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RESEARCH ARTICLE

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Adaptation of movement endpoints to perturbations of visual feedback

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Abstract We investigated the extent to which humans can quickly adapt their goal-directed arm movements to perturbed feedback. We predicted that the magnitude of adaptation to a changed relationship between vision and kinesthesia would depend on the type of perturbation, being largest when the perturbation can be generalized within egocentric frames of reference. To test this prediction we asked subjects to align a real 5-cm cube so that they could feel, but not see, with a simulation that they saw via a mirror. Subjects made successive movements between target locations in a sequence of adaptation and test phases. During adaptation phases, subjects received continuous visual feedback about the position of the real cube. The feedback was either veridical or perturbed. The perturbations were consistent with either a uniform translation, a scaling or a rotation. The latter two were relative to a central position between all the targets. During test phases, subjects received no visual feedback. We compared test movement endpoints after perturbed feedback with ones after veridical feedback. We found about 40% adaptation to translation, 20% to scaling and 10% to rotation. This difference in magnitude is consistent with the ease with which the transformation can be generalized within egocentric frames of reference. Changing the task so that it required different arm postures did not change the magnitude of adaptation, so postural configuration of the arm does not appear to be critical. Nevertheless, transfer to the unexposed arm was incomplete for translations and rotations, though it was complete for scaling, suggesting that at least part of the adaptation is posture based. We conclude that the adaptation to different kinds of perturbations not only differs in extent but also involves different (egocentric) mechanisms.

Keywords Human · Arm · Visuomotor adaptation · Reaching · Perturbation

Introduction

Reaching for a visual object requires complex transformations to link visuospatial information to the muscle activation that will move the hand to the object's location. Integration of visual information about the objects with kinesthetic information about the position of the hand requires information about the orientation of the eye in the head, the head on the trunk, and the orientations of the shoulder and joint angles. These orientations could be considered together within a single transformation, or in a series of transformations leading from an eye-centered frame of reference to a head-centered one, a shoulder-centered one, and so on (Carrozzo et al. 1999; McIntyre et al. 1997; Flanders et al. 1992; Soechting et al. 1990; Soechting and Flanders 1989). Such transformations are under adaptive control, as is illustrated by the ability to generate appropriate motor behavior under changed visual feedback. A common example of such changes is the deformation of visual feedback caused by wearing wedge prisms (for a review see Welch 1986). Prisms change the visual location of an object with respect to the motor commands that are required to reach that object. Thus, wearing prisms induces a mismatch between visual and kinesthetic perception of location. Adaptation is the process of realigning the two so that visual information is again transformed into appropriate motor commands.

The mechanisms by which adaptive realignment gives rise to new visuomotor relationships are not yet clear. Presumably, adaptation is a kind of "best fit" realignment that is restricted by the limited degrees of freedom of the modifiable components of the visuomotor system (Hay et al. 1971). The best fit does not necessarily mimic the spatial characteristics of the mismatches between vision and kinesthesia but will result in a generalized change in the responses of the subject. Wearing prisms could influence visuomotor transformations at several or mul-

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tiple levels (Wallace and Redding 1979; Welch et al. 1974). For instance, the adaptation could involve changes in visual localization (Foley 1974), presumably mediated by changes in the perceived direction of gaze (Craske 1967; Kalil and Freedman 1966). It could involve changes in proprioceptive localization of the arm (Taub and Goldberg1973; Harris 1963) and changes in the perceived orientation of the head (Efstathiou et al. 1967). Finally, it could involve changes in the visuomotor transformations that link visual to kinesthetic information, without changing visual and kinesthetic localization (Kitazawa et al. 1997; Redding and Wallace 1996; Rossetti et al. 1995).

The fact that the same perturbation changes different components in different studies probably results from methodological differences that determine which of the components can best be changed to compensate for the errors in visuokinesthetic alignment. For example, providing continuous visual feedback during exposure, rather than at the end of each movement, can alter the correction mechanisms (Redding and Wallace 1996; Choe and Welch 1974) because it provides information about the frames of reference (e.g., linked to eye, head, shoulder) that could be involved. Hay et al. (1971) compared adaptation to wedge prisms and concave lenses. Compensation was incomplete for both kinds of perturbations but much larger for mismatches induced by prisms (about 50%) than for mismatches induced by concave lenses that reduced all visually perceived dimensions (about 5%). The former, lateral mismatches could be interpreted as errors in judgements of either eye, or of head orientation, or of arm posture. The latter could be interpreted as errors in judging the distance in depth, which would explain the reduced retinal image size, but this implies that both the orientation of the eyes (vergence) and the arm posture are misjudged.

Recent technical developments enable one to study a much wider variety of perturbations than is possible with spectacles, and to switch between them much less conspicuously. The paradigm is to take an interactive task and transform the information about the hand's position before presenting it as feedback to the subject. Through an analysis of the spatial features of the adaptive response, and whatever mismatch exists between it and the perturbations, one can try to assess which of the above-mentioned components are altered. Vetter et al. (1999) studied the generalization of adaptation in pointing movements in three-dimensional space. Their subjects received translated visual feedback about finger position for a single target. They pointed to several targets without visual feedback. The mismatch between actual and displayed finger position at a single location induced changes in pointing over the entire workspace, indicating that the adaptive response generalized over different target positions. This generalization of adaptation was best described as a shift within a spherical coordinate system with its origin between the eyes. This eye-centered frame of reference captured the changes in pointing slightly better than did either a shoulder-centered frame of reference, or a frame of reference based on joint angles, or one based on Cartesian coordinates. This suggests that the best fit to the errors in visuokinesthetic alignment was obtained by changing the perceived eye orientation. However, it is possible that other frames of reference (centered on the head, shoulder or body) were also changed, albeit to a lesser extent.

The results of Vetter et al. (1999) and Hay et al. (1971) are consistent with the main conclusion of Van den Dobbelsteen et al. (2001). In that study we showed that endpoints of natural arm movements towards visual targets were not affected by changes in the starting position of the hand, suggesting that such movements are planned in terms of the final egocentric position (Polit and Bizzi 1979) rather than being planned in terms of a displacement vector (Gordon et al. 1994; Messier and Kalaska 1999; Vindras and Viviani 1998). We therefore hypothesize that adaptation of arm movement endpoints to perturbations of visual feedback requires the ability to account for the imposed changes within egocentric frames of reference. The endpoints of movements toward visual targets are presumably the combined result of numerous transformations, combining retinal eccentricity, eye orientation, posture and muscle properties. Each of these transformations may change during adaptation. Changes in the spatial characteristics of the subject's responses may be hard to relate to any one of these components, because the precise transformations are unknown. We can, however, expect more adaptation when the perturbation is easy to generalize within an egocentric frame of reference, or when compensation could be distributed between several frames of reference.

In a series of experiments we examine adaptation of movement endpoints to four visual perturbations: a uniform translation, a scaling relative to a fixed position in the workspace, and a rotation around either of two different axes through this position. In the experiments, subjects positioned a real 5-cm cube, which they held in their hand but could not see, at the location of a three-dimensional simulation of such a cube. Subjects made natural self-paced movements between different target locations. During feedback phases, subjects received continuous, either veridical or perturbed visual feedback about the position of the real cube. To evaluate whether subjects adapted to the perturbations we removed the feedback in the test phases. We compared test movement endpoints after perturbed feedback with ones after veridical feedback. Our hypothesis was that we would find most adaptation for our uniform translation, because it more or less corresponds with a rotation of the eye, head, or shoulder, so that all of these interpretations may contribute to the changes in endpoints. We expected to find less adaptation for scaling. A scaling of relative positions could be interpreted in terms of a change in distance, but this change in distance requires a re-evaluation of both eye orientation and arm posture and is not accompanied by a corresponding change in the retinal size of the image of the cube. The "best fit" to these errors in visuokinesthetic alignment would therefore

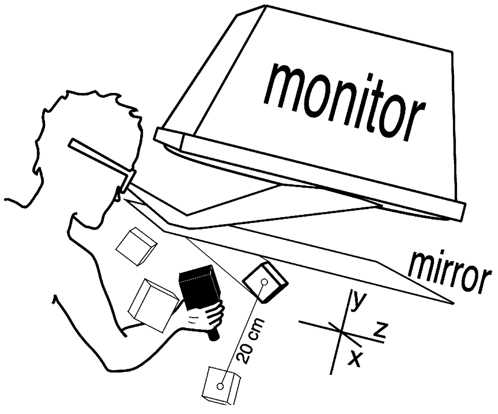

Fig. 1 Schematic view of the setup. Subjects stood in front of a monitor holding a cube attached to a rod. They were asked to align this cube's position and orientation with the position and orientation of a target cube (a simulated wire frame which they saw via the mirror). Four possible positions of the target (those used in the test phases) are shown, but only one target was visible at a time. During adaptation phases, a simulation of the cube in their hand was also visible

be a compromise between a change in perceived distance and a change in perceived size. One of the types of rotations roughly corresponded with a rotation around the viewing axis. This could induce changes in the perceived eye or head orientation so that some adaptation is expected. We did not expect to find any adaptation to the other rotation, because we were unable to relate it to any egocentric frame of reference.

Materials and methods

Subjects

Fourteen subjects, including two of the authors, participated in experiment 1. Eleven of these subjects, including the two authors, participated in experiment 2. All subjects gave their informed consent to participate in this study. The work forms part of an ongoing research program for which ethical approval has been granted by the appropriate committees of the Erasmus University. All subjects reported normal visual acuity (after correction) and binocular vision. There were no evident differences between the data of the authors and the other subjects, so no further distinction is made.

Apparatus

The experimental apparatus is similar to that used by Van den Dobbelsteen et al. (2001). Images were generated with a Silicon Graphics Onyx computer at a rate of 120 Hz. The images were displayed on a Sony 5,000-ps 21" monitor (30.0×40.4 cm; 612×816 pixels), located in front of and above the subjects' head, and viewed by way of a mirror (see Fig. 1). Liquid crystal shutter spectacles (CrystalEyes 2, weight 140 g, StereoGraphics Co., CA) were used to present alternate images to the two eyes at the 120-Hz frame rate (60 Hz/eye for binocular vision).

Subjects held a 2-cm-diameter rod attached to a 5-cm cube (total weight: 145 g) in their unseen hand underneath the mirror. During feedback phases they saw a three-dimensional rendition of a cube at the (transformed) location of the real cube. Their task was to align this feedback cube with a stationary 3D wire frame of a cube (target cube) that appeared beneath the mirror. The feedback cube moved whenever the subject moved the real cube. A spatial discrepancy was sometimes introduced between the real cube and the simulated feedback cube. The monitor and mirror were tilted 12° backwards relative to the horizontal to obtain a large workspace. Images were corrected for the curvature of the monitor screen. Standard anti-aliasing techniques were used to achieve subpixel resolution. The thickness of the edges of the wire frame target cube was one pixel. The luminance of each surface of the feedback cube depended on the orientation relative to a virtual light-source above and to the left of the subject. There was also a virtual diffuse illumination to ensure that all surfaces facing the subject were visible. The surfaces of the feedback cube were translucent and therefore did not occlude the target cube. All images were red because the liquid crystal shutter spectacles have least cross talk at long wavelengths. During the experiment the room was dark, so that subjects were unable to see anything but the virtual cubes.

A movement analysis system (Optotrak 3010, Northern Digital Inc., Waterloo, Ontario) registered the positions of active infrared markers attached to the real cube and to the shutter spectacles at a frequency of 200 Hz. The subjects were free to move their head. We inferred each eye's position (not eye *orientation*) from the positions of markers on the shutter spectacles, so that the images were always rendered with the appropriate perspective for that eye at that moment. The total delay between a movement (of the subject's head or of the real cube) and the adjustment of the image was about 16 ms.

General procedure

Subjects were given the cube attached to the rod and were asked to hold the rod with their hand touching the cube. They touched an edge of the cube with their thumb to prevent the rod from rotating within their hand. This enabled them to feel the location and orientation of the real cube. They were instructed to move the cube as accurately as possible to the position indicated by the simulated wire frame cube (target cube) and to keep it there until the target cube was presented at another position (see Fig. 1). They were not only to bring the cube to the same position, but also to align its orientation with that of the target cube. They were informed that they would receive visual feedback about the position and orientation of the real cube on some trials but not on others. No instructions were given about the speed of the movement.

During trials in which subjects received feedback (feedback phases), the target cube could appear randomly in one of eight positions beneath the mirror. These eight positions were at the corners of two imaginary tetrahedrons that were point-symmetric mirror images of each other, relative to their centers. The length of each edge of the tetrahedrons was 20 cm. The order of target presentation was randomized so the distance between the targets in the feedback phases depended on the subsequent target positions: 14.1 cm, 20.0 cm or 24.5 cm. During trials in which subjects received no feedback (test phases), the target cube was randomly presented in one of four positions beneath the mirror. These four positions were at the corners of only one of the two imaginary tetrahedrons, so that the distance between the targets in the test phases was always 20 cm. The simulated target position did not depend on the kind of feedback (perturbed or veridical).

The subjects were free to move their head, so the distance from eye to target varied somewhat across subjects and movements. However, all target positions were always well within reaching distance. For each movement, the starting position of the hand was the endpoint of the previous movement. A movement was considered to have come to an end when the subject moved the center of the cube less than 2 mm within 300 ms. The movements were smooth and all subjects reported that they were able to align the cubes before the next target cube appeared.

The two experiments consisted of a number of separate measurement sessions, performed on different days. Each experimental session started with the subject holding the cube at an undefined position beneath the mirror. A session involved eight experimental conditions, two for each type of perturbation. The order of the conditions within each experimental session was chosen at random. Each condition had four consecutive phases: a veridical feedback phase, a postveridical test phase, a perturbed feedback phase and a postperturbation test phase. After the last condition, subjects were subjected to an additional veridical feedback phase and test phase. In the *veridical feedback phase* the subjects aligned the real cube with the target cube with continuous veridical visual feedback about the real cubes' position and orientation. The feedback in this phase was provided by the 3D rendition of the cube precisely aligned with the real cube. In the *postveridical test phase* the subjects aligned the real cube with the target cube without visual feedback of the real cube. The *perturbed feedback phase* was identical to the veridical feedback phase except for the introduction of a spatial discrepancy between the position of the simulated feedback cube and the position of the real cube. The feedback cube could be perturbed in different ways. The different types of perturbations are described below (see "Perturbations"). The positions of the target cubes remained unchanged so that when subjects aligned the visual feedback cube with the target cube the final position of the real cube was altered. The *postperturbation test phase* was identical to the postveridical test phase, and was used to evaluate changes in movement endpoints relative to the postveridical test phase as a result of the altered visual feedback during the perturbed feedback phase.

Perturbations

During the perturbed feedback phase of each experimental condition we introduced a spatial discrepancy between the real cube and the visual feedback. This perturbation could be a translation (two of the eight conditions), a scaling (two conditions), and two types of rotation (four conditions). All perturbations were defined within the Cartesian coordinate system within which we registered the positions of the active markers (see Fig. 1). Figure 2 displays projections of the four target positions (open squares) that were used in the test phases (during feedback phases eight target positions were used, including the four shown). The shaded squares show where the feedback cube would be if the subjects were to align the real cube with the target cube. This alignment would result in a 5-cm shift of the feedback cube relative to the real cube for each target under each perturbation. The only difference between the perturbations was the direction of the shift. The simulated *orientation* and *size* of the feedback cube was always equal to that of the real cube. The perturbations only affected its *position*.

Figure 2A represents the two (opposite) translations that we used. For these two perturbations, the shifts of the feedback cube were 5 cm in the same direction for all positions of the real cube. For the other perturbations, the shift between the real cube and the feedback cube depended on the position of the real cube within the workspace.

Figure 2B shows the shifts for the two scaling conditions. The visual feedback about position was expanded or compressed equally in three dimensions relative to an origin that lay at the center of the imaginary tetrahedrons. The scaling factors of 1.41 and 0.59 were chosen to give a 5-cm shift of the feedback cube relative to the real cube when the real cube was aligned with the target. There was no shift when the real cube was at the center of the imaginary tetrahedrons. When the *feedback cube* was aligned with the target cube the shift of the real cube relative to the target cube was 8.5 cm for the expansion and 3.5 cm for the compression.

Figure 2C and D represent the four rotation conditions. The rotations were always around an imaginary axis that intersected the centers of two opposite edges of the imaginary tetrahedrons, because this ensures that the shifts are equal for all target locations, albeit in different directions. There was no shift when the real cube was on the axis of rotation. Figure 2C shows the shifts for two of the four rotations that we used (from now on called *z*-rotations). These rotations were around an axis that is aligned with the *z*-axis of our measurement system, so the shifts are completely within the *xy*-plane. Figure 2D shows the shifts for the other two rotations (from now on called *xy*-rotations). These shifts were of the same size (5 cm) when the cube was on the target but were out of the *xy*-plane.

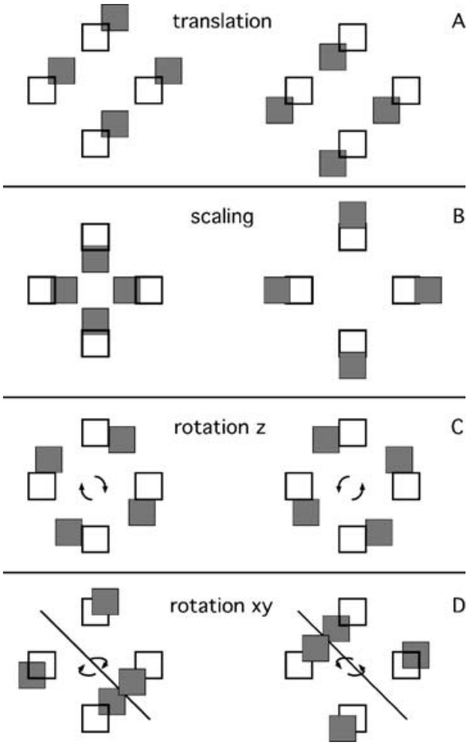

Fig. 2 Projections of the perturbations in the *xy*-plane (see Fig. 1). *Open squares* show the four target positions that were used in the test phases. *Shaded squares* indicate where the feedback cube would be if the real cube were aligned with the target cube. The 3D distance between the real cube and its feedback was always 5 cm in this situation

Experimental design

Experiment 1

Experiment 1 consisted of two sessions that were performed on different days. The subjects performed the task with their right hand throughout the experiment. In the veridical and perturbed feedback phase the eight targets were each presented twice, so subjects made a total of 16 movements. In the postveridical and postperturbation test phases a subset of four targets was presented three times in random order, so subjects made 12 movements. The total number of target presentations in one session was 476. A single session took about 20 min/subject.

In the experiments, subjects were asked not only to bring the real cube to the target position, but also to align its orientation with that of the target cube. In the first measurement session of experiment 1 the orientation of the target cube was fixed. A one-pixel-thick line was drawn, sticking out from the center of the surface of one side of the virtual target cube (perpendicular to this surface) to indicate the way that subjects should align the real cube with the target cube. The subjects were instructed to consider this line as a virtual rod with which they had to align the rod of the real cube that they were holding. In the veridical and perturbed feedback phase the virtual rod always pointed downwards, so that the real cube was above their hand. To be sure that subjects did not simply remember the postures the virtual rod always pointed toward the subject in the test phases. This prevents subjects' from using a movement strategy based on remembered postures (Rosenbaum et al. 1999; Grea et al. 2000) rather than based on perceived target positions.

The magnitudes of the different types of perturbations were chosen so that the magnitudes of the offset when holding the real cube at a target were equal for all perturbations. However, the different perturbations also change the final posture of the arm and the path taken to reach that posture, and this may affect the magnitude of adaptation (Kitazawa et al. 1997). To see whether the kinematics of the movements are critical for the adaptation to the different perturbations we encouraged subjects to change their movements in a second measurement session. We did so by randomizing the orientation of the target cube on every trial, so that the orientation of the hand and the posture of the arm varied to a large extent. If differences in the magnitude of adaptation between the different types of perturbations arise from differences in the kinematics of the movements, then we would expect no or less effect of the type of perturbation in the second measurement session. In this session the orientation of the rod was no longer indicated, so subjects were free to align the cube in one of several ways, leading to even more variability in postural configuration. Differences between the results of session 1 and 2 would show that at least part of the adaptation depends on arm kinematics.

Experiment 2

Experiment 2 consisted of four experimental sessions, which were performed on different days. For each session we used the same eight conditions as in experiment 1. The experimental setup was the same as in the first session of experiment 1 (with a fixed target orientation) except that now the arm that was not used during the veridical and perturbed feedback phase was also tested in a postveridical and postperturbed feedback phase. The veridical and perturbed feedback phases were identical to those in experiment 1. After the 16 trials in these feedback phases, both the feedback cube and the target cube disappeared, and subjects heard a tone. They were instructed that on hearing the tone they should keep the hand that is holding the real cube still and move the other hand to the real cube. After transferring the real cube to the hand that was not used during the feedback phase, a new target cube appeared, and the subjects performed the 12 trials of the postveridical or postperturbed test phase with the previously unused hand. These 12 trials were followed by a second tone in response to which subjects transferred the real cube back to the hand used in the feedback phase and repeated the postveridical or postperturbed test phase. After 12 trials the feedback cube reappeared and subjects continued with the same hand. Thus during a session all feedback phases of all conditions were performed with the same hand. Both hands were tested during the postveridical and postperturbed test phases. The subjects used their right hand during feedback phases in two of the four sessions and their left hand in the other two sessions. We did this to exclude a possible confounding between the arm that was exposed to the perturbation and hand preference.

Analysis

For each subject, session and condition, we determined the average movement endpoint (i.e. the average position of the center of the real cube) for each of the four positions of the target cube in the postveridical and postperturbed test phases. These averages were each based on three movement endpoints. We calculated the adaptation vector ($\boldsymbol{a}$) between the average computed for the postperturbed test phase and the average movement endpoint computed for the preceding postveridical test phase. We did so for each perturbation, subject and target cube position We defined a compensation vector ($\boldsymbol{c}$) as the displacement of the movement endpoint that would realign the feedback cube with the target for that perturbation. For each subject, condition and target position we expressed the projection of the adaptation vector onto the compensation vector as a percentage of the latter to give a measure of adaptation.

$$\text{Percentage adaptation} = 100\frac{\boldsymbol{a} \bullet \boldsymbol{c}}{|\boldsymbol{c}|^2}\%$$

Note that the compensation vector represents the shift in the end position of the real cube that was required to align the feedback cube with the target cube during the perturbed feedback phase.

For each type of perturbation within each session we averaged the percentage adaptation for the two directions of the perturbation and the four target positions to give one value for each subject. For the data of experiment 1, a repeated-measures ANOVA was performed on these mean percentages of adaptation to evaluate the effect of the type of perturbation and of the type of session (target orientation random or fixed). Additional post hoc tests were used to determine which of the perturbations differed from each other. One-group *t*-tests were used to reveal whether the amount of adaptation was significantly different from zero or not. We also performed separate repeated-measures ANOVAs for each type of perturbation to see whether there were effects of the direction of the perturbation and of target position.

We assume that the adaptive response is based on an egocentric generalization of the perturbation (e.g., a translation will be interpreted as an egocentric rotation). Such a generalization does not exactly mimic the mismatches in visuokinesthetic errors to which the subjects were exposed. Therefore, one may expect systematic changes in endpoints that do not always exactly compensate for the perturbation. However, our measure of adaptation only shows the component of the changes in endpoints that can be explained as an adaptive response to the perturbation itself. To evaluate whether subjects' response to the mismatches deviates systematically from this component we also determined the extent to which the changes in endpoints deviate from the shift that can be explained in terms of adaptation to the mismatches induced by the perturbation. To calculate this unexplained response ($\boldsymbol{u}$) we subtracted for each target position the explained adaptation ($\boldsymbol{e}$ = mean percentage adaptation $* \boldsymbol{c}$) from the adaptation vector ($\boldsymbol{a}$) averaged over all subjects. We interpret the length of this difference vector $\boldsymbol{u}$ as the magnitude of the response that cannot be explained as adaptation to the imposed perturbation. We calculated this value for each type of perturbation, direction of the perturbation and target position. As a measure of the extent to which the adaptive response deviated systematically from compensation for the perturbation we defined the *relative unexplained response* as the value of $|\boldsymbol{u}|/(|\boldsymbol{u}| + |\boldsymbol{e}|)$. A large value means that the systematic change in behavior in response to a perturbation has little resemblance to an appropriate compensation for that perturbation. We performed an ANOVA to evaluate whether there were differences in these values between the types of perturbations.

For the analysis of experiment 2 we averaged the percentage adaptation in the four sessions (two in which the left arm was exposed to the perturbed feedback and two in which the right arm was the one that was exposed) to obtain two values for each subject, for each type of perturbation. One value was for the arm that was used during the feedback phases and the other was for the arm that was not. We did a repeated-measures ANOVA to evaluate whether there were differences between the results for the arm that was used during the feedback phases and the arm that was not used, and whether there was an interaction with the type of perturbation. Additional post hoc tests were used to find the perturbations for which the results for the two arms differed from each other. For all analyses statistical significance was set at P=0.05.

Results

Experiment 1

Subjects had no difficulty moving their hand toward the targets, in both the feedback phases and the test phases (in

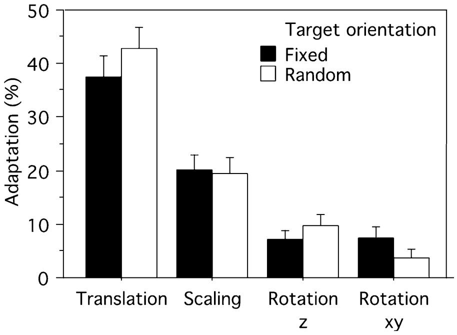

Fig. 3 Percentage of adaptation to the different types of perturbations for the two sessions in experiment 1. The *error bars* show the standard errors in this value across 14 subjects

both phases the target was visible until the hand stopped). Figure 3 shows the difference in movement endpoints between the postveridical and postperturbation test phase, expressed as percentage adaptation. This is shown for each type of perturbation, both for the session with randomized target orientations and for the session with a fixed target orientation. Repeated-measures ANOVA revealed that there were differences between the amount of adaptation for the different types of perturbations ($F_{(3,39)}$=66.0; P<0.0001), but that the factor target orientation was irrelevant (no main effect or interaction with the type of perturbation). Post hoc testing revealed that there was no significant difference between adaptation to *xy*-rotations (mean = 5.5%) and *z*-rotations (mean = 8.4%), but that both adaptation to translation (mean = 40.2%) and to scaling (mean = 19.9%) were different from that to every other type of perturbation. Although adaptation was far from complete, additional one-group *t*-tests showed that the amount of adaptation was significantly larger than zero for each type of perturbation.

Figure 4 shows the average of all the subjects' movement endpoints for each of the perturbations and each target position. Separate repeated-measures ANOVAs were performed for each of the types of perturba-

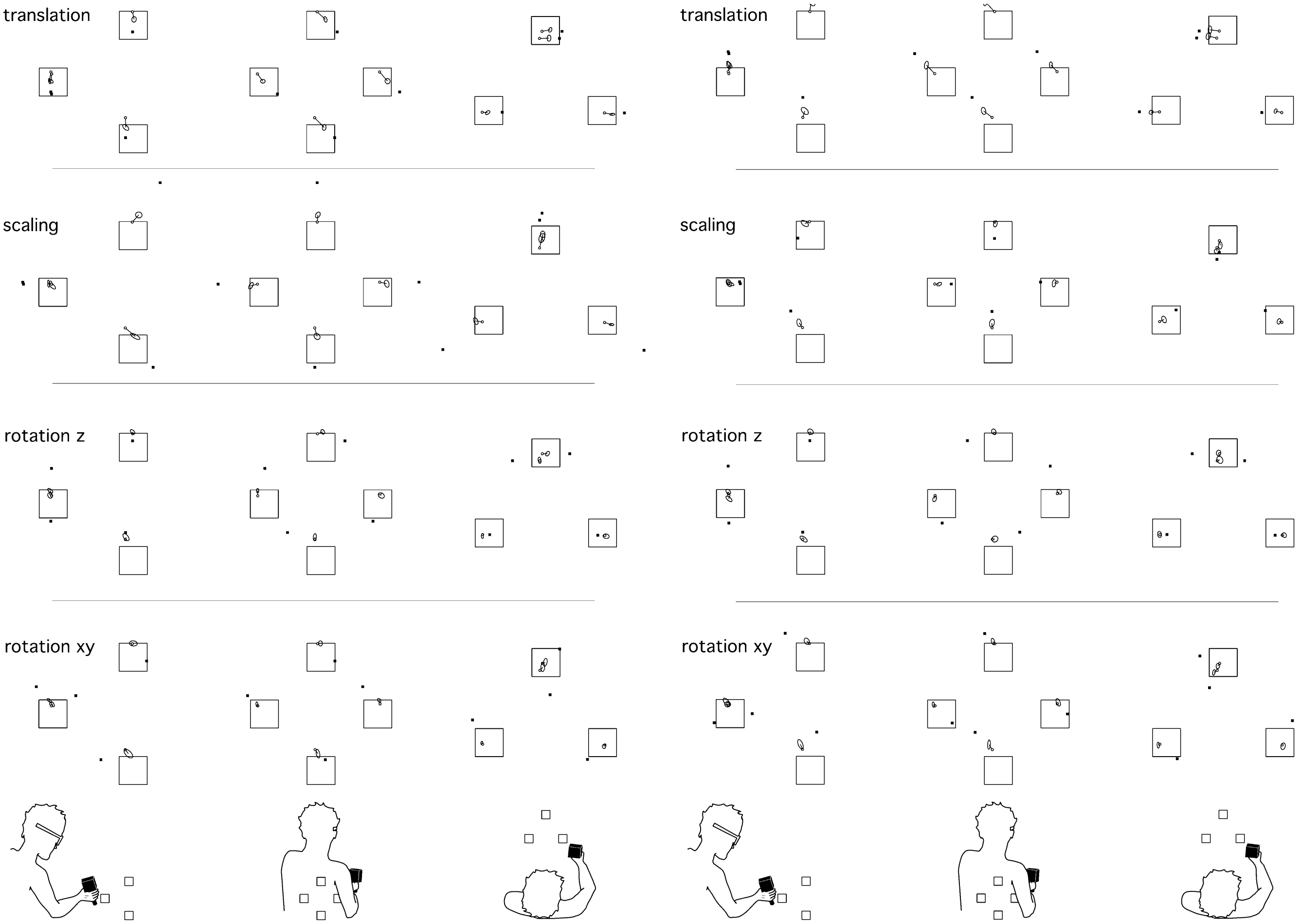

Fig. 4 Projections of the averaged movement endpoints in experiment 1 for each type of perturbation, direction of perturbation and target position. *Open squares* (size 5 cm) show the four targets that were used in the test phases. The *small black squares* show the position that would correspond to a percentage adaptation of 100%. *Circles* show the average endpoints during postveridical test phases. *Ellipses* show the average and the between subject variability for each perturbation (the lengths of the axes correspond to the standard deviations in those directions). The *figures in the bottom row* show the approximate positions of the targets relative to the subject in the three depicted planes

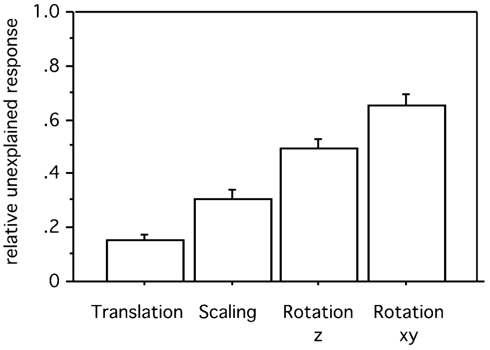

Fig. 5 Relative unexplained response for each type of perturbation. The *error bars* show the standard errors in this value across the direction of the perturbation and the target position

tions to evaluate possible effects of the direction of the perturbation and of the position of the target. None of these analyses revealed effects that were consistent across subjects, indicating that for each of the types of perturbations the magnitude of adaptation was on average equal for all target positions and directions. However, as discussed in "Materials and methods," our measure of adaptation ignores changes in endpoints that are not predicted by a compensation for the perturbation. Figure 4 shows that for scaling (top view of the third panel) the averaged responses were biased toward (right panel) or away (left panel) from the subject. We therefore computed the relative unexplained response for each type of perturbation (see Fig. 5). A small relative unexplained response suggests that the way that subjects were interpreting the transformation was appropriate for generalizing across the four target positions. A large value suggests that it was not. The ANOVA performed on these values showed that the effect of type of perturbation was significant ($F_{(3,28)}$=39.2; P<0.0001). Post hoc testing revealed that the magnitudes of the relative unexplained response for the different types of perturbation were all significantly different from each other.

Figure 5 shows that the relative unexplained response was very small for translations. Interestingly, it was considerably larger for *xy*-rotations than for *z*-rotations. This suggests that although the adaptive response (in terms of percentage adaptation) was equal for these latter perturbations, subjects were less able to pick up the imposed transformation for the *xy*-rotation than for the *z*-rotation.

In summary, subjects adapted to all the perturbations that they were exposed to, but adaptation to translation was more pronounced than adaptation to scaling, and much more pronounced than to rotations of visual feedback. The lack of effect of varying target orientation implies that the adaptation does not involve processes that are specific to the posture of the arm. The changes in endpoints were not always in the direction of the perturbation, the largest deviations being found for the *xy*-rotation.

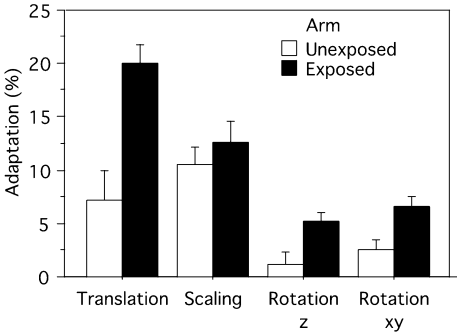

Fig. 6 Percentage of adaptation to the different types of perturbations in experiment 2. The *white bars* indicate the results obtained with the arm that was not used in the feedback phase. The *black bars* indicate the results that were subsequently obtained with the arm that was used in the feedback phase. The *error bars* show the standard errors in these values between subjects

Experiment 2

In Fig. 6 we show the percentage adaptation for both arms tested in experiment 2. We determined whether there were differences in adaptation between the arm that was exposed to the perturbed feedback and the arm that was not. A repeated-measures ANOVA revealed main effects for the type of perturbation ($F_{(3,30)}$=25.2; P<0.0001) and the arm that was tested (exposed vs unexposed, $F_{(1,10)}$=12.2; P<0.0057), as well as an interaction between these variables ($F_{(3,30)}$=4.3; P<0.0121). Post hoc testing revealed that the unexposed arm adapted significantly less than the exposed arm for translations and rotations, but not for scaling.

The differences between the adaptation of the exposed arm for the different types of perturbations are comparable to the differences we found in experiment 1. However, the absolute amount of adaptation is smaller. This could be due to the fact that subjects transferred the real cube between the two hands, because this could give them additional kinesthetic feedback about their actual hand position (from the unexposed arm). Another possibility is that the adaptation decayed spontaneously (Choe and Welch 1974; Clower and Boussaoud 2000) while the other hand was being tested. To examine whether there was spontaneous decay and whether there were differences between the perturbations in the extent to which adaptation decayed during the test phase, we reanalyzed the data of the postperturbation test phase. Instead of computing the overall mean of all settings in this phase, we calculated the mean adaptation for every sequence of three consecutive settings. To evaluate possible effects of transferring the cube between the hands we compared the results for the fixed target orientation in experiment 1 with the results for the exposed arm in experiment 2. To make sure that individual differences could not affect our conclusions, we only included the 11 subjects that participated in both experiments. The results are displayed in Fig. 7.

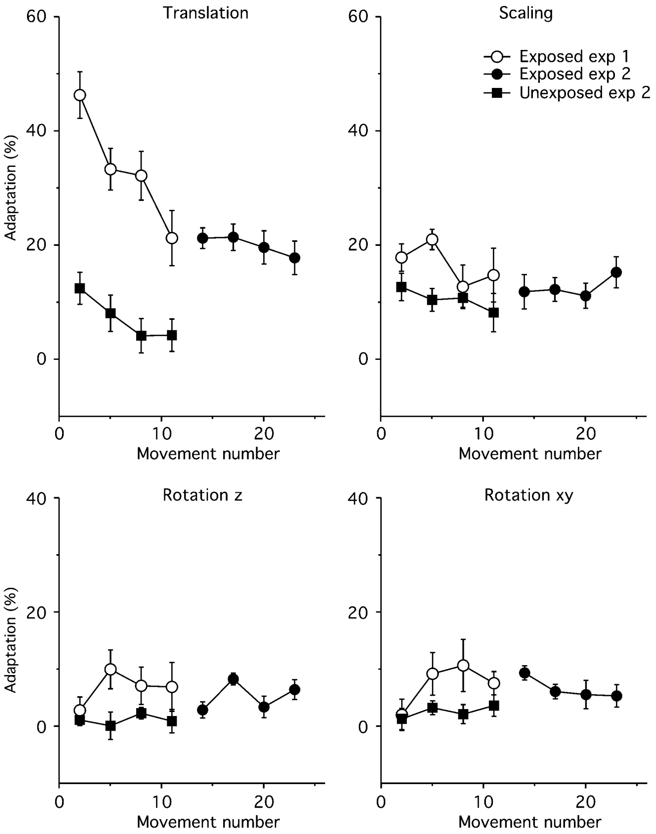

Fig. 7 The development of adaptation during the postperturbation test phase. Results for the four different types of perturbations. Each *symbol* is the average of three consecutive settings for the 11 subjects who participated in both experiments 1 and 2. *Open and filled symbols* show the results for experiments 1 (fixed target orientation) and 2, respectively. *Circles* show the results for the arm that was used during the feedback phase; *squares* indicate the results for the unexposed arm. *Error bars* display standard errors between subjects

Figure 7 shows that the amount of adaptation to translation for both the exposed and unexposed arm clearly decayed during the test phases. The leftmost filled circle follows the pattern of the open circles. Thus, assuming that the decay is spontaneous (Choe and Welch 1974) rather than requiring movement of the exposed arm, there appears to be little influence of transferring the cube (twice) on the amount of adaptation.

Discussion

In this study we attempted to assess the way that natural reaching movements adapt to perturbations of visual feedback. Our subjects aligned a real cube that they held in their unseen hand with a visual simulation of such a cube. Between test phases they received either veridical or perturbed visual information about the position of the real cube. We used different types of perturbations whereby the magnitude of the offset when holding the real cube at a target was equal for all perturbations. Comparing test phase movement endpoints after perturbed feedback with ones after veridical feedback revealed that subjects readily adapt to *translations* of visual feedback. Adaptation to *scaling* was less pronounced. Subjects were able to adapt to *rotations* of visual feedback, but only to a very small extent. In experiment 1 we found that the adaptation of movement endpoints is not affected by varying the postural configuration during the feedback phases. In experiment 2 we found that visuomotor adaptation transfers to the unexposed arm, but that the amount of transfer differs for the different perturbations. Visuomotor adaptation to scaling transferred completely to the unexposed arm, while intermanual transfer for translations and rotations was small. Thus, adaptation is largely effector specific for the latter perturbations, but not for scaling. In addition, adaptation was found to decay during testing for translation.

Adaptation to errors in egocentric parameters

We proposed that to be able to adapt movement endpoints to altered visual feedback of the hand, subjects must be able to interpret the imposed changes as an internal error in egocentrically specified parameters. This is simplest for a translation. The lateral mismatch between vision and kinesthesia could be interpreted as an error in the judged orientation of the eyes or head (Vetter et al. 1999) or in the judged direction of the hand relative to the body (Harris 1963). The incomplete intermanual transfer that we found (see Fig. 7) suggests that the adaptation is partly a change in the interpretation of the kinesthetic information about the arm and partly a change in interpreting information about visual direction (which is not specific to either limb). The extent to which each mechanism contributes to the adaptation is probably a less important finding than the fact that both mechanisms indeed contribute, because the extents will depend on the experimental conditions. Changes in these extents can explain why providing continuous feedback during the movements results in less transfer of adaptation to the unexposed arm than only providing feedback about the endpoint (Cohen 1967), and why transfer is facilitated by an unconstrained head position during exposure (Hamilton 1964).

The scaling of visual feedback about position can be interpreted as an error in the judged distance of the center of the targets, resulting in longer or shorter distances between the targets for the same retinal separation. Note that the information about the cube's size remains the same, so that the subject receives conflicting cues about distance and may therefore be more reluctant to adapt. Moreover, a different distance is in conflict with both vergence and arm posture. We found complete transfer of adaptation for scaling, suggesting that adaptation to scaling is not a modulation of kinesthesia of the arm (which is presumably specific to the exposed arm), but that the perturbation changed components of visuomotor control that transfer across limbs. We observed small biases toward or away from the subjects, which suggests that the perturbation indeed changed the perceived distance of the targets relative to the body to some extent.

Rotations of visual feedback around a single position in space are more difficult to relate to an egocentric frame of reference, and the amount of adaptation is correspondingly low. Nevertheless, there was some adaptation present for both rotations. We expected better adaptation to a rotation around the viewing axis, which can be related to a change in head orientation, but no systematic difference in the magnitude of adaptation between the two types of rotations was found. However, the direction of change in endpoints deviated less from the appropriate compensation vectors for the rotation around the viewing axis than for the other rotation (see Fig. 5). Thus, although the magnitude of the adaptive response was low, we found a closer match between the spatial parameters of the response and the spatial parameters of the rotation around the viewing axis. Perhaps we are too good at determining the direction of gravity, or the conflict with the (unchanged) orientation of the target was too large, for substantial adaptation to occur.

Adaptation to errors in allocentric parameters

Our assumption that subjects use endpoint control for these movements provided the basis for the present experiments. Others have suggested that adaptation can also take place in allocentric coordinates. It was suggested that subjects are able to recalibrate a visuomotor scaling factor and determine a new reference direction to link relative target position to an initial hand position (Abeele and Bock 2001; Krakauer et al. 2000; Ghahramani and Wolpert 1997; Pine et al 1996; Redding and Wallace 1996; Bock 1992).

Redding and Wallace (1996) found that when subjects had simultaneous vision of starting and target locations, adaptation to prisms did not occur (as revealed by postexposure measurements). Robust aftereffects of wearing prisms were observed when subjects had no visual information about the starting position of their hand. According to these authors the lack of adaptation in the former condition resulted from an ability to code visible differences between starting and target locations. They suggested that misalignments are ignored when both the initial and target position are visible, because subjects determine the direction and extent of their movements on the basis of the visual judgements of the relative (initial) positions of the hand and target. In our experiment subjects readily adapted to translations of visual feedback, although both starting location (the initial position of the feedback cube) and target location were visible during perturbed feedback phases. This confirms that under our conditions the movements were not coded as the visual difference between the initial starting location and the target position, but were coded as the target's distance and direction relative to the body (Van den Dobbelsteen et al. 2001).

Krakauer et al. (2000) and Pine et al. (1996) studied the time course and generalization of adaptation to display rotation and altered gain using screen cursor movements on a computer monitor. They found that adaptation to a display rotation was slower than adaptation to a gain change, and generalized less completely to untrained target distances and directions. A longer time constant for adaptation to rotations could explain why we found less adaptation to rotation than to scaling. However, we agree with Clower and Boussaoud's (2000) claim that the use of representational feedback, or feedback that is not perceived to be physically coincident with the position of the hand (as when using a computer mouse), may elicit adaptive responses that do not reflect normal visuomotor control. Different levels of abstraction in the feedback may induce different kinds of adaptation of the visuomotor transformations involved (Norris et al. 2000), or may encourage subjects to use certain egocentric or allocentric cues for guiding their movement (Clower and Boussaoud 2000). We therefore assume that the presumed longer time constant for adaptation to these kinds of rotations results from the need to incorporate allocentric cues for guiding the movement where otherwise egocentric cues would suffice.

Bock (1992) found that the change in gain of arm movements transferred to untrained directions but not to the other arm, suggesting that the adapted parameter is more closely linked to movement execution than to perceptual processes. These results are in contrast with the present study, in which we found almost complete transfer of adaptation to scaling. This contradictory result probably follows from differences in the experimental conditions. In our setup the scaling of visual feedback was equal in all directions. Bock (1992) used a gain reduction to 0.5 for horizontal movements, and at the same time a gain increase to 2.0 for the vertical component. Such a perturbation cannot be interpreted as a change in perceived distance relative to the body. This may have encouraged an interpretation of the errors in terms of changed joint angles, so that the adaptation was restricted to the exposed arm.

Decay of adaptation

Our idea that the adaptation to translation is closely linked to the effector arm is in line with the findings of Choe and Welch (1974), who compared visual and proprioceptive components of prism adaptation. They found rapid decay for the proprioceptive components, but not for the visual components. We too found a rapid decay of the adaptation to translation, suggesting that it was the proprioceptive component that was changed. However, the rate of decay of the small amount of adaptation that did transfer to the unexposed arm was comparable to that of the exposed arm, while one would assume that it is only the visual component of adaptation that transfers (compare the solid squares with the open circles in Fig. 7). An extra complication is that it is unknown whether the decay is a relatively fixed percentage of the initial magnitude of adaptation or whether it saturates at a fixed magnitude of adaptation. Therefore, whether the different components that may adapt display a different time constant in the decay of adaptation remains to be determined.

Realignment or context dependent adaptation

The decay of adaptation without exposure to veridical feedback shows that adaptation does not solely consist of realigning vision with proprioception (Cunningham and Welch 1994; Welch et al. 1993). If the two were realigned one would expect no spontaneous decay, and also a more or less complete adaptation. A possible explanation for the incomplete adaptation is that the adaptation is context dependent. For instance, adaptation is known to depend on head orientation (Seidler et al. 2001) and postural configuration (Ghahramani and Wolpert 1997). If there is no clear context, settings may be a compromise between those appropriate for various contexts (Vetter and Wolpert 2000).

A difference between realigning vision and kinesthesia and switching between contexts is the prediction for the unperturbed trials in our study. In the experiment we used a veridical feedback phase after each postperturbed test phase. Does exposure to the veridical feedback reset adaptation completely? If no realigning occurred during perturbed feedback phases one expects the settings to return to normal during testing after veridical feedback. However, if realignment did occur then veridical feedback is a “perturbation” relative to the current state of alignment, and one would expect a comparable amount of adaptation for this latter “perturbation.” To investigate this we examined whether there were still effects of the translated feedback after the veridical feedback phase. We did this by comparing the averaged movement endpoints of postveridical test phases following the exposure to the translated feedback, with settings of postveridical test phases that subjects made before being exposed to the translated feedback. The results are displayed in Fig. 8.

Figure 8 shows that subjects initially make veridical settings after veridical feedback but gradually alter the endpoints of the movements of the exposed arm in the appropriate direction for the previous transformation. The fact that the influence of the previous perturbation reappears during testing suggests that some alignment between vision and kinesthesia has taken place during the perturbed feedback phase. The change is even consistent with the amount of adaptation to the translated feedback, because the decay of adaptation for translation was saturated at about 20%, so one would expect an increase in the remnants of adaptation up to 80% of this saturation level (16%), which is approximately what we found. No adaptation was expected for the unexposed arm because there was little adaptation at the end of the postperturbation test phase (see Fig. 7). Thus, alignment does appear to take place.

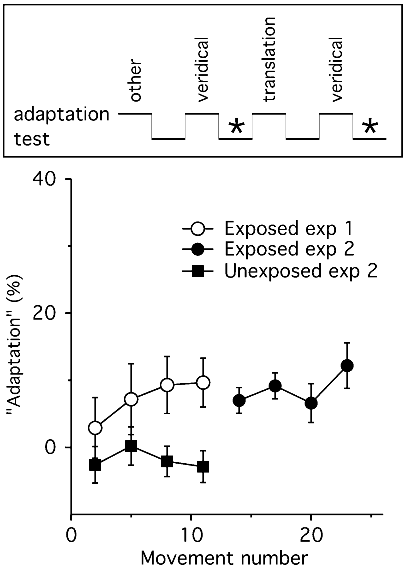

Fig. 8 Remnants of adaptation to translation during the postveridical test phase. “Adaptation” is the error in the movement endpoints after veridical feedback expressed as a percentage of the perturbation in the previous perturbed feedback phase. *Stars in the top panel* show which of the test phases are compared. Each *symbol* is the average of three consecutive settings for the 11 subjects that participated in both experiments 1 and 2. *Open and filled symbols* show the results for experiment 1 (fixed target orientation) and 2, respectively. *Circles* show the results for the arm that was used during the feedback phase; *squares* indicate the results for the unexposed arm. *Error bars* display standard errors across subjects

Conclusions

We conclude that subjects most readily adapt arm movement endpoints to perturbations of visual feedback within egocentric frames of reference, and that adaptation to different types of perturbations is not confined to a single mechanism.

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