Chapter 5

Body-centered visuomotor adaptation

Previous research has shown that humans generalise perturbations of visuomotor feedback in terms of egocentric rotations. We examined whether these rotations are around the eyes or around the shoulder of the arm that was used. Subjects moved a hand held cube between target locations in a sequence of adaptation and test phases. During adaptation phases, subjects received either veridical or perturbed visual feedback about the cube. The perturbations were a change in azimuth either relative to the eyes or relative to the shoulder. During test phases subjects received no visual feedback. Test phases were performed either with the arm that was exposed to the perturbed feedback or with the unexposed arm. We compared test movement endpoints after perturbed feedback with ones after veridical feedback. For the exposed arm, the spatial layout of the changes in endpoints clearly reflected the small differences between the two perturbations. Intermanual transfer of adaptation was incomplete for both types of perturbations. Moreover, the changes in endpoints that we found for the unexposed arm were less consistent with the perturbations than the changes that we found for the exposed arm. These results show that the adaptation involved adjustments both at the level of the eyes and at the level of the exposed arm. The adaptation is distributed and only matches the imposed perturbation when all adjustments are combined, even if the changes in endpoints match the spatial features of a single rotation.

Adapted from: JJ van den Dobbelsteen, E Brenner, JBJ Smeets (submitted) Body-centered visuomotor adaptation.

Introduction

During visually guided reaching movements, visual information about the target's location must be integrated with kinaesthetic information about the position and movements of the hand. Several researchers have proposed that in order to do so the movement endpoint is specified in an egocentric frame of reference (Van den Dobbelsteen et al. 2001, Carrozzo et al. 1999, McIntyre et al. 1998, 1997, Berkinblit et al. 1995 Flanders et al. 1992, Soechting et al. 1990, Soechting and Flanders 1989a). It is assumed that retinal and extra-retinal information are initially combined to determine the target's location relative to the eyes or head. At later stages this position is successively transformed into positions relative to the body and arm by adding kinaesthetic information about the trunk and the effector arm.

Our ability to generate appropriate motor behaviour under changed visual feedback suggests that the above-mentioned transformations are under adaptive control. Vetter et al. (1999) studied the adaptation to mismatches between actual and displayed finger position during pointing movements. A lateral shift of visual feedback about finger position within a small area induced changes in movement endpoints over the entire workspace. This adaptation was best described as a rotation of the workspace around the subjects' eyes (Vetter et al. 1999), suggesting that the adjustments occurred at the level at which the position was coded relative to the eyes or head. According to the hypothesis outlined above, this coding is before effector specific (e.g. kinaesthetic) information is incorporated, so the changes should be the same for the two arms. Other adaptation studies showed however that similar global changes are partly brought about by adaptive processes at the level of the arm. (Van den Dobbelsteen et al. 2003, Cunningham and Welch 1994, Welch et al. 1974, Hamilton 1964). Van den Dobbelsteen et al. (2003) investigated adaptation of arm movement endpoints to translated feedback with a method comparable to that of Vetter et al. (1999). Subjects were exposed to perturbed feedback while they made movements with one of their arms, and were subsequently tested without feedback while they made movements with the unexposed arm. The transfer of adaptation to the unexposed arm was substantial, but incomplete (Van den Dobbelsteen et al. 2003), indicating that the adaptation involved adjustments at a level that is shared by both arms as well as adjustments at the level of the exposed arm.

Transfer studies can reveal differences between the levels at which the modifications take place that cannot be seen in the responses themselves because of the similarity between the predicted effects. In the study of Vetter et al. (1999) a rotation with respect to the eyes captured the changes in pointing slightly better than a rotation with respect to shoulder of the exposed arm. However, it is possible that both adjustments at the level of the eyes and arm were involved. Examining whether adaptation transfers to the unexposed arm can resolve this issue. In the present study we investigate adaptation to perturbations of visual feedback that mimic a change of azimuth relative to the eyes or shoulder. In the experiment, subjects positioned a real 5-cm cube at the location of a three-dimensional visual simulation of such a cube. We compared test (without visual feedback) movement endpoints after perturbed visual feedback with ones after veridical visual feedback. Test phases were either performed with the exposed or the unexposed arm (in two separate sessions). We determined how subjects adapt to eye- and shoulder-centered perturbations, and examined the transfer of adaptation to the unexposed arm.

Materials and Methods

Subjects

Fifteen subjects participated in two experimental sessions that were performed on separate days. All reported normal visual acuity (after correction) and binocular vision. The work forms part of an ongoing research program for which ethical approval has been granted by the appropriate committees of the Erasmus University Rotterdam.

Apparatus

The experimental apparatus is the same as that used in Van den Dobbelsteen et al. (2003). Images were generated at a frame rate of 120 Hz and presented alternately to the two eyes with the help of liquid crystal shutter spectacles for binocular vision. We accounted for individual differences in interocular distance when generating the images. Images were viewed by way of a mirror, which enabled us to present virtual targets and feedback within the arm's workspace. Subjects held a rod attached to a 5-cm cube in their unseen hand and were instructed to align this cube with a stationary 3D wire frame of a cube (target cube) that appeared beneath the mirror. During trials in which subjects received feedback about the position and orientation of the real cube (feedback phases), an additional rendition of a cube was presented at the (transformed) location of the real cube. This feedback cube moved whenever the real cube was moved. A spatial discrepancy was sometimes introduced between the real cube and the simulated feedback cube. 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 that were attached to the real cube, to the distal part of the right shoulder (near the acromioclavicular articulation at the outer extremity of the clavicle), and to the shutter spectacles. Eye position (not eye orientation) was inferred from the positions of markers on the shutter spectacles and used to render the images with the appropriate perspective for that eye at that moment. We defined the location of the shoulder as the position 7 cm below the marker that we attached to the shoulder. Measured eye and shoulder positions were used when introducing the perturbations of visual feedback (see Perturbations). The total delay between a movement and the adjustment of the image was about 16 msec.

Procedure

An experimental session started with the subject holding the cube in his right hand beneath the mirror. Subjects were instructed to move the cube that they held as accurately as possible to the position indicated by the target cube. A movement was considered to have come to an end when the subject moved the centre of the cube less than 2 mm within 300 ms. The starting position of the hand for each subsequent movement was the endpoint of the previous movement. The target cube could appear randomly in one of eight positions beneath the mirror. These eight positions were at the corners of an imaginary 18 cm-cube. During trials in which subjects received no feedback (test phases), this imaginary cube was in an upright position. During feedback phases, the imaginary cube was rotated 45 degrees around a horizontal axis through its center so that the target cube was presented at each of eight other positions. The orientation of the target cube was fixed.

Each of the two sessions involved the same four experimental conditions (see Perturbations). Each condition was repeated six times within one session. The order of the conditions was chosen at random. 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. In the post-veridical 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 and orientation of the simulated feedback cube and those of the real cube (see Perturbations). The post-perturbation test phase was identical to the post-veridical test phase, and was used to evaluate changes in movement endpoints (relative to the post-veridical test phase) as a result of the altered visual feedback during the perturbed feedback phase. In each phase each of the eight targets was presented once.

The veridical and perturbed feedback phases were always performed with the right hand. In the first session subjects also used their right hand during test phases. In the second session they used their left hand during test phases. In the second session the images disappeared at the end of each phase 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. When they had transferred the real cube to the other hand a new target cube appeared, and the subjects performed the next phase with the previously unused hand. Thus, in the first session all phases were performed with the same hand while, in the second session all test phases were performed with the hand that was not used during feedback phases.

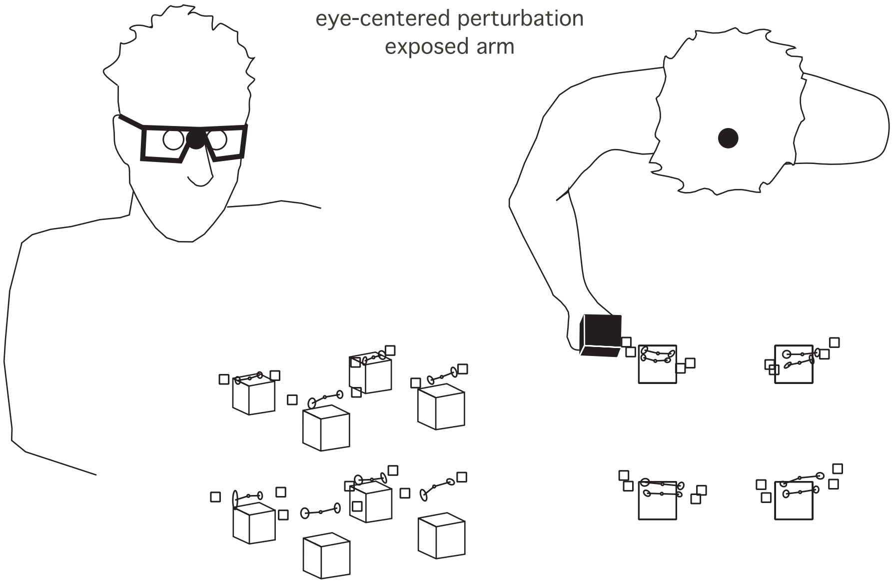
Perturbations

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 an eye-centered rotation (2 conditions) or a shoulder-centered rotation (2 conditions). The two different conditions for each type of perturbation were rotations in opposite directions. For the eye-centered perturbations, we rotated the simulated position and orientation of the feedback cube around a position between the eyes (cyclopean eye). The axis of rotation was orthogonal to a vector from the cyclopean eye to the center of the current target. It lay in the plane defined by this vector and the direction of gravity. For the shoulder-centered perturbations the axis of rotation was similarly defined to be orthogonal to a vector from the estimated shoulder position to the center of the target. The magnitude of the rotation was 4.8 degrees for all perturbations. The perturbations affected both the position and orientation of the feedback cube. The simulated shape and size was always correct for the visually presented position and orientation.

Analysis

We determined each subject's average movement endpoints after veridical and after perturbed feedback for all combinations i of target location and direction of the perturbation. The difference between these endpoints was expressed as a vector ($\vec{a}_i$). To determine whether the changes in endpoints mimicked rotations around the eye or around the shoulder we examined whether these vectors corresponded to one of the rotations. We did this by finding the single rotation around the average position of the cyclopean eye or shoulder that best fits the changes of the average endpoints. The axes of rotation (one for the eye and one for the shoulder) were the same as the ones used to produce the perturbed feedback. To quantify how well this single rotation described the changes in the endpoints we separated each change $\vec{a}_i$ into a component that is accounted for by the common rotation ($\vec{r}$) and a component (the error vector $\vec{e}_i$) that is not. Note that $\vec{e}_i = \vec{a}_i - \vec{r}$.

The common rotation found when fitting the applied perturbation to the data was used to determine the amount of adaptation. The average magnitude of the 16 values of the error $|\vec{e}_i|$ was used as a measure of how well the adaptation is captured by the rotation that was fitted to the data. For each subject, type of perturbation and session (exposed arm, unexposed arm) the average magnitude of the error $|\vec{e}_i|$ was determined both for a rotation centered at the eyes and for one centered at the shoulder (i.e. for the model that corresponded to the applied perturbation as well as for the one that did not). A repeated measures analysis of variance was performed on these measures to evaluate the effect of the type of perturbation (eye-centered, shoulder-centered), session (exposed arm, unexposed arm), and the model fitted (axis of rotation the same as the perturbation, axis of rotation different from the perturbation).


eye-centered perturbation
exposed arm

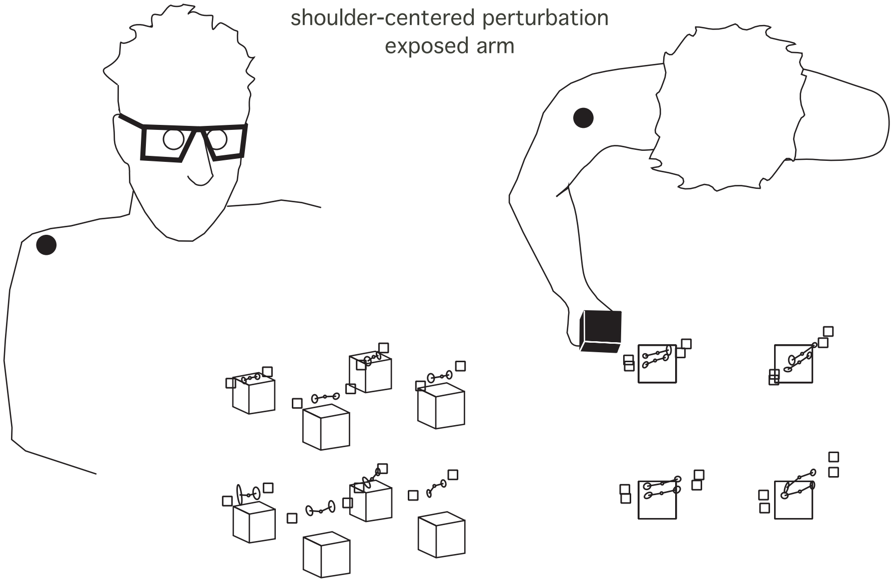

shoulder-centered perturbation
exposed arm

Figure 5.1 *Projections of the average movement endpoints of the exposed arm. Averages are shown for each type of perturbation, direction of perturbation and target position. The left images show the relative positions of the eight target cubes. In the right images (viewed from above) these (overlapping) target positions are represented by the large open squares (size=5 cm). Small solid circles show the average endpoints during post veridical test phases. Note that these averages deviate from the centers of the target cubes due to systematic biases in the perceived position of the target and of the unseen hand. The small open squares show where the perturbation would place these positions. Ellipses show the average (center) and the between subject variability (lengths of the axes correspond to the standard deviations in the direction of highest variability and in the orthogonal direction) of the endpoints during post perturbation phases. The large open circles in the left images show the average positions of the two eyes. The large closed circles show the average center of rotation: the estimated shoulder position for shoulder-centered perturbations and the position of the cyclopean eye for eye-centered perturbations.*

Results

Figure 5.1 shows the averages of all subjects' movement endpoints for each of the perturbations and each target position for the exposed arm. All changes are approximately in the direction of the applied perturbation, showing that the perturbed feedback results in a uniform change that corresponds with the perturbation. The subjects were exposed to rotations of 4.8° for both types of perturbations. For the exposed arm, the common rotation $\vec{r}$ was on average 2.1°, corresponding to 43% adaptation. Figure 5.2 shows the average movement endpoints for the unexposed arm. The changes in endpoints are much smaller for the unexposed arm (an average of 13% adaptation) and less closely match the perturbation. Thus, less than one third of the adaptation found for the exposed arm transferred to the unexposed arm.

A repeated-measures ANOVA performed on the average magnitude of the error $|\vec{e}_i|$ revealed a main effect ($F(1,14) = 24.2; p < .0002$) of the model that was fitted to the data (same rotation as the perturbation or not) as well as an interaction between this factor and the arm that was used ($F(1,14) = 16.1; p < .0013$; see figure 5.3). Post hoc testing showed that fitting the model that corresponds to the applied perturbation always resulted in a lower error, indicating that the changes in endpoints reflected the differences between the two types of perturbations for both the exposed arm and the unexposed arm.

The errors that remain after fitting the applied perturbation were not significantly different for the exposed and unexposed arm (figure 5.3a). However, for both types of perturbations, the difference between the errors obtained by fitting the model that corresponded to the applied perturbation and fitting one that did not, was significantly larger for the exposed arm than for the unexposed arm. This was

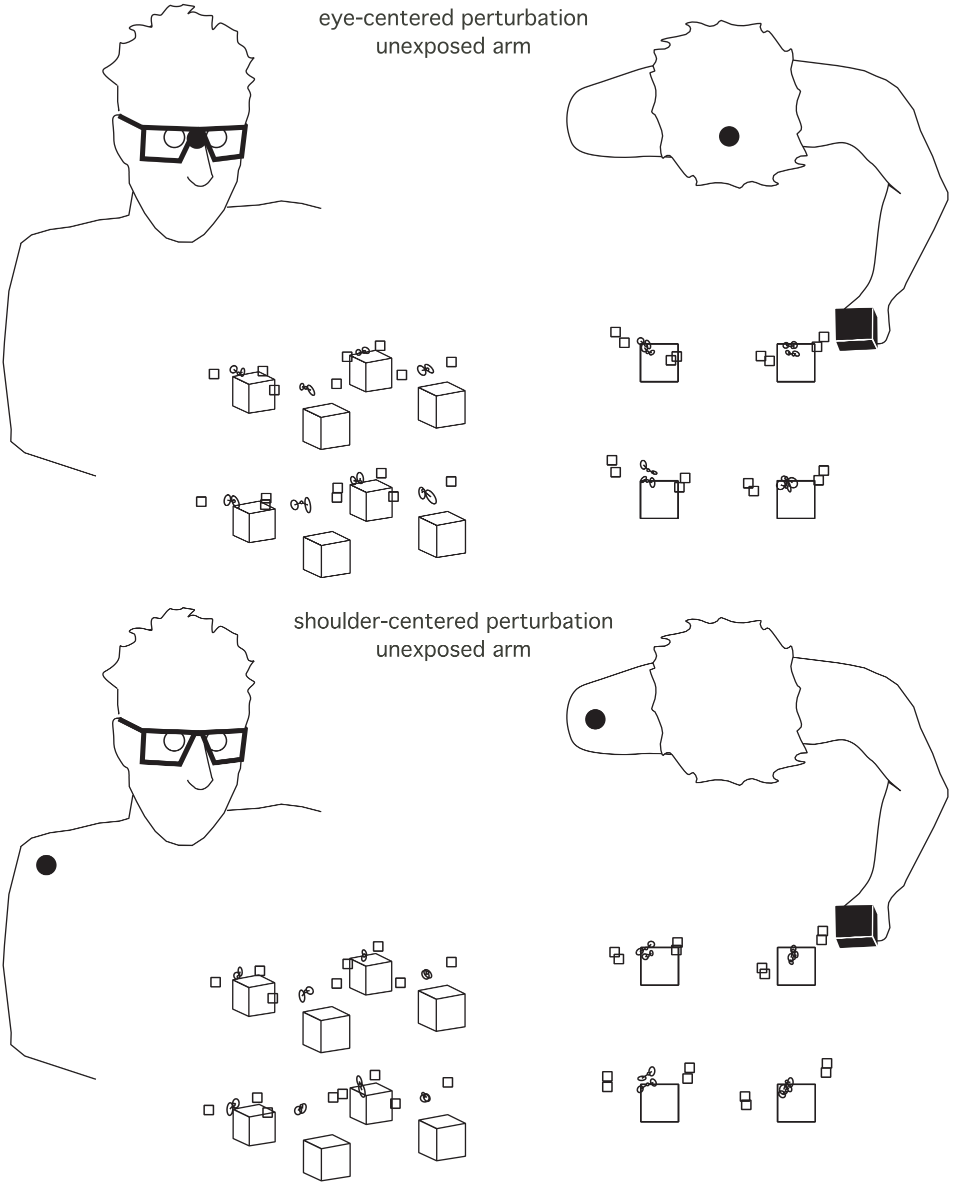


Figure 5.2 *Projections of the average movement endpoints of the unexposed arm. For details see the legend of figure 5.1. Note that the directions of the changes in endpoints after perturbed feedback (lines through ellipses) do not always point toward the small squares. This means that the direction of change is not always consistent with the direction of the perturbation.*

confirmed by analysing the changes in endpoints that were first averaged over subjects (figure 5.3b). With this method we obtain the same values for the common rotations $\vec{r}$ but get rid of much of the random variability. Reducing the random variability makes it clear that the correspondence between the changes in endpoints and the applied perturbation is considerably higher for the exposed arm than for the unexposed arm.

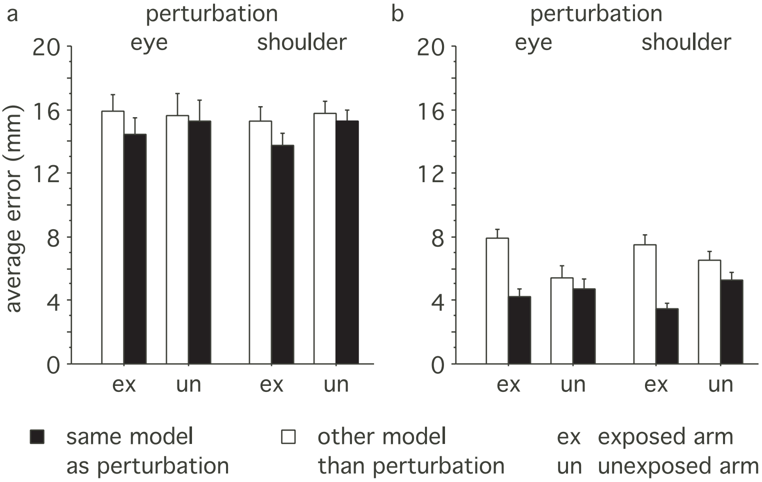


Figure 5.3 *Average errors: the changes in endpoint that cannot be accounted for by a single rotation around the eye or shoulder. Black bars show the results for the model that corresponds to the perturbation. White bars show the results for the model that does not. a) Average errors of individual subjects (with the standard error across subjects). b) Errors in the average of the subjects' endpoints (with standard errors across the two directions of the perturbations).*

Discussion

In this study we investigated subjects' ability to adapt goal-directed movements to eye-centered and shoulder-centered 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 were exposed to either veridical or perturbed visual information about the position and orientation of the real cube. Subjects received feedback during eight movements, and were subsequently tested on eight other target positions than the ones for which feedback had been presented. In separate sessions we tested the hand that was used during exposure to the feedback and the one that was not. Comparing test phase movement endpoints after perturbed visual feedback with ones after veridical feedback revealed changes both for the exposed and unexposed arm. The results show that subjects were able to quickly register the imposed mismatches between vision and kinaesthesia and to alter their visuomotor control to compensate for part of the perturbation. Intermanual transfer of adaptation was present for both types of perturbations but was not complete. This indicates that multiple parameters linked to different parts of the body are changed during adaptation to perturbations of visual feedback. These observations add to the growing body of evidence for egocentric coding of movement endpoints (Van den Dobbelsteen et al. 2001, Carrozzo et al. 1999, McIntyre et al. 1998, 1997, Berkinblit et al. 1995, Flanders et al. 1992, Soechting et al. 1990, Soechting and Flanders 1989a) and confirms that adaptation to perturbations of visual feedback is not confined to adjustments at a single level (Van den Dobbelsteen et al. 2003).

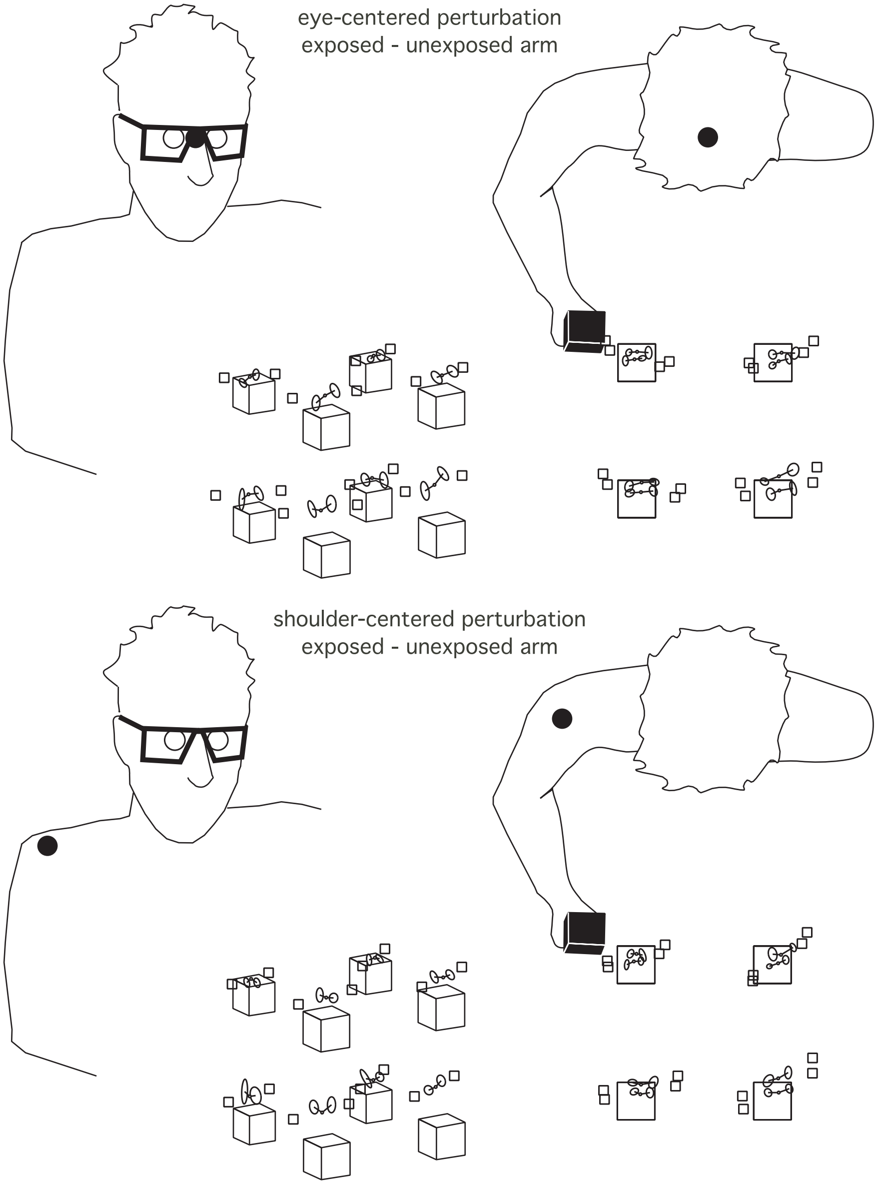
Vetter et al. (1999) proposed that the changes in subjects' pointing behaviour after laterally shifted feedback reflected adjustments within an eye-centered reference frame, because the pattern of generalisation was best captured by a rotation centered near the eyes. Consistent with the results of Vetter et al. (1999), we find that when subjects adapt to eye-centered perturbations, the changes in endpoints are best modelled by a rotation around the eyes. However, if the visuomotor system had achieved this adaptation by a modification at the level of the eyes (i.e. before the divergence point for right and left arm control), then the changes in endpoints should be equal for both arms. This was not the case. The eye-centered perturbations that we used in the present study correspond to prism-induced displacements, and a lack of intermanual transfer is a well-documented finding in that paradigm (Wallace and Redding 1979, Choe and Welch 1974, Welch et al. 1974, Taub and Goldberg 1973, Hamilton 1964, Harris 1963). Thus, adaptation to eye-centered perturbations involves adjustments of parameters that are linked to the arm.

Psychophysical experiments suggest that the transformation of information about target location into a motor command involves the specification of the endpoint of the movement in a reference frame centered at the shoulder (McIntyre et al. 1998, Flanders et al. 1992, Soechting et al. 1990, Soechting and Flanders 1989a). The lack of intermanual transfer is consistent with adjustments within such a shoulder-centered reference frame. Moreover, our subjects were able to adapt appropriately to shoulder-centered perturbations. However, if this adaptation had occurred at the level of the shoulder then the adaptation would not transfer to the unexposed arm, which is contrary to our findings. Thus, adaptation to the shoulder-centered perturbation also involves adjustments of parameters at levels that are common to the two arms.

Our reasoning may appear to indicate that visuomotor adaptation simply involves changes within both eye-centered and shoulder-centered reference frames irrespective of the type of perturbation (eye- or shoulder-centered), and that only the eye-centered component of adaptation has transferred. However, if so, we would expect that the response of the unexposed arm to both types of perturbations corresponded with an eye-centered reference frame. That is certainly not the case for the shoulder-centered perturbations (see figure 5.2).

A similar case can be made for the adaptation that does not transfer. In the present study we cannot determine the spatial characteristics of this adaptation (linked to the exposed arm) directly, but assuming that the different adaptive processes are additive (Wallace and Redding 1979) we can estimate them from the differences in the changes in endpoints for the two arms. For both types of perturbations we subtracted the changes in endpoints that we found for the unexposed arm from the changes in endpoints that were found for the exposed arm. The vectorial differences are displayed in figure 5.4 and reflect the part of the adaptation that did not transfer to the unexposed arm. The spatial characteristics of the vectorial differences in endpoints are comparable for both types of perturbations. Fitting a rotation around the eyes or around the shoulder to the vectorial differences in endpoints results in an average error of equal magnitude for the two types of perturbations (about 21 mm). This indicates that the adjustments that are linked to the exposed arm are neither eye-centered nor shoulder-centered.

The exact nature of the parameters that are changed during visuomotor adaptation is not yet clear. The spatial information required for visuo-kinaesthetic re-alignment is provided by different sensors and encoded in different spatial parameters (e.g. joint angles, muscle stretch, limb orientation). To be able to adapt movement endpoints to altered visual feedback of the hand, the imposed perturbation must be interpreted as changes in these internally specified parameters (Van den Dobbelsteen et al. 2003, Clower and Boussaoud 2000, Hay et al. 1971). The adaptation that we found for the exposed arm shows that rotations around the eye and around the shoulder can be interpreted in this manner. However, for both types of perturbations the spatial characteristics of intermanual transfer indicate that the adjusted parameters differ from the ones that correspond to the perturbation. Part of the adjustments were in the visuomotor processes that are shared by both arms as shown by the transfer of adaptation, but the main part was linked to the exposed arm. The fact that the estimated changes in endpoints are roughly the same irrespective of the type of perturbation suggests that the same parameters linked to the arm are changed during adaptation to eye-centered and shoulder-centered perturbations. The changes in endpoints that we found for the exposed arm are intermediate between eye-centered and shoulder-centered adjustments. Such changes indicate that the adjustments are in the sensorimotor transformations that link visual to kinaesthetic information (Rossetti et al. 1995, Redding and Wallace 1996, Kitazawa et al. 1997).



eye-centered perturbation
exposed - unexposed arm

shoulder-centered perturbation
exposed - unexposed arm

Figure 5.4 *The non-transferred component of adaptation: projections of average movement endpoints of the exposed arm minus the changes in endpoints found for the unexposed arm. For details see the legend of figure 5.1. Note that the directions of the changes in endpoints are comparable for both types of perturbations. In the figure, the positions of the eyes and shoulder, and the average endpoints after veridical feedback are taken from the data obtained for the exposed arm.*

Taken together, our results imply that subjects do not selectively adapt to eye-centered and shoulder-centered perturbations within the matching reference frame, but that combined adjustments at multiple levels of visuomotor control underlie such adaptation. Electrophysiological recordings from single neurons support the view that the brain makes use of multiple spatial parameters and indicate that the parietal cortex is central to the construction of these representations. Neurons at this cortical site are modulated by retinal, eye orientation, and arm-related signals (Buneo et al. 2002, Batista et al. 1999, Lacquaniti et al. 1995, Andersen et al. 1985). A view that emerges is that a single neuron does not explicitly code spatial information in any specific reference frame, but that the spatial representations are distributed over populations of neurons. Subsets of neurons may contribute to multiple representations of space by weighting the convergence of activity differently (Burnod et al. 1999). This raises the interesting possibility that the weighting of different sensory signals changes during adaptation and that this affects movement endpoint specification within multiple frames of reference. In such a coding scheme, the apparent independence of different frames of reference that is reported in psychophysical studies is an emergent property at the systems level, while the neural mechanisms underlying the different reference frames do not operate independently from each other. This is compatible with our conclusion that adaptation to perturbations within one frame of reference is not confined to adjustments at a corresponding level.

We conclude that subjects are able to adapt natural reaching movements to both eye-centered and shoulder-centered perturbations of visual feedback and that during adaptation multiple parameters linked to different parts of the body are altered.