Chapter 3

Visuomotor adaptation to different amplitudes and directions of shifted visual feedback

We investigated the extent to which the perceptual sensitivity for mismatches between vision and kinaesthesia affects the adaptation to such mismatches. One may expect less adaptation if no mismatch is detected, because in that case no corrections can be made. Conversely, one may expect more adaptation if no mismatch is detected, because in that case other (e.g. conscious) compensatory mechanisms can not be used. To examine these possibilities we first determined thresholds for the detection of mismatches between the position of a real 5-cm cube that subjects could feel but not see, and the position of a simulation that they saw via a mirror. The thresholds for detecting mismatches were higher along the viewing direction than in the orthogonal direction. In a second experiment 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 shifted in the same directions as in the threshold experiment. The amplitude of the mismatch was varied close to the detection threshold. The magnitude of adaptation that we found did not depend on the amplitude and direction of the mismatch. We conclude that there is no relation between the perceptual sensitivity for a mismatch between vision and kinaesthesia and the magnitude of adaptation to such a mismatch.

Adapted from: JJ van den Dobbelsteen, E Brenner, JBJ Smeets (submitted) Visuomotor adaptation to different amplitudes and directions of shifted visual feedback.

Introduction

The plasticity of the visuomotor system is particularly evident in the ability to quickly adapt goal-directed arm movements to altered visual feedback. Such visuomotor adaptation presumably involves alterations at multiple levels of movement control (Redding and Wallace 1996, Welch 1986, Welch et al. 1974), and therefore depends on the kind of perturbation (Van den Dobbelsteen et al. 2003) and the conditions of exposure (Norris et al. 2001, Clower and Boussaoud 2000). For instance, it has been suggested that it must be possible for the mismatches between vision and kinaesthesia to be attributed to internal errors if there is to be any adaptation. Errors that can only be interpreted as having an external cause lead to little or no adaptation (Clower and Boussaoud 2000).

Conscious awareness of the mismatch between vision and kinaesthesia does not seem to be a prerequisite for adaptation to occur (Jacobson and Goodale 1989). Noticing the loss of correspondence between arm movements and the visual feedback about these movements has even been reported to hamper the compensatory processes (Kitazawa et al. 1995, Held et al. 1966). Whether or not a mismatch is detected depends on how large the mismatch is in relation to the precision of the visual and kinaesthetic information. This precision has been suggested to determine which of the senses adapt (Van Beers et al. 2001, 1999). However, a systematic analysis of how the sensitivity for the presence of a mismatch enhances or degrades adaptation is not yet available.

If adaptation is a response to a detected mismatch then we expect less adaptation for smaller discrepancies. Both visual and kinaesthetic information are subject to variable errors. Discrepancies between the modalities that are smaller than the variability may therefore remain totally undetected by the brain, and will consequently not induce adaptive processes. Alternatively, if adaptation is a consequence of a constant alignment mechanism, (conscious) detection is irrelevant. Moreover, small discrepancies are less likely to break down the perceived correspondence between the senses and may yield more adaptation than larger mismatches, because no conscious compensation will counteract re-alignment. We therefore examine how the magnitude of a mismatch influences the extent of adaptation.

The precision of visual and kinaesthetic localisation of the hand (Van Beers et al. 2001, 1999) and the variability of endpoints of goal-directed movements (Van den Dobbelsteen et al. 2001, Carrozzo et al. 1999, McIntyre et al. 1998, 1997, Soechting and Flanders 1989a, 1989b) differ for different directions relative to the body. A mismatch in one direction will therefore be easier to detect, and possibly also to accept as an internal error, than a mismatch in another direction. We therefore also compare the effects of two directions of the induced mismatch. By choosing directions that differ in visual and kinaesthetic resolution we can separate the influence of detectability from that of the amplitude itself.

In the present study we examined whether there is a relation between perceptual sensitivity for visual-kinaesthetic mismatches and the magnitude of adaptation to these mismatches. To investigate this issue we first determined the thresholds for detecting mismatches in different directions. Subjects held a real 5-cm cube in their unseen hand while they saw a three-dimensional simulation of such a cube for a brief period of time. The simulated cube could be displaced by up to 5 cm from the real cube. The subjects' task was to move the real cube in the direction of the simulated cube, and thereby to indicate the direction of the mismatch. Previous studies have shown that subjects are less accurate in the alignment of visual and kinaesthetic information along the viewing direction than in the lateral direction (Van den Dobbelsteen et al. 2001, Carrozzo et al. 1999). We therefore used shifts that were roughly in these two directions to maximise the effect of direction of the mismatch on the detection thresholds. In a separate experiment we exposed the subjects to mismatches in the same directions while they made natural self-paced movements between different target locations. To evaluate whether subjects adapted to the mismatches we compared endpoints of pre-exposure movements (without feedback) with post-exposure measures (again without feedback). Comparison of the detection thresholds with the extent of adaptation will reveal whether detecting the mismatch is critical.

Materials and Methods

Subjects

Eight subjects, including two of the authors, participated in the experiment in which we determined the threshold for detection of mismatches between vision and kinaesthesia. Six of these subjects, including the two authors, and six new subjects participated in the experiment in which we determined the extent of adaptation to these mismatches. 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.

Apparatus

The experimental apparatus is similar to that used in Van den Dobbelsteen et al. (2001) Images were generated with a Silicon Graphics Onyx computer at a frame rate of 120 Hz. The images were displayed on a Sony 5000 ps 21" monitor (30.0 cm × 40.4 cm; 612 pixels × 816 pixels), located in front of and above the subjects' head, and viewed by way of a mirror (see figure 3.1). Liquid crystal shutter spectacles (CrystalEyes 2, weight 140 g., StereoGraphics Corporation, California) were used to present alternate images to the two eyes at the 120 Hz frame rate (60 Hz per eye for binocular vision).

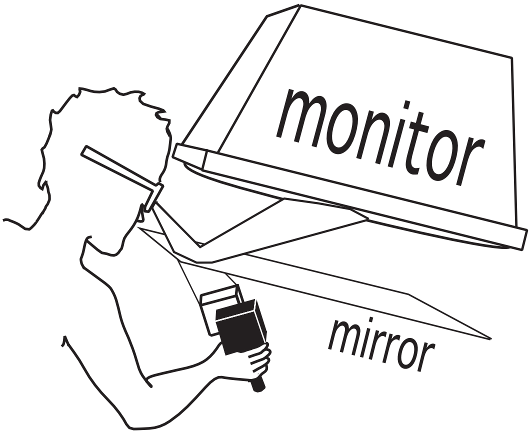

Figure 3.1 *Schematic view of the setup. Subjects stood in front of a monitor holding a cube attached to a rod. In the threshold experiment they had to indicate the direction in which the visual feedback about the real cube (a simulated solid cube which they saw via the mirror) was perturbed. In the adaptation experiment the subjects aligned the real cube's position and orientation with the position and orientation of a target cube (a simulated wire frame cube).*

Subjects held a 2-cm-diameter rod attached to a 5-cm cube (total weight: 145 g) in their unseen hand underneath the mirror. The monitor and mirror were tilted 12° backwards relative to the horizontal to obtain a larger workspace. During the first 480 ms of each trial in the threshold experiment and during the feedback phases of the adaptation experiment subjects saw a three-dimensional rendition of a cube at the location of the real cube. This simulated cube moved and turned whenever the subject moved or turned the real cube. Our main manipulation was that its position was sometimes shifted from that of the real cube. The luminance of each surface of the virtual cube depended on its 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. In the test phases of the adaptation experiment subjects also saw a wire-frame rendition of a cube that served as a target. All images were red because the liquid crystal shutter spectacles have least cross talk at long wavelengths. Images were corrected for the curvature of the monitor screen. Standard anti-aliasing techniques were used to achieve sub-pixel resolution. During the experiments the room was dark, so that subjects were unable to see anything but the simulated cubes.

A movement analysis system (Optotrak 3010, Northern Digital Inc., Waterloo, Ontario) registered the positions of active infrared markers that were 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 msec.

Procedure in the Threshold experiment

Subjects were given the cube attached to the rod and were instructed to hold the rod with their right hand. They touched an edge of the cube with their thumb, so that they could feel the location and orientation of the real cube. This prevented the rod from rotating within their hand without them noticing it. The subjects were asked to hold the real cube in front of them, roughly in the middle of the workspace (i.e. centered underneath the mirror). They were told that on every trial a simulated cube would appear, that was not aligned with the position of the real cube. This simulated cube was visible for 480 ms. It was explained to them that the mismatches between the position of the real cube and the position of the virtual cube could be of any amplitude and in any direction. They were to detect the mismatch between the cubes and to move the real cube in the direction of the simulated cube). They were asked to continue to move the real cube in that direction after passing the simulated cube. The direction was registered when the real cube had moved 5.0 cm, even when the amplitude of the mismatch was smaller than 5 cm. If subjects did not detect any difference between the position of the real cube and the simulated cube they still had to move in a 'randomly' chosen direction to continue the experiment. After each movement they had to return to the center of the workspace and wait until the next simulated cube appeared.

Experimental design in the Threshold experiment

The position of the simulated cube could either be shifted laterally or in depth, relative to the position of the real cube. In each direction the mismatches also differed in amplitude. We used mismatches of five different amplitudes (1 to 5 cm) in each direction resulting in a total of 20 different mismatches. Each of them was presented ten times. The different kinds of mismatches were presented in a random order. Between every two trials with a mismatch there was a trial with veridical feedback (thus it was not at all the case that the simulated cube was never aligned with the real one). These trials were included to get rid of any adaptation to the previous mismatch.

Analysis of the Threshold experiment

As a measure for the direction that the subject indicated we used the vector between the initial position of the real cube and its position once it had moved 5.0 cm. For each vector we determined whether it was in the direction of the perturbation or not. Although the movements could be in any direction, we only checked whether the direction was within 90 degrees of the direction of the mismatch. This gave us binary values (1 for movement directions that deviated less than 90 degrees from the direction of the mismatch, 0 for movement directions that deviated more than 90 degrees). The values for each of the 20 mismatches were expressed as a percentage of correct responses. A value of 50% correct responses indicates that subjects responded at chance level, presumably because they did not detect the mismatch. Values higher than 50% indicate that the subjects detected the mismatch on some trials. A repeated-measures ANOVA was performed to evaluate whether there were consistent effects of the direction or the amplitude of the mismatch across subjects. To obtain the detection threshold for each of the two directions we fitted a sigmoid through the values averaged over subjects and took the intersection with the 75%-correct line. The sigmoid was:

$$y = 50 + \frac{50}{1 + e^{a-bx}},$$

where x is the magnitude of the mismatch and y is the average percentage correct responses. The values of a (the shift across the abscissa) and b (the steepness of the curve) were fitted.

Procedure in the Adaptation experiment

Subjects held the cube attached to the rod as in the threshold experiment. They were instructed to move the cube as accurately as possible to the position indicated by a simulated wire frame cube (target cube) and to keep it there until the target cube was presented in another position. 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, 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. The symmetry point was the center of the tetrahedron. The length of each edge of the tetrahedrons was 20 cm. The order of target presentation was randomised so the distance between the targets could be 14.1 cm, 20.0 cm or 24.5 cm. During trials in which subjects received no feedback, the target cube was randomly presented in one of four positions beneath the mirror. These four positions were at the corners of one of the two imaginary tetrahedrons, so that the distance between the targets was always 20 cm.

The subjects were free to move their head, so the distance from eye to target varied somewhat across subjects and movements. 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. This threshold corresponded with the subjects' own judgement of movement end, as they reported that they were able to align the cubes before the next target cube appeared.

The adaptation experiment consisted of two separate sessions, performed on different days. Each session started with the subject holding the cube at an undefined position beneath the mirror. Each examined ten experimental conditions in which the visual feedback about the real cube was shifted. In one session subjects were exposed to five of the ten lateral mismatches and five of the ten mismatches in depth. The remaining conditions were performed in the other experimental session. The order of the conditions within each experimental session was chosen at random. The order of the sessions was counterbalanced across subjects.

Each condition had four consecutive phases: a veridical feedback phase, a post-veridical test phase, a perturbed feedback phase and a post-perturbation 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 was provided by the 3D rendition of the cube precisely aligned with the real cube. In the post-veridical test phase the subjects aligned the real cube with the target cube without visual feedback about the real cube. The perturbed feedback phase was identical to the veridical feedback phase except for there being a spatial discrepancy between the position of the real cube and the position of the simulated feedback cube. The feedback cube could be shifted relative to the real cube in different ways. The different mismatches that were used were the same as the ones used in the Threshold experiment. 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 post-perturbation test phase was identical to the post-veridical test phase. It was used to evaluate changes in movement endpoints relative to those in the post-veridical test phase as a result of the altered visual feedback during the perturbed feedback phase.

Analysis of the Adaptation experiment

For each subject, amplitude of the perturbation and direction of the perturbation (left, right, closer, and further away) we determined the average movement endpoint (i.e. the average position of the center of the real cube) in the post-veridical and post-perturbed test phases. These averages were each based on 12 movement endpoints (three endpoints per target). We calculated vectors between the average movement endpoint computed for the post-veridical test phase and the average computed for the post-perturbed test phase. We did so for each subject, amplitude of the perturbation and direction of the perturbation. This gave us the adaptation vector, $\vec{a}$. We defined a compensation vector ($\vec{c}$) as the displacement of the movement endpoint that was needed to align the feedback cube with the target under that perturbation. Thus 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. We could then express the projection of the adaptation vector onto the compensation vector as a percentage of the latter to give a measure of adaptation.

$$\text{Adaptation} = 100\frac{\vec{a} \bullet \vec{c}}{|\vec{c}|^2}\%$$

A repeated-measures ANOVA was performed on these values to evaluate the effect of the amplitude and direction of the mismatch on the extent of adaptation.

Results

Threshold experiment

Figure 3.2 shows the mean percentages of correct responses. The percentage of correct responses is close to 50% for the smallest mismatches, indicating that subjects could not distinguish small shifts in the feedback from veridical feedback. Percentages of correct responses increased with increasing amplitudes of the perturbations. This increase was larger for lateral mismatches than for mismatches in depth. A repeated-measures ANOVA revealed that there was a main effect of the amplitude of the mismatch ($F(4,28) = 14.7; p < .0001$). There was no main effect of the direction of the mismatch, but the direction of the mismatch did interact with the amplitude of the mismatch ($F(4,28) = 4.2; p < .009$). The percentage of correct responses was highest for the large mismatches in the lateral direction.

We determined the 75% correct thresholds for detecting a lateral mismatch and a mismatch in depth by fitting a sigmoid through the averaged values for each of the two directions. For lateral mismatches this threshold was 3.7 cm. For mismatches in depth a threshold of 5.9 cm was found.

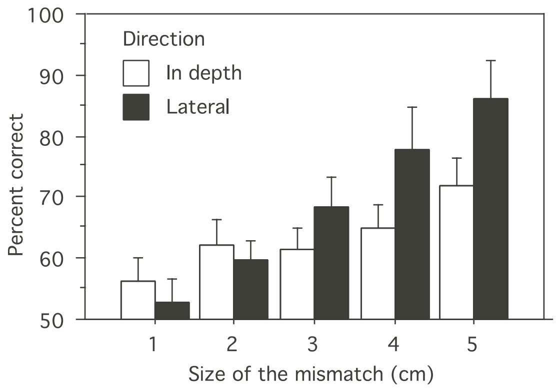

Figure 3.2 *Results of the Threshold experiment. Means and standard errors of the eight subjects' percentages.*

Adaptation experiment

Figure 3.3 shows the difference in movement endpoints between the post-veridical and post-perturbation test phase, expressed as a percent adaptation. The percentage of adaptation is roughly the same for most mismatches (about 40%). The repeated-measures ANOVA revealed no differences between the amount of adaptation for the different directions or for the different amplitudes of the perturbations (no main effect or interaction with the direction of perturbation). The lack of effect of the direction and amplitude of the mismatch suggests that there is no clear relation between detection of a mismatch and whether or not a subject adapts to it.

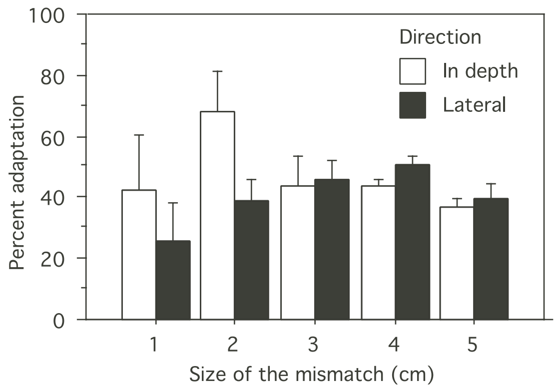

Figure 3.3 *Results of the adaptation experiment. Means and standard errors of the twelve subjects' percentages. The percentage adaptation was about 40%, independent of the amplitude and direction of the mismatch.*

Discussion

In this study we investigated whether there was a relation between the perceptual sensitivity for mismatches between vision and kinaesthesia and the magnitude of adaptation to these mismatches. We looked for a dependency between adaptation and the sensitivity for mismatches in two different directions. Subjects were exposed to either veridical or shifted visual information about the position of a cube that they held in their unseen hand. In the threshold experiment subjects were asked to indicate the direction of the mismatch by moving the real cube in the direction of the simulated cube. The results show that the range of mismatches that we chose yields percentages of correctly identified directions of between just above chance and over 85%. In the adaptation experiment our subjects aligned the (unseen) real cube with a visual simulation of such a cube. Comparing test phase movement endpoints after shifted feedback with ones after veridical feedback revealed that subjects readily adapt to the different shifts of visual feedback, with no difference in the magnitude of the effect (when expressed as a percentage of the amplitude of the mismatch) for the different amplitudes and directions.

Adaptation to perturbations in different directions

We have previously provided evidence that in a similar task subjects control the endpoints of movements to visual targets within an egocentric frame of reference (Van den Dobbelsteen et al. 2001). It has been suggested that during adaptation the visuomotor system modifies the judged orientation of the eyes, head, shoulder or elbow (Van den Dobbelsteen et al. 2003, Vetter et al. 1999). If so, then in order 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 error in judging some such egocentrically specified orientation (Clower and Boussaoud 2000).

Whether or not this is possible will partly depend on the direction of the mismatch. In order to adapt arm movement endpoints to various kinds of altered visual feedback one may require several different judgements to change (Redding and Wallace 1996, Welch 1986, Welch et al. 1974). This may involve changes in visual localisation mediated by changes in the perceived direction of gaze (Craske 1967, Kalil and Freedman 1966), and changes in the proprioceptive localisation of the arm (Taub and Goldberg 1973, Harris 1963) mediated by changes in the perceived shoulder and joint angles. In an adaptation paradigm, Van Beers et al. (2001, 1999) investigated how visual and proprioceptive localisation are combined to generate a single estimate of hand position. They found that the weighting of visual and proprioceptive information varies with the direction. For lateral mismatches subjects relied more on visual information while for mismatches in depth proprioceptive information was weighted most heavily. Thus, the visuomotor system uses knowledge about the direction-dependent precision of visual and kinaesthetic information when combining the two so that the mismatches in different directions are treated differently (Van Beers et al. 2001, 1999).

The differences in precision of the various sources of information can undoubtedly explain why the patterns of variable errors are anisotropic when making arm movements to visual targets (Van den Dobbelsteen et al. 2001, Carrozzo et al. 1999, McIntyre et al. 1998, 1997). We are better in judging the direction of object than its distance. Consequently, a lateral mismatch between vision and kinaesthesia may less readily be interpreted as an internal error than a mismatch in depth. However, we found no difference between adaptation to lateral mismatches and mismatches in depth, although we did find the expected difference in detectability for the very same stimuli.

Adaptation to perturbations of different amplitudes

We looked at adaptation to mismatches for which the amplitude was near detection threshold. Much larger perturbations, which are readily noted, will presumably lead to task-dependent performance changes based on knowledge of results. This makes it hard to distinguish strategic changes of arm movements from adaptive alignment of vision and kinaesthesia (Redding and Wallace 1996). We were specifically interested to see whether detection of a mismatch would influence re-alignment of vision and kinaesthesia. Therefore, we limited the range of mismatches to those that were just below or above the detection threshold. Within this range the amount of adaptation is a fixed percentage of the magnitude of the mismatch.

The lack of effect of the amplitude of the mismatch on the magnitude of adaptation is in contrast with Efstathiou (1969), who suggested that the strength of prisms critically affects the magnitude of adaptation. Efstathiou (1969) investigated adaptation to 2, 4, 8, 16 and 24-diopter wedge prisms, corresponding to mismatches of about 1, 2, 4, 8 and 12 cm at the target distance used in his experiment. He found that 2 and 4-diopter prisms failed to generate any adaptation. In our study we found adaptation of equal magnitude to such small mismatches, although variability was high. This large variability is probably due to errors that were not related to the perturbation, such as modest visual-proprioceptive drift (Van den Dobbelsteen et al. 2001, Wann and Ibrahim 1992) that affects both post-veridical baseline measurements and post-perturbation measurements of the arm movement endpoints. The variability can be as large as the mismatches, making it hard to reliably determine which part of the change in mean hand position is an adaptive response. It is also possible that drift counteracts the changes induced by the prisms so that no clear adaptation is found. Adaptation is known to decay rapidly after removal of the altered feedback (Van den Dobbelsteen et al. 2003, Choe and Welch 1974). In the study of Efstathiou (1969) the period of time between exposure and post-exposure measurements was longer than in the present study, making it possibly more susceptible to drift and decay of adaptation. The exact mechanisms by which drift and decay of adaptation occur are not known.

Our results are consistent with those of Jakobson and Goodale (1989) who found comparable adaptation on the reach trajectory when wearing 5 and 20-diopter prisms. Their subjects were permitted full visual feedback of their moving hand at all times, so they made no endpoint errors. However, the curvature of their movements changed significantly. Their subjects did not detect the small mismatches caused by the 5-diopter prisms while they did do so for the 20-diopter prisms, indicating that the sensitivity for the mismatches was not critical. However, Jakobson and Goodale (1989) made no quantitative comparison between the effects of the different prisms. Our study extents their findings by showing that the adaptation is a fixed percentage of the amplitude of the mismatch.

To summarise, we found comparable adaptation to different amplitudes and different directions of mismatches between vision and kinaesthesia. Although the perceptual sensitivity for the mismatches differs between these perturbations, the adaptation is a fixed percentage of the magnitude of the mismatch in all cases.