesi, & Singhal, 2006; Culham & Valyear, 2006). Based on the involvement of the parietal cortex in reaching movements as well as egocentric spatial judgments, it appears likely that visually guided hand movements would rely predominantly on egocentric visual information (Neggers et al., 2006). Yet, it is obviously the case that human beings can perform visually guided hand movements based on allocentric visual information alone (Thaler & Todd, 2009a, 2009b). Consider for example the two pointing tasks illustrated in Figure 1. The "endpoint" task illustrated in the left-hand panel requires egocentric processing because the subject is instructed to move her hand based on visual information that defines the location of a point with respect to the her own body (i.e., eye, head, shoulder, hand). In contrast, the "allocentric" task illustrated in the right-hand panel requires allocentric processing because the subject is instructed to move her hand based on visual information that defines the location of a point with respect to another point that is external to the subject.

Based on neuroimaging research, it would appear that hand movements performed in the allocentric task should require ventral
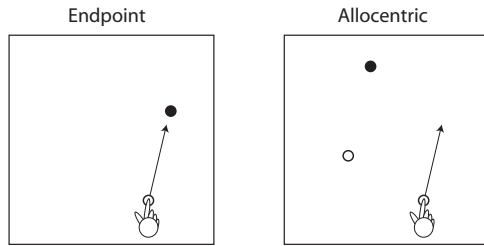
Figure 1. Illustration of two different visuomotor tasks. In the "endpoint" task, subjects are instructed to move their hand from the starting position to a location indicated by a black target dot. In the "allocentric" task, subjects are instructed to move their hand from the starting position to a location whose position with respect to the hand starting point is identical to the position of the black dot with respect to the white dot.

visual stream function, whereas hand movements performed in the endpoint task should require dorsal visual stream function. Consistent with this idea, Schenk (2006) found that performance of a patient with intact dorsal but lesioned ventral visual stream areas (patient DF) was worse than matched control subjects in the allocentric task in Figure 1, but normal in the endpoint task.

Performing visually guided hand movements requires complex visuomotor transformations that link visual spatial information to movement parameters. Given the plethora of behavioral, neurological, and neuroimaging results, the question arises how allocentric and egocentric visual visuomotor transformations are related. One possibility is that the human central nervous system (CNS) employs separate visuomotor transformations for hand movements performed in the endpoint and allocentric tasks illustrated in Figure 1. If this were the case, the human CNS would have two separate visuomotor mappings, one that maps allocentric visual information onto movement parameters and one that maps egocentric visual information onto movement parameters. Alternatively, it is also possible that allocentric and egocentric visual information are mapped in a combined fashion onto movement parameters. The results in DF (Schenk, 2006) are not relevant to this question, because her impairment could be caused both by the disruption of an allocentric visuomotor mapping as well as by the loss of allocentric visual input to a combined visuomotor mapping. In the current paper, we use visuomotor adaptation to investigate if allocentric and egocentric visual information are mapped independently from each other onto motor parameters.

Visuomotor adaptation refers to the phenomenon that visually guided motor behavior changes in response to visual feedback. Since von Helmholtz's (1867) pioneering work on prismatic adaptation, many studies have investigated adaptation to a variety of forms of altered visual feedback (for a review, see Redding & Wallace 1996, 1997; Welch 1986). Studies on visuomotor adaptation consistently show that subjects change their visuomotor behavior to minimize the errors that they visually perceive, even when these changes increase the physical discrepancy between hand and target or between the desired and actual physical trajectory (i.e., Bedford, 1989; Cunningham, 1989; Ghahramani, Wolpert, & Jordan, 1996; Krakauer, Pine, Ghilardi, & Ghez, 2000; Mon-Williams & Bingham, 2007; Pine, Krakauer, Gordon, & Ghez, 1996; van den Dobbelsteen, Brenner, & Smeets, 2004; Wolpert, Ghahramani, & Jordan, 1995). This situation occurs, for

example, when visual feedback is distorted with respect to the physical movement of the hand. One possibility to quantify feedback-induced changes in visuomotor mapping is to measure the degree to which changes in visuomotor performance that are required in response to visual feedback persist after visual feedback is removed and subjects are instructed to move their hands to the physical target to the best of their abilities. The change in performance that persists after visual feedback has been removed can then be used as a measure of feedback induced changes in visuomotor mapping.

If egocentric and allocentric visual representations were mapped independently from each other on movement parameters in endpoint and allocentric visuomotor tasks, a change in performance that is acquired in the presence of feedback in an egocentric task should not transfer to an allocentric task, when feedback is removed, and vice versa. Thus, a task switch between feedback and no-feedback phase should dramatically affect performance if subjects use independent ego- and allocentric visuomotor mappings in endpoint and allocentric tasks. In contrast, if there is only one shared mapping from visual representations to movement parameters, that is used in both endpoint and allocentric tasks, a task switch between feedback and no-feedback phases should not affect performance and changes in performance should transfer 100% from one task to the other.

The current experiments were designed to test these predictions. Subjects performed visually guided movements in endpoint and allocentric tasks. First, we measured performance in baseline conditions. We then gave visual feedback that was distorted with respect to the actual physical movement and measured how subjects' performance changed compared to baseline. We then removed visual feedback and measured, to what degree changes in performance persisted. When visual feedback was removed the task could either be the same as when feedback was available, or the task could be switched. We found that changes in performance persisted in all conditions. However, we also found that changes persisted more when the same task was used during feedback and no-feedback phases, compared to when the task was switched. Our experiment was designed to ensure that the effects could not be explained by fatigue, differences in the actual physical movements during the feedback phase, or differences in visual feedback. Therefore, our results suggest that subjects use partially independent egocentric and allocentric visuomotor mappings.

Method

Subjects

Nine subjects (five men: two left-handed; four women: one left-handed), including the authors, participated in the experiment. Subjects gave informed consent before the experiment, and all subjects except the authors were paid for their participation. All subjects had self-reported normal or corrected-to-normal vision. All subjects, but the first author, were naïve about the distortions employed and the specific conditions tested in each session.

Apparatus

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 (26 cm to either surface). Thus, the mirror prevented subjects from seeing their hand and at the same time stimuli appeared to be in the same plane as the digitizing tablet, on which subjects moved their hand.

Hand movements were recorded with a stylus on the digitizing tablet (AccuGrid, Model A90; Numonics Corporation, Montgomeryville, PA; 1,200 (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 1,024 (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 to avoid changes in head position. Subjects' eyes were located approximately 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. The relative position between rear projection surface and tablet was fixed. 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.

Stimuli and Task

The two basic tasks are illustrated in Figure 1. In endpoint conditions, subjects saw a black target dot (5 mm diameter) and were instructed to move their hand from their starting position to the target. In allocentric conditions, subjects saw a white and a black dot (both 5 mm diameter), and they were instructed to move their hand to a location whose position with respect to their hand starting point was identical to the position of the black dot with respect to the white dot. The white dot in allocentric conditions was located 70 mm to the left and 150 mm to the front of the starting point of the hand. We used two positions of the black target dot with respect to the starting position of the hand (or the white dot; Position 1: 20 mm right, 120 mm front; Position 2: 60 mm right, 140 mm front). Subjects started each movement from the same starting position located 50 mm in front of their sternum on the recording surface. A small tactile marker was placed on the digitizing tablet at the hand starting point. Visual indicators of hand starting position were different in feedback and no-feedback conditions (see Procedure). Setup and stimuli for left-handed subjects was mirror symmetric to that of right-handed subjects described above. All stimuli were presented in front of a light-gray background covered with 2,500 small, randomly positioned points. Random positions were recomputed on every trial.

Movements were performed in baseline and adaptation conditions. In both adaptation and baseline conditions, visual feedback could be available (feedback blocks) or not (no-feedback blocks). In no-feedback blocks, subjects never received any visual feedback about their hand movement. In feedback blocks, visual feedback was available but it was different in baseline and adaptation conditions. In feedback blocks in baseline sessions, coordinates of a subject's hand on the digitizing tablet were used to project a green cursor dot (3 mm diameter) in between trials. Because subjects viewed the projection of the green dot in a mirror, the green dot appeared to move with the subject's hand in real

time (max. delay ~ 16 ms due to 60-Hz projector refresh rate). The cursor dot would appear only after subjects had moved their hands at least 30 mm away from their final hand position on any given trial. During a trial, feedback was not available. Choosing to give visual feedback this way in baseline conditions gave subjects a veridical estimate of their physical hand position in between trials, but prevented them from changing their natural motor behavior in response to task-relevant feedback.

In feedback blocks in adaptation sessions, feedback about the hand movement was provided at the end of each trial in the form of a movement trace that was a distorted version of subjects' original movement trace in that trial. The distorted version of subjects movement trace was obtained by rotating subjects' original movement traces 17° in the clockwise direction (in the counter clockwise direction for left-handed subjects) and by stretching the original movement amplitude to 110% of its original length. The coordinates of the distorted trace were indicated by green 3 mm diameter dots. The first coordinate of the distorted movement trace always coincided with the first coordinate of the original movement trace, that is, the hand starting point. To enable subjects to evaluate their performance in allocentric conditions, the white and black target dots were translated onto the subjects hand starting position during the feedback phase. Please note that this feature of our feedback schedule enabled us to provide the same visual feedback in endpoint and allocentric conditions.

Procedure

In the beginning of a trial, subjects saw only the movement surface, and they were instructed to move their hand toward the hand starting point that was indicated by a small tactile marker on the digitizing tablet. A trial was initiated when subjects had remained for at least 1 s within a distance of 3 mm to the starting position. Then, a 100-ms beep would indicate the start of the trial. Synchronous with the beep, the target(s) would become visible; and in feedback trials, the starting point of the hand would become visible as well. No instructions about movement speed were given, but it was emphasized to subjects that they should move in one smooth movement once they had started moving. A trial was terminated when subjects had moved less than 15 mm during the last 450 ms. After another 100 ms, another beep would indicate the end of the trial. In feedback blocks in adaptation sessions, the feedback trace would become visible synchronous with that beep and remain visible for 1.2 s. In allocentric feedback conditions, the target dots would also be translated. After those 1.2-s feedback, starting point and the old target(s) would disappear and subjects could initiate the next trial by moving the hand to the starting position indicated by the tactile marker. Because the feedback movement trace was only shown in feedback blocks in adaptation sessions, the new target(s) would appear synchronous with the beep and thus without a 1.2-s delay in all other conditions.

The experiment was performed in four sessions on four separate days. Every subject first performed in two baseline sessions (Sessions 1 and 2) and then two adaptation sessions (Sessions 3 and 4). Each session consisted of four feedback blocks and four no-feedback blocks that were presented in alternating order. The task used in feedback blocks did not change within a session, but the task used in no-feedback blocks was alternated. Thus, within each session subjects had two no-feedback blocks that required a task

switch and two no-feedback blocks that used the same task as feedback blocks. To counterbalance the order of no-feedback blocks, we used two basic experimental designs (Design A and B), both of which are sketched in Table 1. Five subjects performed Design A, and four subjects performed Design B. To counterbalance the order of sessions (with the restriction that baseline session were performed before adaptation sessions), each subject in Design A or B performed sessions in a different order, that is, Order 1, 2, 3, 4; 1, 2, 4, 3; 2, 1, 3, 4; or 2, 1, 4, 3. Because five subjects performed in Design A, order 1, 2, 4, 3 was performed by two subjects in Design A. Because tasks in no-feedback conditions were alternated, each session consisted of two structurally equivalent parts (Parts 1 and 2). The only difference between Parts 1 and 2 was that subjects had received on average more feedback in part 2.

Counterbalancing the order of sessions and the order of no-feedback blocks across subjects enables us to control the effects of those variables on performance in task-switch and no-task-switch blocks. However, if we want to know how performance on any given adaptation trial was affected by visual feedback, we have to evaluate performance in any adaptation trial against performance in a matched baseline trial. For example, factors such as muscular fatigue and visuo-kinesthetic drift (Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006; Wann & Ibrahim, 1992) as well as no-feedback–related effects of task switching might systematically affect subjects' visuomotor performance irrespective of feedback induced changes in visuomotor mapping. As evident in Table 1, we were able to control for the effects of these variables because structure of baseline and adaptation sessions was matched perfectly for each subject.

Within each feedback and no-feedback block, subjects performed 20 movements to each target configuration (Points 1 and 2). The presentation of order of points 1 and 2 was pseudorandomized within each block, so that the same configuration could not appear more than three times in direct succession. Each session consisted of $8 \times 40 = 320$ movements and took approximately 45 min. In the beginning of each session, subjects were made familiar with the task and procedure by performing at least three practice movements in each condition to each target. Practice trials were equivalent to experimental trials in every respect (feedback, timing, etc.).

Before the start of each session, written instructions were given to each subject by the experimenter (first author). Instructions were different in baseline and adaptation sessions. In baseline sessions, subjects were instructed to move as accurately as possible in all conditions. In adaptation sessions in feedback blocks, subjects were instructed to work with the visual feedback and to perform movements that would minimize the errors that they visually perceived at the end of each trial. In no-feedback blocks, subjects were instructed to perform movements that they felt would minimize the physical error between their movement and the movement that was indicated on a trial.

Summary of Experimental Design

Subjects had to compute an allocentric representation of the visual stimulus in allocentric tasks. In contrast, endpoint tasks permit the use of egocentric visual representation. In baseline conditions, we measured subjects' natural response in allocentric

Table 1

Outline of the Two Basic Experimental Designs That Were Counterbalanced Across Subjects

Variable	Part 1				Part 2			
	Feedback	No feedback	Feedback	No feedback	Feedback	No feedback	Feedback	No feedback
Design A								
Session 1 (Baseline)	Endpoint	Endpoint	Endpoint	Allocentric (task-switch)	Endpoint	Endpoint	Endpoint	Allocentric (task-switch)
Session 2 (Baseline)	Allocentric	Endpoint (task-switch)	Allocentric	Allocentric	Allocentric	Endpoint (task-switch)	Allocentric	Allocentric
Session 3 (Adaptation)	Endpoint	Endpoint	Endpoint	Allocentric (task-switch)	Endpoint	Endpoint	Endpoint	Allocentric (task-switch)
Session 4 (Adaptation)	Allocentric	Endpoint (task-switch)	Allocentric	Allocentric	Allocentric	Endpoint (task-switch)	Allocentric	Allocentric
Design B								
Session 1 (Baseline)	Endpoint	Allocentric (task-switch)	Endpoint	Endpoint	Endpoint	Allocentric (task-switch)	Endpoint	Endpoint
Session 2 (Baseline)	Allocentric	Allocentric	Allocentric	Endpoint (task-switch)	Allocentric	Allocentric	Allocentric	Endpoint (task-switch)
Session 3 (Adaptation)	Endpoint	Allocentric (task-switch)	Endpoint	Endpoint	Endpoint	Allocentric (task-switch)	Endpoint	Endpoint
Session 4 (Adaptation)	Allocentric	Allocentric	Allocentric	Endpoint (task-switch)	Allocentric	Allocentric	Allocentric	Endpoint (task-switch)
Trial within session	0 to 40	40 to 80	80 to 120	120 to 160	160 to 200	200 to 240	240 to 280	280 to 320

Note. Sessions were performed on separate days. Only one possible order of session types (1, 2, 3, 4) is shown, but order of sessions was counterbalanced across subjects as well, with the restriction that baseline sessions (1 & 2) were performed prior to adaptation sessions (3 & 4). Thus, at least one subject in each design performed sessions in order 1, 2, 3, 4; 1, 2, 4, 3; 2, 1, 4, 3; or 2, 1, 3, 4. Each session consisted of two structurally equivalent parts (Parts 1 & 2) that differed only with respect to their order, that is, Part 2 was performed after Part 1 in each session.

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and endpoint tasks in feedback and no-feedback conditions and after task-switch or no task-switch. In adaptation conditions, we measured subjects' motor responses during and after distorted-visual feedback under the same conditions as in baseline sessions. Counterbalancing the order of tasks and feedback schedules across subjects enabled us to control for the effects of those variables on the group level. At the same time, matching the order of those variables across sessions for each individual subject enabled us to control for effects of muscular fatigue, visuo-kinesthetic drift, and effects of task switching that are unrelated to adaptation. Furthermore, visual feedback in allocentric and endpoint adaptation conditions was identical. It follows that any difference in the change in performance compared to baseline that we might observe in task-switch and no-task-switch blocks must be due to differences in the visuomotor mapping that subjects use to generate hand movements in endpoint and allocentric tasks.

Data Analysis

Movement trajectories were filtered using a Butterworth filter with a 7-Hz cutoff. Movement onset was defined as the first time movement speed exceeded 1 cm/s. Movement end was defined as either the first time movement speed fell below 1 cm/s or the first time movement speed fell to a local minimum after having reached a global maximum. Movement speed was obtained by numerical differentiation of smoothed velocity traces.

To avoid that differences in the shape of movement trajectories affect our analyses, we computed the curvature of each trajectory as the maximum absolute distance of any point on the trajectory to the straight line joining start and endpoint, divided by the length of the straight line joining start and endpoint (Atkeson & Hollerbach, 1985). We then multiplied this ratio by 100 to obtain a measure in percentage. A value of 50% corresponds to a semicircular trajectory. For every subject and experimental condition separately, we then excluded any trajectories whose curvature exceeded the 25th percentile − 2*iqr or the 75th percentile + 2*iqr (iqr = interquartile range). This resulted in the exclusion of 1.5% of the trajectories ($n = 178$).

In feedback conditions in adaptation session, subjects were instructed to produce movements that would minimize the errors that they visually perceived at the end of each trial. The visual feedback was rotated 17° clockwise (counterclockwise for left-handed subjects) with respect to the physical movement direction and the amplitude was stretched to 110% of its original length. Thus, to produce a movement endpoint that resulted in correct performance as indicated by visual feedback, subjects had to move in a direction 17° counterclockwise (or clockwise for left-handed

subjects) compared to the visual target direction and over a distance that was 91% shorter than the visually indicated movement distance. Physical target locations that would result in correct performance with respect to the visual feedback in adaptation conditions were thus located to the left (or to the right for left-handed subjects) and front of the physical locations of the visual targets. We will refer to these new locations as *adaptation targets* in subsequent sections.

To quantify how subjects' motor behavior changes in response to the distorted-visual feedback, we used an analysis similar to the one introduced by van den Dobbelsteen, Brenner, and Smeets (2003). A graphical illustration is given in Figure 2. For every trial in adaptation sessions, we computed vector **a** pointing from the final hand position in the corresponding baseline trial to the final hand position in the adaptation trial (*adaptation vector*). The adaptation vector denotes the change in performance in adaptation trials with respect to performance in corresponding baseline trials. For the corresponding baseline trial, we also computed vector **c** pointing from the final hand position toward the adaptation target (*compensation vector*). The compensation vector denotes to the change in performance that would have realigned the visual feedback with the target in adaptation trials. To obtain a measure of the change in performance that is consistent with distorted visual feedback on any given trial we then computed the projection of the adaptation vector onto the compensation vector as the explained response, $e = \frac{a \cdot c}{|c|^2} c$. To obtain a measure of the change in performance that is inconsistent with distorted visual feedback we computed the vectorial difference between the adaptation vector and the explained response as unexplained response, $\mathbf{u} = \mathbf{a} - \mathbf{e}$. To obtain a measure of adaptation in percentage for every trial, we then computed the difference in length between vector **e** and **u**, divided the difference by the sum of the lengths, and multiplied by 100. Thus, for every trial,

$$\text{Adaptation (\%)} = 100 \frac{|e| - |u|}{|e| + |u|}.$$

Differences in adaptation between feedback and no-feedback blocks, that is, $d_A = \text{Adaptation (\%)}_{feedback} - \text{Adaptation (\%)}_{no\text{-}feedback}$, indicate to what degree behavioral changes acquired during feedback blocks carry over into no-feedback blocks. The larger d_A, the smaller is the carry-over effect. We computed d_A by averaging percentage adaptation across all trials separately for feedback and no-feedback blocks and computing the difference between the averages.
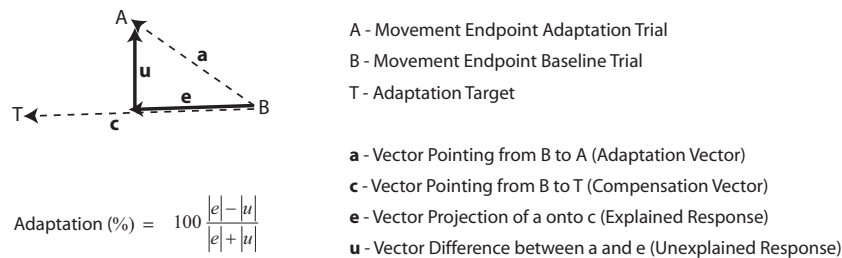

Adaptation (%) = $100 \frac{|e| - |u|}{|e| + |u|}$

A - Movement Endpoint Adaptation Trial
B - Movement Endpoint Baseline Trial
T - Adaptation Target

a - Vector Pointing from B to A (Adaptation Vector)
c - Vector Pointing from B to T (Compensation Vector)
e - Vector Projection of a onto c (Explained Response)
u - Vector Difference between a and e (Unexplained Response)

Figure 2. Graphical illustration of the analysis used to quantify changes in visuomotor behavior due to distorted-visual feedback. Please see text for details.

Results

After each baseline and adaptation session, all subjects (but the first author) were questioned by the first author regarding the difficulty of the task and if they had noticed anything unusual. Following baseline sessions, none of the subjects reported anything unusual. However, following adaptation sessions all but one subject reported that it was difficult to perform well, and they noted that this might have had something to do with the way feedback was given. Four subjects explicitly pointed out that they thought that the feedback had been rotated with respect to their actual movement.

Movement curvature was overall low (M = 2.4, SD = 1.3, median = 2.2, min = 0.3, max = 7.8) and did not differ across the different experimental conditions. Thus, subjects' movement traces were mostly straight in all conditions. 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, Figures 3 & 5; Desmurget, Jordan, Prablanc & Jeannerod, 1997; Thaler & Todd, 2009b).

Figure 3 shows adaptation in percentage averaged across subjects and spatial configurations (Points 1 and 2) on a trial-to-trial

basis. The upper panel shows changes in conditions in which feedback was given in the endpoint task; the lower panel shows shifts in conditions were feedback was given in the allocentric task. For ease of presentation, data for all subjects have been plotted according to Design A (cf. Table 1). However, as mentioned in the Method section, four subjects had performed the experiment according to Design B, such the actual order of no-feedback blocks for those subjects had been allocentric-endpoint-allocentric-endpoint. There was no significant difference in movement shifts between Points 1 and 2. Gray areas around each curve represent 95% confidence intervals around the mean across subjects. Dashed horizontal lines denote 0% adaptation.

Positive values in Figure 3 indicate that subjects change their movements to minimize the errors that they visually perceive. The difference in adaptation between feedback and no-feedback blocks indicate the change in behavior that persist after feedback has been taken away. If the curve drops rapidly at a transition from feedback to no-feedback blocks, the carry-over effect is small. If the curve continues at about the same level, the carry-over effect is large.

It is evident from Figure 3 that subjects shift their movement endpoint toward the adaptation target when visual feedback is
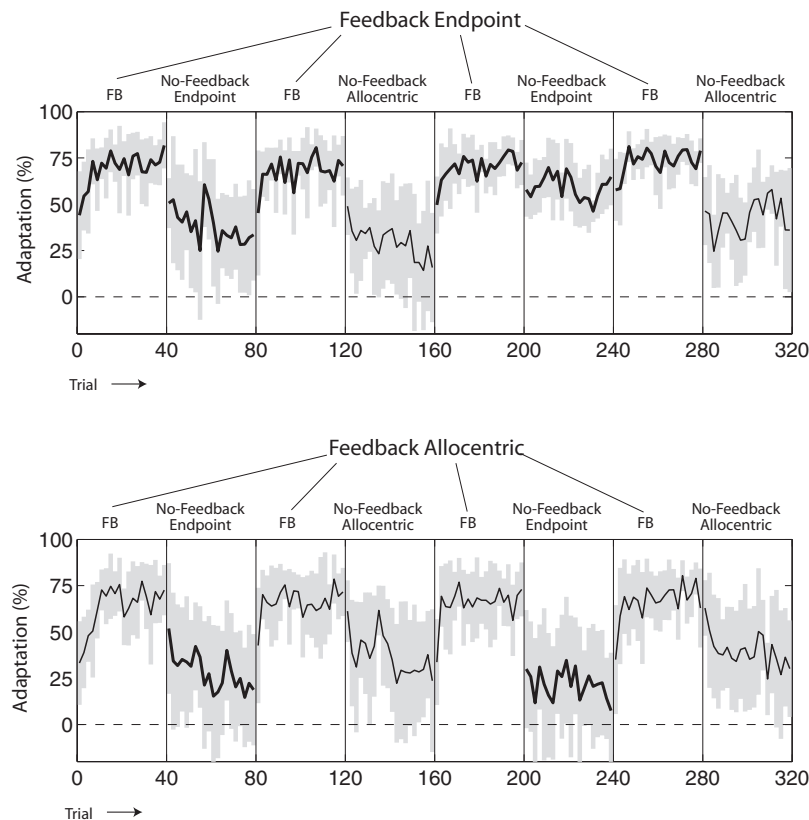

Figure 3. Percentage Adaptation on a trial-to-trial basis. Sessions in which feedback was obtained in endpoint and allocentric tasks are shown in the upper and lower panels, respectively. In each panel, solid vertical lines indicate breaks between feedback and no-feedback blocks, and the task performed in each block is denoted on top. Dashed horizontal lines indicate zero adaptation. Curves show average adaptation across subjects and points 1 and 2. For ease of presentation, thick and thin lines denote average adaptation in the endpoint and allocentric tasks, respectively. Gray areas around each curve represent 95% confidence intervals around the mean across subjects. FB = feedback.

available in both endpoint and allocentric tasks. In both endpoint and allocentric tasks, the feedback induced shift is significantly different from zero, except for the very first feedback trials within a session. This indicates that subjects follow the instructions and change their motor behavior in order to minimize the errors they visually perceive in both endpoint and allocentric feedback conditions.

In no-feedback blocks, the shift with respect to baseline depends on the amount of feedback that was received as well as on the task that was used during feedback and no-feedback trials. When feedback is obtained in the endpoint task (upper panel in Figure 3), the shift that is acquired during feedback trials in Part 1 of a session does not carry over to the no-feedback trials. For example, when feedback is given in the endpoint task several confidence intervals in endpoint and allocentric no-feedback blocks in Part 1 of a session include zero. However, in Part 2, in which more feedback has been obtained, the carry-over effect in endpoint no-feedback blocks is larger compared to allocentric no-feedback blocks. The opposite pattern of results is evident when feedback is obtained in the allocentric task (lower panel in Figure 3), in which case the carry-over effect in allocentric no-feedback blocks is larger, compared to endpoint no-feedback blocks. In fact, when feedback was obtained in the allocentric task, several of the confidence intervals in endpoint no-feedback blocks include zero.

To summarize, the change in motor behavior that is acquired during feedback carries over to subsequent no-feedback blocks in all conditions, but the degree to which feedback-induced changes in visuomotor behavior carry over to a subsequent no-feedback phase depends on the task that is used during feedback and no-feedback phases. When the same task is used during feedback and no-feedback phases, and thus subjects can rely on the same type of representation, the carry-over effects appear to be larger.

To obtain a single measure of adaptation and transfer in the different conditions, we computed average percentage adaptation for feedback and no-feedback phases as well as the difference in average adaptation in feedback and no-feedback phases, d_A, for the second part of each session. The reason for only considering the second part of a session is that subjects had received on average more feedback in those trials and that the changes in visuomotor performance appear to be more stable. Figure 4 shows average adaptation (in percentages) for the different feedback and no-feedback conditions (white bars) and the difference in adaptation (d_A) between feedback and no-feedback blocks (gray bars). Error bars denote 95% confidence intervals. In general, the larger d_A, the smaller is the carry-over effect.

It is evident from Figure 4 that the average data agree with the trial-by-trial results. Specifically, carry-over effects are larger when the same task is used during feedback and no-feedback
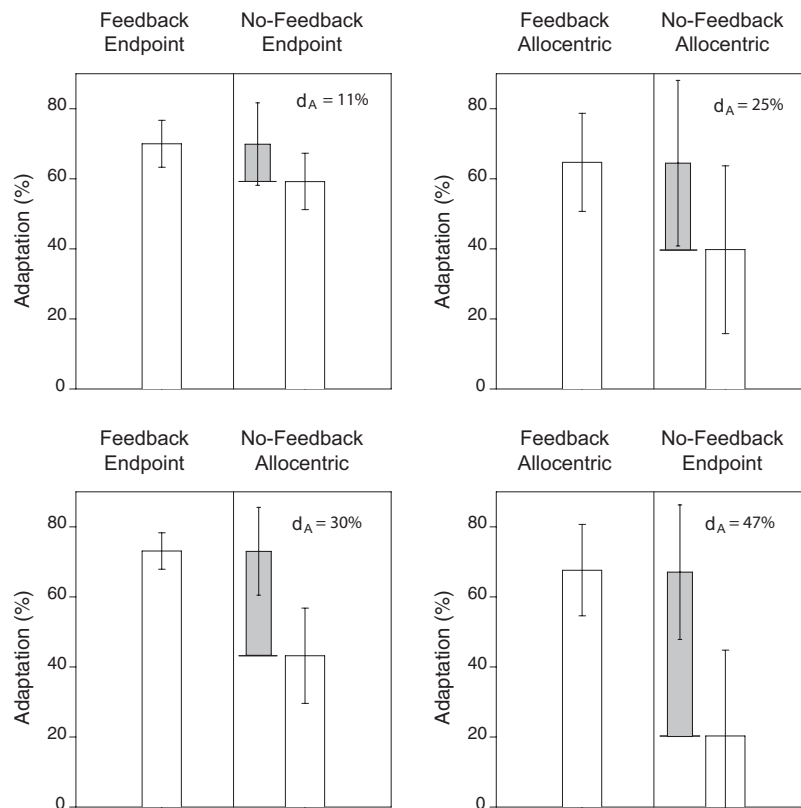

Figure 4. Average adaptation (white bars) and differences in average adaptation, d_A(Adaptation (%)$_{feedback}$ − Adaptation (%)$_{no-feedback}$), (gray bars) in percentages. Averages were computed across subjects, points 1 and 2 and trials, for each condition within the second part of a session. Error bars represent 95% confidence intervals across subjects. d_A was used to quantify carry-over effects: The smaller d_A, the larger the carry-over effect. Thus, shorter gray bars in the top and bottom panels indicate larger carry-over effects.

phases. Furthermore, feedback in the endpoint task appears to result in smaller d_A values, and thus larger changes in visuomotor behavior, respectively, than feedback in the allocentric task. To assess the reliability of these effects we applied a repeated-measured analysis of variance (ANOVA) to d_A, with feedback task and task switch as repeated-measures factors. The results reveal significant main effects of task switch, $F(1, 8) = 10.563$, $p = .012$. The effect of feedback task shows a trend to be significant, $F(1, 8) = 4.294$, $p = .072$. The interaction effect was not significant, $F(1, 8) = .053$, $p = .824$.

The analyses described so far focus on group averages. However, we can also investigate how our results hold up for the individual subjects by treating each trial that a subject performed as an independent measurement of that subject's performance in a certain condition. If we average adaptation values across configurations (Points 1 and 2) and focus only on the last four blocks performed in each session, we obtain eight blocks with 20 adaptation values each for each subject. Based on the 20 shift values in each block, we can then compute the average adaptation within a block, $\bar{X}_{\text{adaptation}}$, and the variance

within that block, $\sigma^2_{\text{adaptation}}$, for each subject. To calculate d_A values for each subject we treat the relevant feedback and no-feedback blocks as independent samples. For example, to compute $d_{A(\text{feedback endpoint} - \text{no-feedback endpoint})}$ for a subject we compute $\bar{X}_{\text{adaptation(feedback endpoint)}} - \bar{X}_{\text{adaptation(no-feedback endpoint)}}$. Because the two blocks are considered independent samples the variance of $d_{A(\text{feedback endpoint} - \text{no-feedback endpoint})}$ is given by $\sigma^2_{\text{adaptation(feedback endpoint)}} + \sigma^2_{\text{adaptation(no-feedback endpoint)}}$. Based on these d_A statistics we can compute an ANOVA with task and switch as between-group factors for each subject. Again, for the purpose of this analysis all trials for a subject are treated as independent samples. Thus, the error variance is obtained by averaging variances of d_A across blocks for each subject and the error term has $(20 - 1) * 4 = 76$ degrees of freedom. It is important to note that the subject specific analysis differs from the repeated-measures ANOVA applied to the group averages, because the subject specific analysis considers each subject's variability.

Figure 5 shows d_A values for each subject (white bars) as well as the group average shift (gray bars). Gray bars in Figure 5
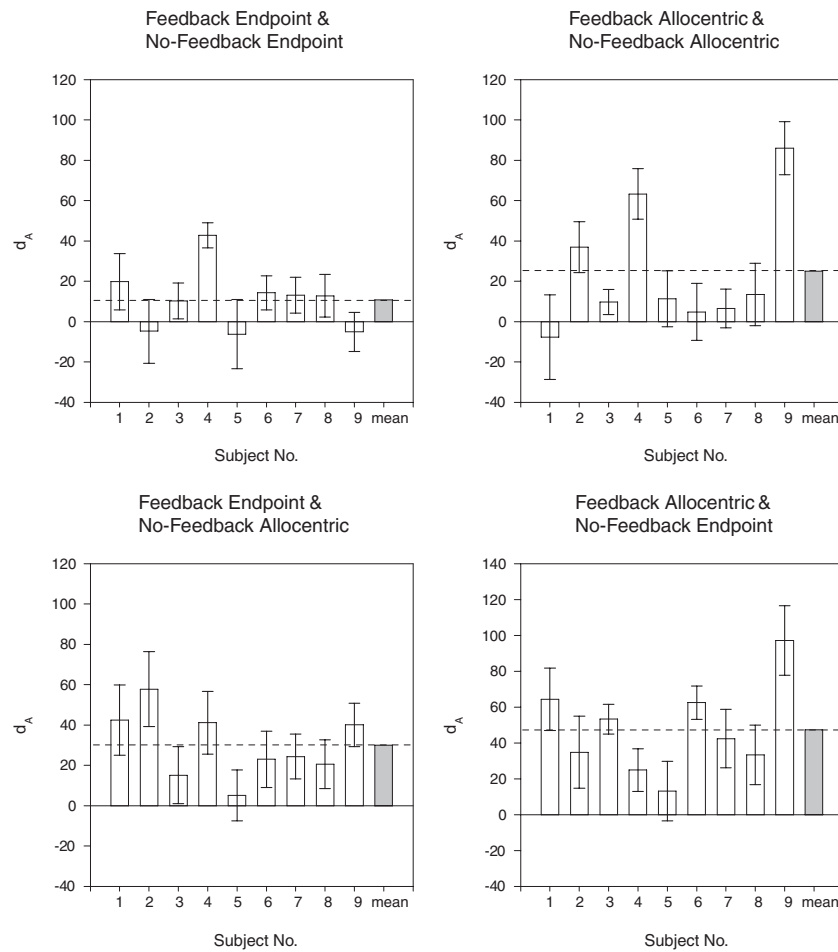

Figure 5. The d_A (Adaptation (%)$_{\text{feedback}}$ – Adaptation (%)$_{\text{no-feedback}}$) values for individual subjects (white bars) and averaged across subjects (gray bars). Dashed horizontal lines indicate the group average. Error bars denote 95% confidence intervals around the mean. To obtain averages and variances of d_A for each subject, each trial was considered an independent sample (for details see text). Subjects 1 and 5 are the authors.

correspond to the gray bars in Figure 4. Error bars in Figure 5 denote 95% confidence intervals around the mean. It is evident from Figure 5 that d_A is larger when the task is switched for most subjects. However, variability between subjects is evident as well. Thus, for some subjects carry-over effects when the task is switched can be the same or even exceed those compared to when the task is not switched. Table 2 summarizes the results of the statistical analyses for the individual subjects. The statistical analyses agree well with Figure 5 and show that even though there is a strong trend that task switches reduce carry-over effects, there are differences between subjects, too. We found it interesting that almost all subjects that showed a significant main effect of task switch also showed a significant interaction, suggesting that there are task specific differences in carry-over effects. However, inspection of Figure 5 reveals that these task specific differences are unsystematic, which explains the nonsignificant interaction on group level.

Overall, the individual subject's results agree with our results obtained on the group level. Specifically, the degree to which feedback induced changes in visuomotor behavior carry over to a subsequent no-feedback phase appear to depend on the visual representation that subjects have to use to perform a certain visuomotor task. When the same representation is used, (i.e., egocentric or allocentric) in feedback and no-feedback phases, the carry-over effects are larger than when a different representation is used.

Table 2
Summary of Results of Statistical Analysis of Individual Subjects

Effect	Subject	$F(1, 76)$	p
Task	1	0.054	.816
	2	0.664	.427
	3	8.022	.012*
	4	0.068	.798
	5	1.568	.228
	6	3.561	.077†
	7	0.516	.483
	8	0.518	.482
	9	63.172	.000***
Switch	1	15.810	.001***
	2	6.885	.018*
	3	13.379	.002**
	4	6.065	.026*
	5	0.415	.528
	6	17.459	.001***
	7	8.669	.009**
	8	2.136	.163
	9	9.108	.008**
Task × Switch	1	4.320	.041*
	2	7.892	.013*
	3	8.479	.010*
	4	5.110	.038*
	5	0.213	.650
	6	9.500	.007**
	7	2.350	.145
	8	0.411	.531
	9	3.335	.087†

Note. Results were obtained by applying a 2 × 2 factorial analysis of variance to each subject's d_A (Adaptation $(\%)_{\text{feedback}}$ − Adaptation $(\%)_{\text{no-feedback}}$) values. For the purpose of the analysis, that is, to obtain averages and variances of d_A for each subject, each trial was considered an independent sample (for details, see text). Subjects 1 and 5 are the authors.
† $p = .1$. * $p = .05$. ** $p = .01$. *** $p = .001$.

The conclusion that the magnitude of carry-over effects is smaller in task-switch than no-task-switch blocks is only valid if visuomotor behavior is equivalent in feedback blocks that precede task-switch or no-task-switch blocks. Otherwise, the magnitude of carry-over effects is confounded with the degree of adaptation or with certain movement kinematics in the preceding feedback block. To rule out these possible confounds, we computed average adaptation as well as average movement distance, direction, speed, and curvature for feedback blocks in the second part of each session (data not shown). We then analyzed each of these data sets with a 2 × 2 repeated-measures ANOVA with task and task switch as within-subject variables. Neither main effects nor interactions were significant for any of these measures, indicating that both the physical movement as well as the feedback-induced shift were equivalent in the different feedback conditions in our experiment.

Discussion

Using visuomotor adaptation, we found that visual feedback in both endpoint and allocentric tasks changes visuomotor performance. We observe carry-over effects in all conditions, but also that carry-over effects are larger when the same task is used during feedback and no-feedback phases, compared to when the task is switched. Smaller carry-over effects after task switch suggests that subjects use two different visuomotor systems with different visuomotor transformations in endpoint and allocentric tasks. However, the fact that we observe carry-over effects in task-switch conditions also suggests that there is cross-talk between egocentric and allocentric visuomotor transformations.

It is important to keep in mind that movement kinematics as well as visual feedback were the same in endpoint and allocentric tasks in our experiment. Thus, differences in carry-over effects cannot be explained based on behavioral or methodological differences during feedback phases. The fact that physical movements as well as visual feedback were the same in endpoint and allocentric tasks also rule out a simple explanation of our results in terms of a generalization gradient. A generalization gradient can be observed when behavioral changes in response to distorted-visual feedback weaken with increasing distance to the location at which feedback was provided (Mon-Williams & Bingham, 2007). In our experiment, feedback was provided in the same location and in the same fashion in either task (see Method section). In subsequent no-feedback phases, subjects were required to perform movements at the same physical locations at which feedback had been provided in both tasks. It follows that a generalization gradient cannot explain task dependent differences in carry-over effects. Furthermore, our experimental design carefully counterbalanced order of feedback and no-feedback tasks across subjects. In addition to ruling out behavioral or methodological confounds and generalization gradients as possible explanations, our experimental designed also controlled for external factor such as fatigue, visuokinesthetic drift, or no-feedback related task-switch effects. Therefore, we believe that the most parsimonious explanation of our findings is, that differences in performance between conditions that switched the task and conditions that did not, are caused by differences in the representation that subjects have to compute to perform a given visuomotor task. This interpretation of our results is consistent with the idea that egocentric and allocentric visuomotor mappings have some degree of independence. It is interest-

ing to note in this context that it has been shown that spatial errors of movement endpoints in response to egocentric target locations and in response to allocentric shape parameters can only be partially explained by a common underlying representation of space (Bingham, Crowell, & Todd, 2004). This finding is consistent with our current results and further supports the idea that human subjects may employ two partially independent visuomotor systems that rely on egocentric and allocentric visual spatial information. As mentioned in the introduction, there are various possible egocentric coordinate systems that subjects might use, that is, centered on the eye, head, shoulder, or hand. The current experiments as well as previous (Bingham et al, 2004) results do not distinguish between the different types of egocentric coordinate systems. It follows that the role played by the different egocentric coordinate systems remains to be investigated in future research.

Even though there is a common trend in our data, the individual results also show variability between subjects. It is possible that subjects' response strategies are partially responsible for these individual differences. For example, it is possible that subjects notice the distortion in feedback trials in adaptation sessions and consciously undo this distortion in no-feedback trials. This type of behavior would be a deliberate modification of motor responses based on knowledge obtained in the very beginning of a feedback block. It would be reasonable to expect that a deliberate conscious strategy would be easier to turn off when feedback is removed than an unconscious recalibration of the relevant visual-motor mapping (Mon-Williams & Bingham, 2007). In this context, we want to point out that a conscious strategy might depend on the degree to which subjects notice the properties of the visual distortion and that debriefing of our subjects revealed that they differed with respect to their awareness of the geometrical properties of the visual distortion (see the beginning of Results section). This further supports the idea that differences in response strategy might be responsible for intersubject variability in our experiments.

We find it interesting that our findings can be interpreted as consistent with previous findings on visuomotor adaptation that have been reported by other researchers in a different context, specifically in the context of movement control. One of the questions that have been studied extensively over the years in this context concerns the issue, whether the human motor system employs trajectory or final position control mechanisms during movement execution (for review, see Desmurget, Pelisson, Rossetti, & Prablanc, 1998). In our opinion, the distinction between allocentric and egocentric visuomotor transformation processes that is emphasized in the current paper is related to the distinction between trajectory and endpoint control processes. For example, the allocentric task could be considered a task in which subjects use predominantly trajectory control because the visual instruction given to subjects specifies the movement trajectory, that is, movement distance and direction. In contrast, the endpoint task could be considered a task in which subjects may rely more on endpoint control. Consistent with the idea that the two tasks employed in the current experiment may recruit different movement control processes, we found recently that subjects employ predominantly endpoint control processes in the endpoint task and predominantly movement distance and direction control processes in the Allocentric task (Thaler & Todd, 2009a). The major difference between the current paper and the discussion in the context of movement control is that the current paper emphasizes possible differences

between processes that are active during the transformation from visual into movement parameters, that is, during the visuomotor mapping. In contrast, the issue of different movement controllers emphasizes possible differences between processes that are active after the visuomotor mapping has been completed.

In the current paper, we argue that the human visuomotor system may employ partially independent allocentric and egocentric visuomotor transformation processes. Similarly, several researchers have proposed independent mechanisms for controlling trajectory and final position of a moving limb (Brown, Rosenbaum, & Sainburg, 2003; DiZio & Lackner, 1995; Gottlieb, 1996; Hirayama, Kawato, & Jordan, 1993; Lackner & DiZio, 1994; 1998; Sainburg, Ghez, & Kalakanis, 1999; Sainburg & Wang, 2002; Scheidt & Ghez, 2007). Support for the idea of independent mechanisms for trajectory and endpoint control for example is provided by adaptation studies that investigate transfer effects between the right and left hand (DiZio & Lackner, 1995; Sainburg & Wang, 2002). A seminal study in this context was reported by DiZio and Lackner (1995) who asked subjects to move their hands toward a visible target in a slowly rotating room, which introduces a coriolis force field. When subjects reach toward a target in these condition coriolis forces act on the moving hand that are proportional and perpendicular to the velocity of the moving hand. When exposed to this force, subjects first produce trajectories that show a convexity away from the straight-line trajectory directed at the target and they show a final position error that is biased toward the direction of the convexity (DiZio & Lackner, 1995; Lackner & DiZio, 1994, 1998). Over time, subjects adapt to the coriolis force present during movement execution such that both convexity and final position errors are greatly reduced. When subjects are trained with their dominant (right) hand and subsequently tested with their nondominant (left) hand in the same environment, final position adaptation transfers from the dominant to the nondominant hand, but trajectory adaptation does not (DiZio & Lackner, 1995). This finding has been interpreted as evidence for the idea that endpoint control mechanisms can be adapted independently from trajectory control mechanisms.

If we assume that subjects rely more on trajectory control mechanism in the allocentric task, but more on endpoint control mechanisms in the endpoint task, differences in carry-over effects in our experiments could not only be taken as evidence for two partially independent visuomotor mappings, but also as evidence for partially independent trajectory and endpoint control mechanisms. However, if we accept an interpretation of our results in terms of adaptation of control mechanisms, either instead of or in addition to an adaptation of visuomotor transformation processes, our results support a conclusion that we have drawn previously. Namely, the conclusion that different types of visual spatial information alone can be used to tap into trajectory or endpoint control mechanisms (Thaler & Todd, 2009a). This conclusion is warranted, given that in our experiment the actual visual feedback as well as the physical movements were the same in egocentric and allocentric tasks during adaptation phases. In this respect, our results are different from those that were obtained in previous studies on control mechanisms, because those investigated the existence of multiple mechanisms by invoking different forms of visual feedback, different physical movements, or different effectors during learning and test (i.e., DiZio & Lackner, 1995; Ghez, Scheidt, & Heijink, 2007; Sainburg & Wang, 2002; Scheidt &

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Ghez, 2007). In summary, we believe that our results are consistent with previous findings from movement control and that they extend them. Furthermore, we believe that the paradigm introduced here could be useful, possibly in combination with changes in effector or physical movement properties, to provide further insights into egocentric versus allocentric visuomotor transformation and endpoint versus trajectory movement control mechanisms and their interactions. For example, van den Dobbelsteen et al. (2003) found that subjects' arm movements adapted more readily to perturbations of visual feedback within egocentric frames of reference, than to perturbations of visual feedback within allocentric frames of reference. However, those authors only investigated performance in a task that required subjects to move their hands toward visible targets, that is, they used a task similar to our endpoint task. Based on our current results, therefore, we might speculate that perturbations of visual feedback within allocentric frames of reference tested by those authors might be more effective in tasks similar to our allocentric task.

It has been reported that a patient with damage to the ventral stream of the visual system (patient DF) has impaired visuomotor performance in an allocentric task, but normal performance in an endpoint task (Schenk, 2006). Based on this finding Schenk (2006) suggested that endpoint and allocentric tasks rely on different types of visual-spatial information. As mentioned in the Introduction, this result is consistent with several behavioral and neuroimaging studies. However, as also mentioned in the Introduction the results are inconclusive with regard to the question if the human CNS employs two visuomotor system with separate visuomotor mappings from allocentric and egocentric visual information onto movement parameters, or if egocentric and allocentric visual information are simply two inputs into a single visuomotor system. Our results are in agreement with Schenk's results and extend his findings in that they suggest that human beings engage two visuomotor systems in endpoint and allocentric tasks. Furthermore, our results also suggest that the two visuomotor systems are only partially independent and show cross talk. In contrast, DFs preserved performance in the endpoint task, in the presence of severely impaired performance in the allocentric task suggests that the two systems are independent from each other. One of the major differences between our and Schenk's study is of course that subjects in our experiment had an intact brain. Thus, the possibility arises that the two visuomotor systems show cross talk in healthy subjects (see also Neggers et al., 2005, 2006), but that they can function independently from each other in principle.

During the last decades, there has been a longstanding debate about the functional role played by the ventral and dorsal visual streams. In a very influential account, it has been suggested that the ventral visual stream processes visual information for perceptual reports, whereas the dorsal visual stream processes visual information for motor action (Goodale & Milner, 1992; Milner & Goodale, 1995). More recently, an alternative distinction of dorsal and ventral visual stream function into different types of visual spatial processing for both perceptual processing and visuomotor control has been suggested (Schenk, 2006; Smeets, Brenner, de Grave & Cuijpers, 2002), and support for this idea comes from behavioral results in a patient with isolated lesions to the ventral visual stream (Schenk, 2006). However, in a recent rebuttal an explanation of these results in the context of the perception-action dissociation has been given (Milner & Goodale, 2008). The dis-

tinction into egocentric and allocentric visuomotor processes suggested here is in agreement with a functional distinction of ventral and dorsal stream function into different spatial processing modes (Schenk, 2006; Smeets et al., 2002). At the same time, the neural underpinnings of the different functional visuomotor units outlined here remain to be investigated. In a related proposal, it has also been suggested that behavioral differences between perceptual and visuomotor tasks might as well be explained using a distinction into processing of absolute and relative spatial information (Vishton, Rea, Cutting & Nunez, 1999). The current paper does not distinguish between relative and absolute and egocentric and allocentric spatial processing. However, we have shown elsewhere that different types of egocentric and allocentric coordinates can provide a more accurate description of performance than a distinction into absolute and relative spatial processing (Thaler & Todd, 2009b).

Conclusions

The current paper addresses the question if the human central nervous system employs separate visuomotor systems to transform egocentric and allocentric visual information into motor commands, or if egocentric and allocentric visual information provide a joined input into a single visuomotor system. Using visuomotor adaptation, we found that changes in visuomotor performance in response to distorted-visual feedback were larger when the same task was used during feedback and no-feedback phases, compared to when the task was switched. We conclude that human observers have two partially independent visuomotor systems that rely on different types of visual spatial information.

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