The ability to align vision and kinaesthesia

Het vermogen om visus en kinesthesie te matchen

Proefschrift

ter verkrijging van de graad van doctor aan de
Erasmus Universiteit Rotterdam
op gezag van de Rector Magnificus

Prof.dr.ir. J.H. van Bemmel

en volgens besluit van het College voor Promoties.
De openbare verdediging zal plaatsvinden op
vrijdag 14 maart 2003 om 13.30 uur
door

Johnny Johannes van den Dobbelsteen

geboren te Geldrop

Promotiecommissie

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Chapter 1

General introduction

Many human actions are directed toward objects, and many of them with are executed the use of tools. Van Lawick-Goodall (1970) defines tool use as the use of an external object as a functional extension of the body to attain an immediate goal. This definition illustrates one of the main difficulties that one encounters when using tools. The tool is an extension of the body, but as opposed to other body parts, the external object lacks the sensors that inform us about its position, orientation and movements. The problems in using tools are therefore largely related to sensorimotor integration. When manipulating objects directly, what you see is generally consistent with what you feel. The visuomotor system integrates the visual information with the sensory information about the position (proprioception) and movements (kinaesthesia) of our limbs to generate appropriate motor commands to the muscles. Most tools, however, change the link between the activation of one's muscles and the consequences of one's actions. One way to cope with such changes is to modify the spatial relation between what we see and feel. In other words, we must adapt to the new relationship between visual information and proprioceptive-kinaesthetic information. The manner in which these adaptive responses come about is likely to provide important clues about the normal operation of the visuomotor system. By altering the normal relationship between vision and kinaesthesia we introduce a mismatch. The adaptation serves to overcome such a mismatch but is constrained by the way the visuomotor system is organised. The characteristics of the adaptive responses therefore reflect the properties and functions of the system.

Scope of the thesis

In this thesis we investigate the ability to re-align vision and kinaesthesia to reveal how the visuomotor system uses these two types of sensory information to control goal-directed arm movements. More specifically, we ask ourselves what spatial information provided by these senses is incorporated in the motor commands that generate a visually guided arm movement to an object, and how the spatial information used to control and coordinate such movements is represented. To answer these questions, we designed a number of experiments to determine how the motor commands specify end positions of arm movements to visual targets and how this is changed during adaptation to discrepant sensory information. In the following, we first describe the concepts and methods underlying our approach.

Position coding and vector coding

Researchers have studied a large variety of goal-directed arm movements under different conditions and constraints. These studies show that vision of the hand is not essential for movement control. Movement accuracy is relatively preserved when the hand is occluded to prevent visually guided corrections (Baud-Bovy and Viviani 1998, Van Beers et al. 1998, Prablanc et al. 1986, 1979). Moreover, studies in humans and monkeys deprived of proprioceptive-kinaesthetic afferents suggest that accurate movements are possible in the absence of any sensory feedback (Bard et al. 1999, Polit and Bizzi 1979). Yet, what information is required to plan a reaching movement is still a matter of considerable debate. A key issue is whether the visuomotor system needs to know the position of the hand prior to movement onset.

Most models of the visuomotor system are in between two more general concepts of movement control: position coding and vector coding. Position coding holds that the motor commands only specify the intended final position of the hand relative to one self, i.e. in egocentric coordinates. The notion of position coding derives from the equilibrium point hypothesis. According to this hypothesis a muscular equilibrium point is selected which can be reached without knowledge of the initial state of the motor apparatus. The idea is the muscles behave like springs whose stiffness is controlled by the brain. By setting the length-tension properties of all muscles so that the torques exerted by agonist and antagonist muscles are in balance when the hand is at the desired position, one is able to move the hand irrespective of knowledge about its starting position (Polit and Bizzi 1979). In contrast, other models assume that both information about the initial hand position and the desired hand position are incorporated in the motor command. Evidence for the importance of accurate information about the initial position of the hand is provided by several studies showing that viewing the hand prior to movement onset greatly improves endpoint accuracy (Desmurget et al. 1997b, Rossetti et al. 1994, 1995, Prablanc et al. 1979). Information about the initial hand position would be required to program the movement as a displacement of the hand from its starting position to the desired end position. The hand displacement can theoretically be encoded in two different ways. The vector coding model states that the motor command specifies a distance and direction that will bring the hand from its initial position to the desired position. These parameters are estimated from visual cues that signal the spatial difference between hand and object in allocentric (or external) coordinates (Gordon et al. 1994, Bock and Eckmiller 1986). Other models, however, assume that the required displacement is determined from the positions of the hand and target in egocentric coordinates (or internal) (Buneo et al. 2002, Cohen and Andersen 2002, Engel et al. 2002, Flanders et al. 1992). Thus, apart from the question whether the visuomotor system requires knowledge about the initial state of the motor apparatus, the problem of motor planning is further complicated by the fact that it is unclear in what way the positions are represented.

Frames of reference and sensorimotor transformations

In order to specify a position in space, there must be some physical reference relative to which that position can be described, i.e. one needs a frame of reference. The frame of reference defines the origin of the coordinate system in which positions are represented. To specify the location of a point one also needs to define a set of coordinate axes for the frame of reference. One way to do so is by choosing three orthogonal coordinate axes. Any position can now be characterised as a distance from the origin along these three axes, i.e. a Cartesian frame of reference. One can also define the distance and direction relative to the origin of the coordinate system. The direction is given by two angles (e.g. azimuth and elevation) that describe the rotation of the distance vector relative to the axes, i.e. a spherical frame of reference.

In the case of reaching, the task is to move the hand to the object. It may therefore be convenient to represent its position relative to the hand, i.e. in a hand-centered frame of reference. However, most researchers agree that reaching requires localisation of the object relative to the body and propose that the movement endpoint is specified in an egocentric spherical coordinate system. (Vetter et al. 1999, Carrozzo et al. 1999, McIntyre et al. 1998, 1997, Flanders et al. 1992, Soechting et al. 1990, Soechting and Flanders 1989a, 1989b). Information about object location is provided by the visual system so we can imagine an egocentric reference frame that is fixed to the retina of the eye, i.e. in a retinocentric frame of reference. However, because the eyes can move in the head and the head on the body, one needs to integrate the retinal information with information about the orientation of these body parts to obtain a description of the position relative to the body. Egocentric coding of movement endpoints could therefore involve transformations of the target position into an eye-centered, a head-centered and a body-centered reference frame (Carrozzo et al. 1999, McIntyre et al. 1998, 1997). Moreover, goal-directed arm movements require additional sensorimotor transformations because the visual information about target location needs to be transformed into a pattern of muscle activity that brings the hand to the target. Because this involves receptors that sense muscle stretch, elbow joint angles and shoulder angles, one can also imagine reference frames fixed to these limb segments, i.e. the shoulder and the upper arm (Flanders et al. 1992, Soechting et al. 1990, Soechting and Flanders 1989a).

Neural codes for visuomotor control

The idea that the visuomotor system may utilise the above-mentioned spatial descriptions to encode motor commands is supported by studies that show correlates between the characteristics of the hypothesised reference frames and activity at the neural level (for reviews see Cohen and Andersen 2002, Burnod et al. 1999, Lacquaniti and Camaniti 1998, Lacquaniti 1997, Jeannerod 1997). These studies show that the neural circuitry for visuomotor performance, mainly identified in primates, encompasses a large number of both subcortical and cortical areas and that there is no area uniquely responsible for reaching.

The functional specialisation and hierarchy of areas in the network for reaching is not clearly segregated. Electrophysiological studies show that reach-related signals, like retinal target location, orbital eye orientation, head orientation and limb position and movement direction modulate the activity of neurons in multiple parts of this distributed network. For instance, it is well known that the superior colliculus is involved in the control of eye and head movements, but recent studies show that a substantial population of cells in this oculomotor structure is also devoted to the control of arm movements (Stuphorn et al. 2000, Kutz et al. 1997, Werner et al. 1997a, 1997b). Stuphorn et al. (2000) found that part of the neurons in the superior colliculus discharge only when the monkey reaches for targets at specific retinal coordinates.

The activity of neurons in the visuomotor network is often modulated by more than one signal. The properties of these neurons might indicate that they are involved in the coding of spatial information in multiple frames of reference. A merging of signals is required to represent information from one reference frame into another and may reflect reference frame transformations. Anderson et al. (1985) identified cells in the parietal cortex of which the activity in response to retinal stimulation was gain modulated by shifts in the orientation of the eye. The output of a population of gaze-dependent neurons with receptive fields in different retinal locations could converge to form an eye-centered representation (Xing and Andersen 2000, Zipser and Andersen 1988). Galletti et al. (1993) found that for the majority of neurons in the parieto-occipital cortex the receptive field shifted with gaze. However, for some of the cells the receptive field remained anchored to the same spatial location regardless of eye orientation so that they only respond to stimuli placed at certain positions relative to the eye (Galletti et al. 1993). The parietal cortex could, therefore, be involved in the transformation of retinal visual information into eye-centered visual information.

Neurons whose activity is changed by eye orientation signals have been reported in both parietal (Battaglia-Mayer et al. 2000, 1998, Cohen and Andersen 2000, Snyder 2000, Batista et al. 1999, Ferraina et al. 1997, Galletti et al. 1993, Anderson et al. 1985) and frontal areas (Cisek and Kalaska 2002a, Boussaoud and Bremmer 1999, Schlag-Rey et al. 1992) of the visuomotor network. To obtain a head-centered representation of visual information one needs to integrate both eye orientation signals and head orientation signals. Neurons that combine these signals through gain modulation have been found in the lateral intraparietal area (Snyder et al. 1998, Brotchie et al. 1995). Few neurons have been found that code positions in explicit head-centered coordinates. Populations of neurons whose activity is modulated by eye orientation and head orientation could constitute a distributed head-centered representation (Snyder 2000, Xing and Andersen 2000).

Neurons with above-mentioned properties that are also activated during arm movements could be involved in the specification of movement endpoints in egocentric coordinates. Batista et al. (1999) and Buneo et al. (2002) report neurons with these properties. Buneo et al. (2002) found that some neurons in area 5 strongly code target locations in retinotopic coordinates but are gain modulated by the initial position of the hand. These authors suggest that this area could code both the target position and hand position in retinotopic coordinates to obtain a difference vector for movement encoding in egocentric coordinates (Buneo et al. 2002). Neurons in area 5 also respond to other somatosensory stimuli and their receptive fields may enclose both the trunk and the shoulder (Burbaud et al. 1991). In a study of Lacquaniti et al. (1995) monkeys were trained to make arm movements to visual targets in different part of the workspace. The activity of most neurons in area 5 was related to the position of either the target or the hand relative to the head and body, irrespective of the starting position of the hand and, therefore, the direction of the movement. The fact that the activity was related to the target position, although this had not yet been reached, suggests that these neurons are involved in encoding desired end positions.

There is also substantial electrophysiological evidence for vectorial coding of movement direction in allocentric coordinates. Parietal areas connect through the premotor cortex to the primary motor cortex. Neural activity in these areas is modulated by several reach-related parameters (Boussaoud and Bremmer 1999, Scott et al. 1997). Recordings of whole populations of cells have revealed a vector code of movement direction (Cisek and Kalaska 2002a, 2002b, Messier and Kalaska 2000, Wessberg et al. 2000, Camaniti et al. 1990, Georgopoulos et al. 1988, 1983, Kalaska et al. 1983). The activity of many neurons at these sites is directionally tuned, in that activity is highest for a given movement direction (‘preferred direction’) and decreases gradually with increasing angles between the preferred direction and the direction of actual movement. Each of these neurons could contribute a vector in its preferred direction with an amplitude proportional to its level of activity so that the sum of these vectors (i.e. the population vector) points in the direction of the movement.

Identifying frames of reference

The electrophysiological studies mentioned in the previous section show that multiple spatial descriptions of target, hand and movement direction exist in the brain. These spatial descriptions may correspond to the hypothetical representations of end positions of goal-directed movements that have been proposed in psychophysical studies. One approach used in these studies has been to characterise the errors in final hand positions to identify the reference frames (McIntyre et al. 2000, 1998, 1997, Carrozzo et al. 1999, Gordon et al. 1994, Soechting and Flanders 1989a, 1989b). In this approach, one assumes that the endpoint errors arise from errors in the encoding of positions within the frames of reference, or from errors in the transformation of positions from one reference frame into another. There are two types of endpoint errors for repeated movements to the same target: constant (or systematic) errors, representing the deviation of the mean endpoint from the target, and variable errors, representing the distribution of endpoints around the mean. Constant errors may reflect biases in the parameters that are specified relative to a particular reference frame. Variable errors may result from noise in the specified parameters. Differences in the precision of the encoding of independent parameters will result in patterns of endpoint errors that have a larger distribution in one direction than another (Gordon et al. 1994). Such anisotropic patterns of endpoint errors are invariant relative to axes of the reference frame. Thus, a lack of correlation between endpoint variability along the different coordinate axes of a certain reference frame suggests that this reference frame is used to encode the movement endpoint.

The analysis of endpoint errors may help to determine what spatial information is used to specify end positions of arm movements. The approach is however complicated by the fact that the specification of movement endpoints is susceptible to errors added at multiple levels of visuomotor control. This may result in ambiguous patterns of endpoint errors and may conceal the actual transformations that are involved (McIntyre et al. 2000). We therefore study movement endpoint control with a method that accounts for the various (unknown) sources of errors. It relies on the assumption that when the visuomotor system is confronted with an altered relationship between visual and kinaesthetic information it adjusts its parameters to compensate for the mismatches (Hay et al. 1971). Possible sources of error added at different levels will affect the endpoints before and after adaptation in a similar manner. By analysing the changes in endpoints after adaptation to the new relation one tries to characterise the modifications. The spatial features of these modifications may help to determine how movement endpoints are represented. The earliest experiments on adaptation to mismatches between vision and kinaesthesia reveal the basic paradigm that will be used in the present experiments. Its principles are described below.

Visuomotor adaptation

There is a long tradition of experiments in which the relationship between visual and kinaesthetic information is manipulated with wedge prisms (for reviews see Welch 1986, 1978). Placing prisms before the eyes displaces the visual information relative to the kinaesthetic information (see figure 1.1). As a consequence, when reaching for an object the subject initially reaches in the direction of the displacement. These errors are, however, quickly overcome. Reaching errors occur again upon removal of the prisms, but this time in the opposite direction of the perturbation, showing that the subject has adapted to the changed relationship. The latter movements are usually performed without visual feedback to prevent corrective movements and compared with movements without feedback performed before exposure to the discrepant information.

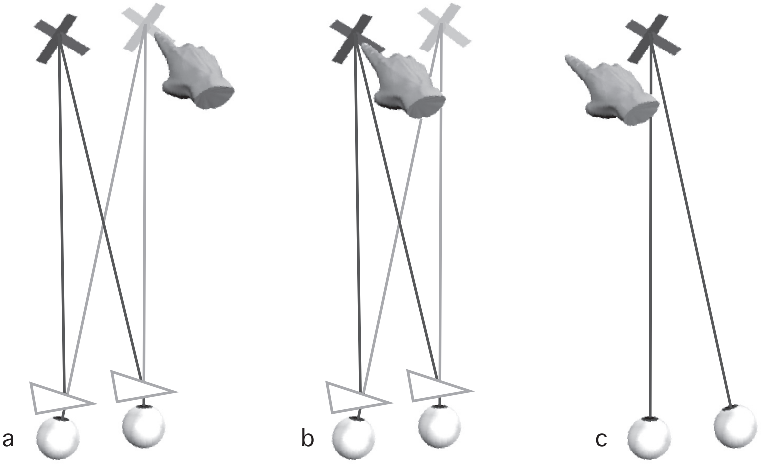


Figure 1.1 *A schematic representation of the principle of prism adaptation. a) Prisms placed in front of the eyes displace the visual image (grey cross) of a target (black cross) so that reaches initially deviate in the direction of the displacement. b) During prolonged exposure to the effects of the prisms the errors are reduced. c) After removal of the prisms subjects point in the direction opposite to the displacement, showing that they adapted to the perturbation.*

Wearing prisms could influence several components of the visuomotor system. The adaptation could involve changes in vision, changes in kinaesthesia or changes in the sensorimotor transformations that link vision and kinaesthesia. Moreover, kinaesthetic adaptation could occur at the level of the wrist, elbow, shoulder, neck or eye muscles (the latter is, however, often considered as visual adaptation so that the distinction between the types of adaptation is not absolute), so that there are many potential reference frames or sensorimotor transformations of which the parameters could be altered (e.g. at the level of the eyes, head, shoulder etc). As with the analysis of endpoint errors, one can infer the parameters in which the movement endpoints are represented if the parameters are specified independently from each other. Finding that the spatial characteristics of the changes in endpoints are invariant relative to one reference frame, but not relative to others, could indicate that the visuomotor system altered parameters that are specified relative to this reference frame. With use of prisms one is, however, limited in the types of perturbations to which a subject can be exposed so that one is also limited in the adjustments that one may expect. The studies described in this thesis are therefore done with use of an experimental setup that enabled us to control the visual information about arm movements presented to the subjects, and to expose subjects to a much wider diversity of perturbations of visual feedback.

General methods and outline of the thesis

The studies presented in this thesis investigate the motor commands that generate arm movements to visual targets and how sensory information used to encode these programs is represented. With the above-mentioned concepts and paradigms in mind, we evaluate subjects' ability to align vision and kinaesthesia under different conditions and constraints. To avoid biases caused by subjects' proficiency at using certain types of tools or dealing with tasks that could bring about stereotyped responses we designed a simple task that in its abstract form required moving the hand to a position in space. In the experiments, the subjects held a cube in their hand that they had to align with a visual simulation of such a cube. The simulated cube was presented by way of a mirror that prevented subjects from seeing their hand and the real cube (see figure 2.1). In some of the experiments subjects received feedback about their movements by way of another simulated cube that moved along with the real one. This feedback could be perturbed in different ways so that we were able to investigate the adaptive responses to different kinds of mismatches between the visually and kinaesthetically perceived position of the real cube. We analysed the variability in subjects' performance and their adaptive responses to perturbations of visual feedback to identify the spatial parameters used by visuomotor control. All analyses were done on measurements of the endpoints of movements that were performed without visual feedback.

In chapter 2 we address the question whether the nervous system uses the initial hand position to plan the movements of the arm to a visual target as a distance and extent of the required displacement. We evaluate the spatial dispersion of movement endpoints in terms of variability in the encoding of intended final positions and in terms of variability in the encoding of vectorial displacements to determine whether the endpoints were position coded or vector coded. Chapter 3 presents an experiment in which we assess whether the magnitude of an adaptive response to a mismatch between vision and kinaesthesia is independent from the variability in visual-kinaesthetic alignment we observed in chapter 2. At some locus in the visuomotor system the sensory discrepancy needs to be detected otherwise no compensation mechanisms will be recruited. The detectability of the mismatches depends on the size and direction of the mismatch, because the precision of the visual and kinaesthetic information differs for different directions from the body. This may affect the magnitude of adaptation to perturbations in different directions. In Chapter 4 we deal with the adaptability of the visuomotor system to different types of perturbations. Whether one adapts to these perturbations will depend on the properties of the internal parameters used by the visuomotor system. We investigate adaptation to translation, rotation and expansion of visual feedback and examine whether the adaptive responses, and therefore the modified parameters, are linked to the arm that was exposed to the perturbed visual feedback. In the study described in chapter 5 we specifically investigate whether one adjusts parameters specified at the level of the eyes or at the level of the shoulder by exposing subjects to visual feedback that was rotated relative to the eyes or shoulder.

Chapter 2

Endpoints of arm movements to visual targets

Reaching out for objects with an unseen arm involves using both visual and kinaesthetic information. Neither visual nor kinaesthetic information is perfect. Each is subject to both constant and variable errors. To evaluate how such errors influence performance in natural goal-directed movements we asked subjects to align a real 5-cm cube, which they held in their hand but could not see, with a three-dimensional visual simulation of such a cube. The simulated cube was presented at one of four target locations at the corners of an imaginary tetrahedron. Subjects made successive, self-paced movements between these target locations. They could not see anything but the simulated cube throughout the experiment. Initial analysis of the spatial dispersion of movement endpoints demonstrated that the major source of errors under these conditions was visual. Further analysis of the relationship between variability of the starting positions and endpoints showed that the errors were primarily in judging the endpoint, rather than the direction or amplitude of the required movement vector. The findings support endpoint control of human goal-directed movements.

Adapted from: JJ van den Dobbelsteen, E Brenner, JBJ Smeets (2001) Endpoints of arm movements to visual targets. *Experimental Brain Research* 138, 279-287.

Introduction

In daily life we come across many tasks that require reaching to, manipulating and displacing objects. In spite of the apparent ease with which we perform these simple motor tasks, the control of such targeted movements is rather complex. Although this issue has received considerable attention in both psychophysical and neurophysiological studies (for a review, see Lacquaniti and Caminiti 1998) the principles for controlling the movements are still largely unknown. A simple movement could either be controlled in terms of the intended endpoint (position coding; Polit and Bizzi 1979), or in terms of the required displacement from the initial arm posture (vector coding; Desmurget et al. 1998, De Graaf et al. 1996, Bock and Eckmiller 1986). In both cases it has been suggested that the coding is in terms of distance and direction (Rosenbaum 1980, Georgopoulos 1991). The endpoints of movements are thought to be coded as either the target's distance and direction relative to the body (Flanders et al. 1992) or the distance and direction of the required movement of the hand (Gordon et al. 1994).

A number of different techniques have been used to investigate the way goal-directed movements are controlled. One approach is to characterise the endpoint distributions of repetitions of the same intended movements. Higher variability in the distance from the subject than in the orthogonal direction suggests that errors in the intended endpoint play an important role (Carrozzo et al. 1999, McIntyre et al. 1998, 1997, Berkinblit et al. 1995, Flanders et al. 1992, Soechting and Flanders 1989a, 1989b). Similarly, greater variability along the axis of movement than along the orthogonal axis suggests that errors in the intended displacement play an important role (Messier and Kalaska 1999, 1997, Vindras and Viviani 1998, Gordon et al. 1994). Other support for the notion that movements are programmed as the vectorial difference between the initial and final hand positions comes from studies that show that endpoint accuracy is affected by information about the initial hand position (Vindras et al. 1998, Desmurget et al. 1997b, Rossetti et al. 1995, 1994). Moreover, errors for sequential movements accumulate (Bock and Arnold 1993, Bock and Eckmiller 1986).

The analysis of movement endpoints is complicated by the fact that their distributions reflect a combination of localising the target and executing the movement. It relies on both visual and kinaesthetic localisation, each with its own anisotropies (Haggard et al. 2000, Van Beers et al. 1998). Moreover, the experimental procedures often involve removal of vision of the hand to avoid corrections based on simultaneous vision of the hand and the target (Bock 1986, Prablanc et al. 1986, 1979). Occluding the arm removes the information that could be used to keep vision and kinaesthesia in register, allowing them to drift apart (Wann and Ibrahim 1992). In the present study we attempt to separate these influences.

We examine the dispersion of endpoints when the target, but not the hand, is visible throughout the movement. In the experiment, 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. They made self-paced movements between different target locations in a manner that allowed us to separate movement direction from viewing direction and arm configuration. We addressed the question whether the nervous system uses the initial hand position to encode the intended final hand position. We used an analysis that enabled us to evaluate possible effects of drift.

Materials and Methods

Apparatus

Images were generated by 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; 816 pixels × 612 pixels), located in front of and above the subjects' head, and viewed by way of a mirror (see figure 2.1). Subjects saw a three-dimensional rendition of a cube beneath the mirror. They also held a 2-cm-diameter rod attached to a 5-cm cube (total weight: 145 g) in their unseen hand underneath the mirror. They held the rod with their hand touching the cube. Monitor and mirror were tilted 12° to increase the available workspace. The rationale behind using a cube on a hand-held rod instead of a hand-held cube was to reduce the conflict with occlusion that would otherwise arise when subjects fail to see their hand and therefore interpret the visible cube as being in front of the hand. Using liquid crystal shutter spectacles (CrystalEyes 2, weight 140 g., StereoGraphics Corporation, California), alternate images were presented to the two eyes for binocular vision. Images were corrected for the curvature of the monitor screen. A newly calculated image was presented to each eye every 16.7 ms. Standard anti-aliasing techniques were used to achieve sub-pixel resolution.

Sets of active infrared markers were attached to four sides of the real cube and to the shutter spectacles. A movement analysis system (Optotrak 3010, Northern Digital Inc., Waterloo, Ontario) registered the positions of these markers to within 0.1 mm at a sample frequency of 200 Hz. To create images with the appropriate perspective, eye position was inferred from the positions of the markers on the shutter spectacles (by eye position we mean eye position in space, not eye orientation in the orbit). This allowed the subject to move his head without introducing conflicts with information from motion parallax. The total delay between a movement of the subject's head and the presentation of the appropriate image was about 16 msec.

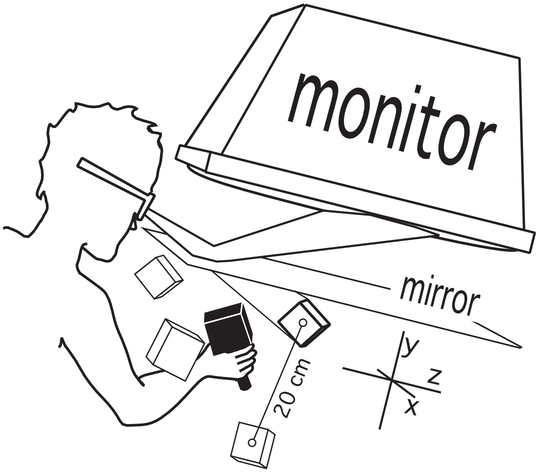


Figure 2.1 *Schematic view of the setup. Subjects stood in front of a monitor holding a cube attached to a rod. The only thing they could see was a three-dimensional rendition of the cube in one of four target locations. They were asked to align the position and orientation of the real cube with the position and orientation of the simulated cube.*

Stimuli

The simulated cube was presented in one of four positions beneath the mirror. These four positions were at the corners of an imaginary tetrahedron (each position was 20 cm from all others). Because the subjects were free to move their head, the distance from eye to target varied across subjects and movements. The overall average distance from eye to target was 44 cm. All target positions were well within reaching distance: the range was 33 to 62 cm. The orientation of the simulated cube was randomised. The luminance of each randomly textured, Lambertian surface of the simulated 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 virtual image of the cube was 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 cube.

Subjects

Eight subjects participated in the experiment, including two of the authors. The local ethics committee approved the use of human subjects for this study. One subject used bifocal spectacles and responded overtly differently to the targets that were presented in his lower visual field. Therefore, this subject was excluded from the analysis. One subject used his left hand. Biases in the proprioceptively perceived position of the hand are known to be mirror symmetric for the left and right arm (Haggard et al. 2000). We thus mirrored the hand and head position data of the left-handed subject in the off-line analysis. There were no evident differences between the data of the left-handed subject, the authors and the other subjects.

Procedure

Subjects were given the cube attached to the rod and asked to hold the rod with their hand touching the cube, so that they could feel the location and orientation of the real cube. They touched the edges of the real cube with their thumb to prevent rotation of the rod within the whole handgrip. They were instructed to move the cube as accurately as possible to a target position indicated by the simulated cube and to keep it there until the simulated cube was presented in another position. They were not only to bring the real cube to the target position, but also to align the orientation of the cube with the orientation of the simulated cube. No instructions were given about the speed of the movement, and the subjects received no feedback about their performance. The experiment started with the subject holding the cube beneath the mirror and the experimenter turning off the light in the room.

The total number of target presentations in the experiment was 120. As the starting position for the movement to the first target was not defined, we only analysed 119 movements. The sequence of target presentations was pseudo-random and consisted of 10 repetitions of the 12 possible movements between pairs of targets (movement configurations). 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 trial started. The whole experiment took less than 8 minutes per subject.

Analysis of movement endpoint variability

Variability was pooled over subjects after subtracting each subject's average movement endpoint (i.e. the constant error) for the relevant movement configuration from the individual movements. This prevented differences in constant errors between subjects from affecting our measure of variability. Endpoint variability is presented graphically as projections of oriented ellipsoids in 3D. For each movement configuration, this ellipsoid was determined by computing the normalised eigenvectors of the Jacobi transformed (McIntyre et al. 1997, Press et al. 1988) 3 × 3-matrix **A**, whose elements are given by:

$$\mathbf{A}_{jk} = \sum_{i=1}^{n} \delta_{ij}\delta_{ik},$$

where the deviation $\delta_i = \vec{p}_i - \overline{\vec{p}}$, $\vec{p}_i$ is the endpoint of movement i along one of three orthogonal axes (rows and columns $j,k \in \{x,y,z\}$) and $\overline{\vec{p}}$ is the mean position over n trials. To determine the size and shape of the ellipsoid we computed the standard deviations of the endpoints along the axes described by these normalised eigenvectors. This is equivalent to taking the square roots of the eigenvalues; $SD_j = \sqrt{d_j / n}$, where d_j is the eigenvalue of the eigenvector j and n the number of trails. Each axis shows the mean ± the standard deviation of the endpoint settings along that particular axis.

The subjects were not constrained in any way. Therefore, head movements and possible variations in the distance of the targets as a result of body sway may affect movement endpoint variability. We evaluated the variability of the location of the eyes in the same manner as we analysed movement endpoint variability to see whether head movements contributed to endpoint variability.

Interpreting the variability

Vector coding

If movements are controlled as vectors, one assumes that two factors contribute to differences in endpoints between repeated movements: variability in the displacement and variability in the starting position of the hand. Moreover, these sources of variability should be independent. To establish whether this kind of encoding is important we constructed new (fictional) movement endpoints by combining observed displacements with observed initial positions of other movements that were made within the same movement configuration. If the two are independent, the variability in the fictional endpoints should be no different from the observed variability (see figure 2.2). Thus, finding a ratio of 3D variability of the measured endpoints and 3D variability of fictional endpoint (the explained variability) close to 100% would support the hypothesis of vectorial coding. As a measure of 3D variability in endpoints we calculated the volume of the ellipsoids that describe the variability in endpoints relative to the mean endpoint. The volume of this ellipsoid is given by: $V = \frac{4}{3}\pi r_1 r_2 r_3$,

where $r_{1,3}$ are half the standard deviations of the endpoints along the axes of the ellipsoid. Each movement configuration was repeated ten times so that all volumes for both the measured endpoints and the fictional endpoints were based on ten settings. We did this for each of the seven subjects and each of the 12 movement configurations resulting in 84 values for the variability of observed endpoints and 84 values for the variability of fictional endpoints.

Position coding

A comparable strategy can be used to determine whether the controlled variable is the desired endpoint. If so, variability in measured endpoints results solely from variability in the specification of the endpoint of the movement. Since variability in

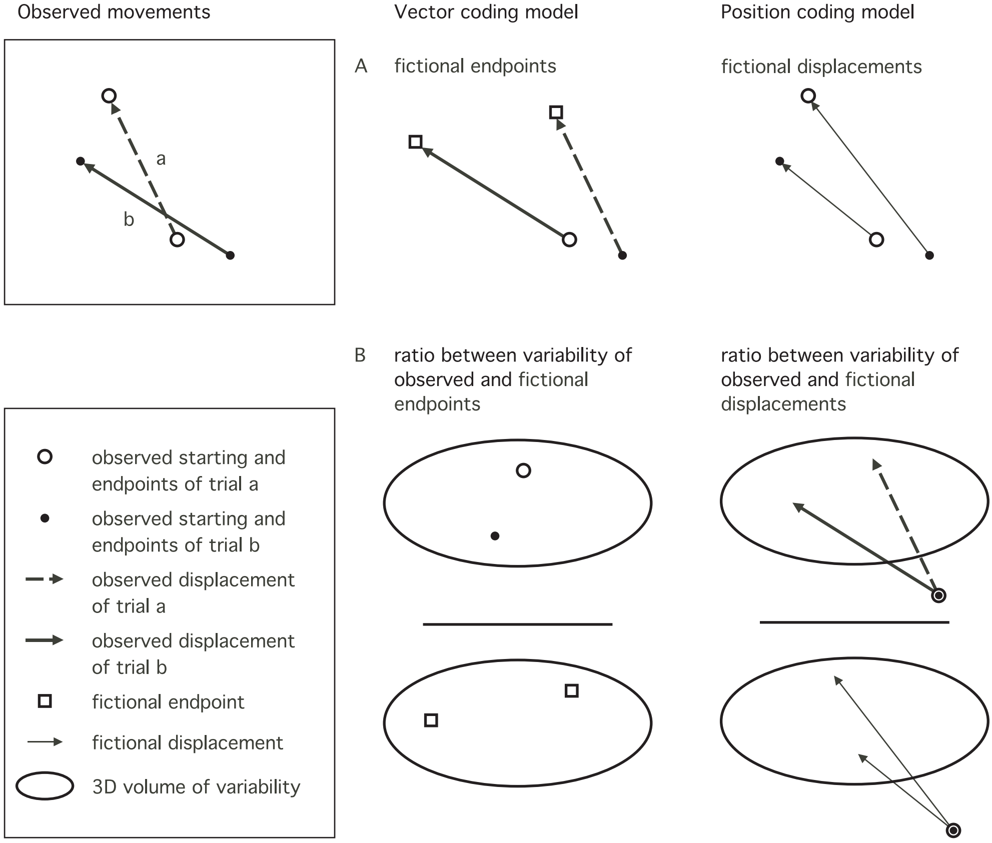


Figure 2.2 *Movement encoding models. The graph shows (using only two trials) the principles behind our method that uses the variability to study movement encoding models. A) Generation of fictional endpoints by combining observed starting positions with observed vectorial displacements from different trials (vector coding model), or of fictional vectorial displacements by combining observed starting positions with observed endpoints from different trials (position coding model). B) Ratios between volume of variability of observed and fictional data. The variability in the displacements (position coding model) was calculated by superimposing the initial positions and determining the variability in the endpoints. To evaluate whether the 3D variability in the fictional data is different from the variability in the observed data, we calculated the ratios of the volumes of the ellipsoids and expressed them as a percentage. We then averaged these values over all subjects and movement configurations.*

the initial position of the hand plays no part in the variability of endpoints, it should be independent of the latter, so that the vectorial displacements measured should be no different from ones constructed by combining arbitrary start- and endpoints. We tested this hypothesis by combining an observed endpoint of one movement with the initial position of one of the other movements to derive new (fictional) vectorial displacements (see figure 2.2). Again we used combinations of start- and endpoints within the 12 movement configurations. The values for both the measured displacements and the fictional displacements were each based on ten settings. As a measure of 3D variability we calculated the volume of the ellipsoids that describe the variability in endpoints of the vectorial displacements relative to the mean endpoint, after superimposing the initial positions. We compared the 3D variability of the observed displacements with the 3D variability of the fictional displacements. The position coding model predicts that the ratio of 3D variability of fictional and observed data (the explained variability) is close to 100%.

Drift

Both the vector coding model and the position coding model assume that no other factors than the controlled variables and the constant errors affect the endpoints of movements. If this is so we could suffice with a much more simple analysis of our data (described in the appendix). However, in the current study, vision of the hand was prevented throughout the entire experiment. The constant errors might have changed over the course of the experiment due to drift between vision and kinaesthesia (Wann and Ibrahim 1992). This could also affect the results of the analysis we used, because we combine starting positions with endpoints of other movements, which took place some time earlier or later. We therefore combined initial positions with endpoint settings that were performed at specific times during the experiment, to evaluate the extent to which drift could have affected the results (also see the legend of figure 2.4).

Orientation matching

In order to minimise systematic effects of bio-mechanical factors (e.g. limb orientation) (Rosenbaum et al. 1999a, 1999b) on endpoint variability we asked subjects to align the orientation of the real cube with the orientation of the simulated cube, which was presented at random orientations. We analysed the errors in orientation matching to see whether the subjects successfully aligned the orientation of the real cube with that of the virtual cube. We limited our analysis to the 3D error in the orientation of the normal to one surface of the real cube relative to the normal to the nearest surface of the virtual cube. This gave one angle for each setting. Due to the symmetry of the simulated cube, the orientation error could not exceed 54.7° (orienting an axis at equal angles relative to three orthogonal axes gives the highest possible angle α, i.e. $\cos\alpha = 1/\sqrt{3}$).

Results

Subjects had no difficulty moving the real cube with their unseen hand toward the (continuously visible) targets. We analysed the spatial distribution of the movement endpoints. In figure 2.3 we show the projections of endpoint ellipsoids and target locations (squares) and the positions of the eyes, in the sagittal, fronto-parallel and horizontal plane. Each thick ellipsoid represents the variability in repeated responses for one of the 12 movement configurations. The two thin ellipsoids within the head show the variability in the position of the eyes over all movements.

The endpoint ellipsoids are close to the squares (i.e. most mean constant errors are less than 3 cm). The largest constant error (3.5 cm) was found for the most distant target. In this case the mean response is shifted toward the head. For most movement configurations the directions of highest variability converge toward the head of the subject (figure 2.3). Extrapolating the axes of highest variability enables us to determine the point in space for which the summed distance from all these lines is minimal. This position is slightly below and to the right of the subjects' eyes. Note that the directions of highest variability are sometimes almost perpendicular to the movement direction (e.g. for the movements from left to right and vice versa) and perpendicular to the variability of the position of the eyes.

Movement encoding

We analysed the variability in our data to see what it can tell us about the principles according to which a movement is encoded. Vector coding predicts that variability in the final hand position is the combined result of variability in the encoding of the displacement and variability in the initial hand position. We generated a collection of fictional endpoints, using observed displacements and initial positions, and contrasted them with the observed endpoints (see figure 2.2). The results are shown in figure 2.4 (filled squares). A value of 100% means that the volume of variability of observed endpoints is equal to the volume of variability of fictional endpoints. Lower values indicate that the observed variability is smaller than the variability of fictional endpoints. The observed variability is less than 30% of the newly synthesised variability, indicating that movements are not determined by independent variability in a vector and an initial position. The explained variability found is the same whether we constructed fictional endpoints from observed displacements and starting positions that were measured few (on average 12) or many (up to 60) trials apart.

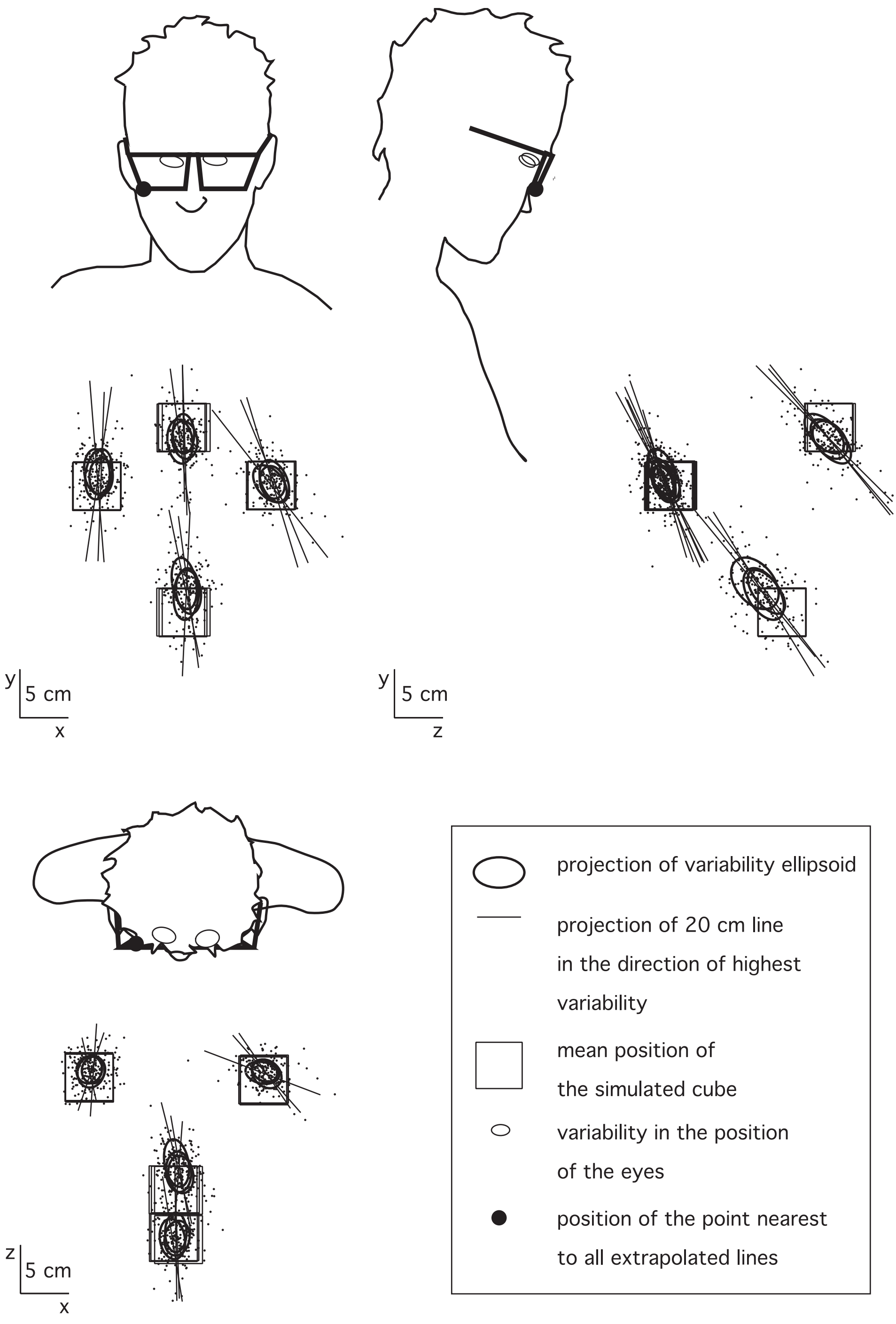

y
5 cm
x
y
5 cm
z
z
5 cm
x
projection of variability ellipsoid
projection of 20 cm line in the direction of highest variability
mean position of the simulated cube
variability in the position of the eyes
position of the point nearest to all extrapolated lines

Figure 2.3 *Movement endpoints. Projections of endpoint ellipsoids and target locations in the sagittal, fronto-parallel and horizontal plane for each of the 12 movement configurations. For each movement configuration, we computed the average positions of both the simulated cube and the real cube relative to the cyclopean eye over all subjects. Squares show the mean location (and the size) of the simulated cube, relative to the observer. Variability of eye position is shown by the two thin ellipsoids. The positions of the targets relative to the eyes show small systematic shifts because subjects turn their head when shifting gaze. The positions of the thick ellipsoids relative to these targets show the constant errors pooled over subjects. The shape and size of these ellipsoids show the variability in the settings. The length of each axis of the ellipsoids is equal to twice the standard deviation along that axis. Lines represent projections of a 20-cm line aligned with the longest axis of each endpoint ellipsoid. The filled circle is the point for which the summed distance from all (extrapolated) lines is minimal. Dots are the projections of movement endpoints of individual movements relative to the overall mean for one movement configuration (i.e. corrected for individual biases by subtracting each subject's mean endpoint for that movement configuration).*

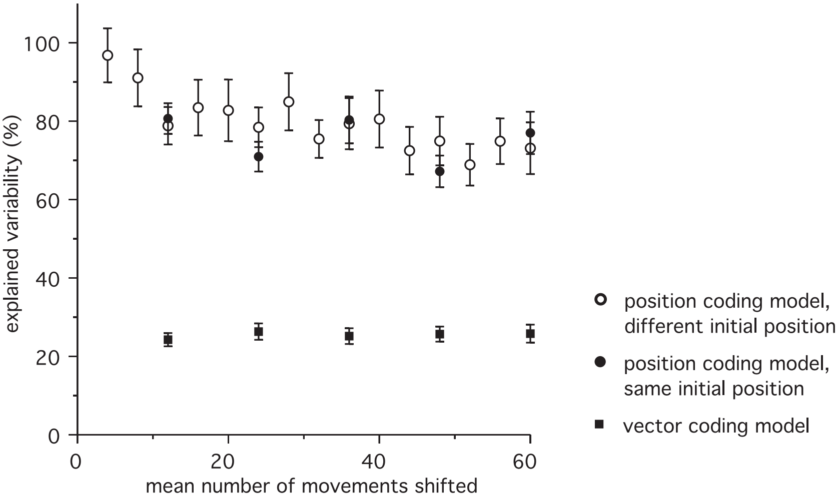


Figure 2.4 *The percentage variability explained by combining components of pairs of movements as a function of the time difference between the movements. For the position coding model the observed starting positions were combined with endpoints of movements that occurred a number of movements later. For the vector coding model the observed starting positions were combined with vectorial displacements a number of movements later. When only movements with the same initial position were considered the average shifts were multiples of 12 movements (filled symbols). Otherwise it was 4 (open circles). The error bars show the standard errors in the explained variability across subjects and movement configurations.*

To evaluate whether only the positions are relevant (position coding) we generated fictional displacements using new combinations of observed initial positions and observed endpoints. According to the hypothesis, variability in the vectorial displacements emerges from variability in encoding of the endpoint, independent of the initial position. As can be seen in figure 2.4 (filled circles), the variability in observed displacements is almost as large as for fictional displacements, suggesting that our data can best be explained by the hypothesis of position coding. However, the explained variability is below 100% indicating that additional sources of variability must have affected the displacements. The percentage tends to decrease with increasing time shifts. One possible factor could therefore be drift, because we combined endpoints with initial positions that occurred earlier in time. We did an additional analysis to see whether the deviation from the predicted value of 100% can be attributed to drift or whether it is related to the starting position of the movement.

In the former analysis, we only combined initial and final positions that were recorded within the same movement configuration. However, if movements are encoded according to the principles of position coding the initial positions are irrelevant, so we can also use combinations of initial and final positions from different movement configurations. Thus, we also generated new vectorial displacements for all 12 movement configurations using the endpoints recorded for each target, instead of the endpoints recorded for each movement configuration. This allowed us to determine the ratio of observed and constructed displacements for trials separated (on average) by multiples of 4 rather than 12. Differences between the results of the latter analysis and the results based on positions recorded within movement configurations would be attributed to the influence of starting position. As shown in figure 2.4, the results are the same whether we used initial and final positions derived from the same movement configuration (filled circles), or combined initial positions with final positions derived from all movement configurations that were directed toward the same target (open circles). Thus, the starting points have no influence on the endpoints. The deviation from 100% explained variability can presumably be attributed to drift. A simple linear regression analysis of the effect of time shifts on explained variability reveals a slight negative slope (-0.34% per number of movements shifted, p=0.004). In table 2.1 we show that explained variability for the position coding model is higher than for the vector coding model for all subjects. Thus, these results also hold at the individual level.

Orientation matching

If one would orient the cube randomly, the chances to make any particular orientation error are asymmetrically distributed. Therefore, interpreting the 3D error in orientation can be difficult. For instance, it is meaningless to simply calculate the

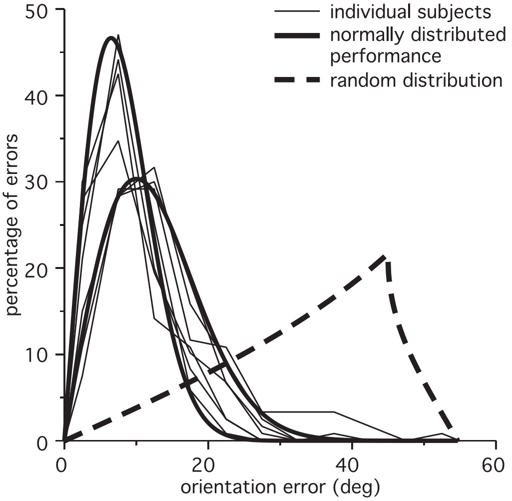


Figure 2.5 *Errors in the alignment of orientation. Due to the symmetry of the cube the orientation errors could not exceed 54°. The dashed line shows how the distribution of errors would look for random performance. This distribution is not flat, due to the unequal probability of obtaining each angular error. Thin lines represent the distributions of errors for individual subjects. The thick bell shaped curves show normally distributed performance with a standard deviation of 12.3° and 14.4°, obtained by multiplying these normal distributions with the distribution for random performance. Performance of individual subjects lies within this range.*

standard deviation of the error. We therefore compared the measured distribution of errors with normal distributions that were multiplied with this asymmetric random distribution. Distributions of orientation errors are plotted for each subject in figure 2.5. This analysis shows that subjects varied the orientation of their hand in accordance with variations in the orientation of the simulated cube.

Discussion

In the present experiment we attempted to assess the way the nervous system controls the endpoint in natural reaching movements to a visual target. Our subjects aligned a cube that they held in their unseen hand with a visual simulation of such a cube. Analysis of the distribution of movement endpoints revealed anisotropic patterns of variable errors. Endpoints were mainly scattered along the line of sight. The origin of the lines of highest variability was shifted a few cm to the lower right of the eyes, in the direction of the effector arm. Thus, visual localisation affected endpoint variability to a higher degree than kinaesthetic localisation. These results are in line with previous studies, which have shown that the accuracy of visual depth perception is particularly low for isolated objects in the dark (Brenner and Smeets

2000, Brenner and Van Damme 1999, Foley 1980, Gogel 1969). However, body-centered distributions of errors have also been found (Carrozzo et al. 1999, McIntyre et al. 1998, 1997, Soechting et al. 1990)

The directions of highest variability were slightly different for the various movement configurations but not related to the direction of movement. This is in contrast with previous reports of spatial dispersions of endpoints that suggest larger variations in movement amplitude than in movement direction (Vindras and Vivianni 1998, Messier and Kalaska 1999, 1997, Gordon et al. 1994). Such findings have been interpreted as evidence for vector coding. However, they can be reconciled with control of final position. Forces that arise when moving against a constraining surface are not necessarily accounted for by a position control system. External forces could induce distortions in the execution of movements (Desmurget et al. 1997a) resulting in a mismatch between the desired state and the actual movement endpoint. Thus, the effects of starting point manipulations do not necessarily relate to variability in coding of a displacement but could be due to non-conservative forces, which add variability in the direction of movement. In our study, the arm movements were unconstrained and we imposed large variations in hand and arm orientation by asking subjects to align the orientation of the cubes. Forcing the subjects to vary limb orientation changes the configuration of the arm and thus gravitational torques and muscle lengths on each setting. Furthermore, it ensures that for each setting subjects produce a hand position and do not reproduce a remembered posture. This presumably gets rid of systematic influences of external forces and anatomical constraints on the subject’s settings, although it may increase total variability.

Implications for movement control

Our results show that the motor system uses only intended final position to control these simple movements. Other studies showed that vision of the hand prior to movement onset improves endpoint accuracy (Desmurget et al. 1997b, Rossetti et al. 1995, 1994), and that errors in the kinaesthetic estimation of the initial arm position are correlated with endpoint errors (Vindras et al. 1998), suggesting that information about the initial position is important too. Such observations imply that the accuracy of targeted movements does not only depend on the goal of the effector, but also on knowledge about its initial state and the starting point. However, we argue that these results do not contradict the idea of position coding. Our reasoning is that the nervous system may use afferent kinaesthetic signals to adjust the motor plan (Smeets 1992). Occlusion of the arm almost instantaneously produces a drift between visual and kinaesthetic information (Wann and Ibrahim 1992). If afference is involved in specifying final positions, correlations between errors in the estimation of initial positions and final positions emerge as a result of lack of correspondence between the visual and kinaesthetic modality. Vision of the hand before movement will improve endpoint accuracy since it enables alignment of the afferent visual and kinaesthetic information.

The same argument holds for the observation that successive errors in pointing at sequentially presented targets tend to accumulate (Bock and Arnold 1993, Bock and Eckmiller 1986). After each pointing movement vision and kinaesthesia are perceptually aligned, even though there is a lack of correspondence (as shown by the presence of pointing errors). The perceptual correspondence may prevent correction of the mismatch between vision and kinaesthesia. If kinaesthesia is calibrated by vision or vice versa, then this should yield error accumulation so that pointing errors are related to initial errors. This idea is supported by a study of Vetter et al. (1999). They showed that introducing a mismatch between visual and kinaesthetic feedback for pointing movements toward a single target induced a corresponding bias in pointing toward other targets. Thus, drift, whether it is induced or spontaneous, will bias endpoint error in sequential pointing movements. Moreover, in that case corresponding errors for starting points and endpoints will leave the movement vectors between the targets unaffected.

Our method enabled us to delineate the effects of drift and starting position on endpoint settings. The results we obtained for the position coding model showed that the subjects' settings were slightly affected by an additional variability factor that developed in time, but did not depend on the starting position. A simple linear regression analysis of the data showed a significant negative slope between the explained variability we obtained for the position coding model and increasing time shifts, which indicates the presence of drift (Wann and Ibrahim 1992). The explained variability for the vector coding model remained unaffected throughout the experiment. Together these findings suggest that the small error accumulation in the subjects' endpoint settings is a result of drift between vision and kinaesthesia. It should be noted here that our method relies on the quantitative comparison of the volumes of observed ellipsoids and fictional ellipsoids and not directly on the comparison of orientations of the ellipsoids. The orientations of observed and fictional ellipsoids could have been used to test the position coding model. However, the orientation of an ellipsoid can only be characterised reliably if one eigenvalue is significantly different from the other two. We tested whether this was so for all ellipsoids using a χ^2 test described by Morrison (1990, p.336) and McIntyre et al. (1997). For 14 of the 84 ellipsoids (16.7%) the largest eigenvalue was significantly different from the other two. For 13 of the 84 ellipsoids (15.5%) one of the eigenvalues was significantly shorter than the others. Thus, two-third of all distributions is isotropic and cannot be evaluated in terms of orientation. We therefore relied on the increased volume that is expected instead.

Abrams et al. (1994, 1990) reported evidence for a hybrid model. They showed that the type of eye movement (pursuit or saccade) toward the target affected the initial phase but not the end of the arm movement (Abrams et al. 1990). Accordingly, they proposed that different parts of the movement involve different types of specification. Distance and direction of the required movement vector may be used for planning the initial phase, while the final phase may be based on a specification of the desired endpoint. The latter phase compensates for variability in the first part and exhibits properties corresponding to the tendency to correct errors that was described by Bock and Arnold (1993) for sequential pointing. In our experiment, subjects made slow, self-paced movements toward the target positions, which gave them ample time to make corrections. Therefore, an alternative explanation of our findings is that error correction based on endpoint compensated for errors related to the direction of movement. If this is so, preventing subjects from making corrective movements by increasing the required movement speed should affect the final endpoints. Adamovich et al. (1994) investigated the effect of movement speed on pointing toward remembered visually defined targets. They found that neither constant nor variable pointing errors increased with higher arm velocity. However, this could mean that subjects make no corrections for movements toward remembered targets, while they do for continuously visual targets, or that they still had enough time to make corrections (Adamovich et al. 1999, 1994).

Studies on the cortical representations of arm movements also show a variety of frames of reference. Several brain areas are involved in the initiation and control of reaching. Electrophysiological recordings in the motor cortex of the behaving monkey reveal correlations between a population vector formed by many neurons and the movement of the arm (Georgopoulos et al. 1988, 1983); the direction of movement corresponds to a vector, coded by a population of cells on the basis of the preferred direction and the change of activity of individual cells. However, vectorial coding by a neural population implies that patterns of neural activity should be the same for movements of equal length along parallel directions but from different initial positions. Caminiti et al. (1990) studied the effects of workspace on directional tuning for reaching movements and showed that neural activity differs for similar movements but different starting points. This may indicate that the movements were encoded relative to the body rather than relative to the starting position of the hand. Further, the activity of many cells in various areas of the visuomotor pathways that are involved in reaching is modulated by the orientation of the eye, head and gaze (Stuphorn et al. 2000, Boussaoud and Bremmer 1999, Andersen et al. 1995) and could be devoted to the coding of endpoints in egocentric coordinates.

In summary, the simplest explanation of our findings is that intended final positions rather than intended displacements guide natural movements toward visual targets.

The effects of (information on) initial position on endpoint accuracy that have been reported can be explained by either drift or non-conservative external forces.

Appendix

The analysis we presented in this article to evaluate the vector and position coding model is a refined version of the following analysis. Given a population of vectors formed by the sum or difference of pairs of vectors drawn from two independent populations, the standard deviation of the sum or difference is equal to the root of the summed squared standard deviations of the two component populations. We can test whether this is so for both models by comparing the following variables: SD_i = 3D variability of initial positions, SD_f = 3D variability of final positions, SD_d = 3D variability of displacements. If the initial position and displacement are controlled independently, then $SD_f = \sqrt{SD_i^2 + SD_d^2}$ and therefore $SD_f > SD_d$. Conversely, if the initial position and final position are controlled independently, then $SD_d = \sqrt{SD_i^2 + SD_f^2}$ and therefore $SD_d > SD_f$. In table 2.1 we show the mean values (averaged over movement configuration) for the 3D variability of final positions and displacements for each subject. SD_d is higher than SD_f for all subjects in agreement with the results we obtained with our initial analysis.

subject	1	2	3	4	5	6	7
vector coding model (%)	30.2	15.1	27.2	29.7	25.6	19.7	28.8
position coding model, same initial position (%)	57.9	134.2	50.3	99.4	60.1	91.0	69.3
position coding model, different initial position (%)	47.7	104.3	56.4	128.3	58.1	87.2	73.5
3D variability of final positions (cm^3)	0.9	2.8	1.2	0.5	2.3	2.7	0.3
3D variability of displacements (cm^3)	1.5	7.8	2.3	1.2	3.9	7.5	0.6

Table 2.1 *Individual measures for various variables. The percentages of explained variability were calculated for a shift of 36 movements. The 3D variability was computed as the volume of the variability ellipsoid, and averaged over movement configuration.*

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).

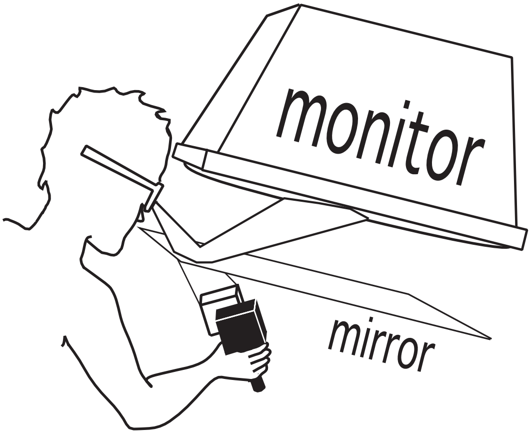


Figure 3.1 *Schematic view of the setup. Subjects stood in front of a monitor holding a cube attached to a rod. In the threshold experiment they had to indicate the direction in which the visual feedback about the real cube (a simulated solid cube which they saw via the mirror) was perturbed. In the 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.

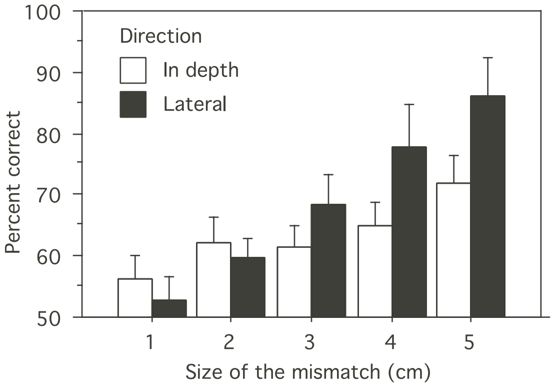


Figure 3.2 *Results of the Threshold experiment. Means and standard errors of the eight subjects' percentages.*

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.

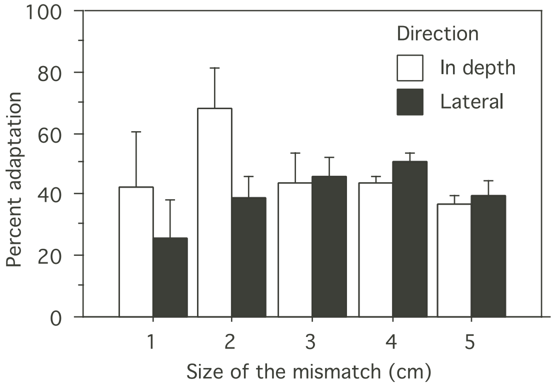


Figure 3.3 *Results of the adaptation experiment. Means and standard errors of the twelve subjects' percentages. The percentage adaptation was about 40%, independent of the amplitude and direction of the mismatch.*

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.

Chapter 4

Adaptation of movement endpoints to perturbations of visual feedback

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 kinaesthesia would depend on the type of perturbation, being largest when the perturbation can be generalised within egocentric frames of reference. To test this prediction we asked subjects to align a real 5-cm cube 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. 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 generalised 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.

Adapted from: JJ van den Dobbelsteen, E Brenner, JBJ Smeets (2003) Adaptation of movement endpoints to perturbations of visual feedback. *Experimental Brain Research*, in press.

Introduction

Reaching for a visual object requires complex transformations to link visuo-spatial information to the muscle activation that will move the hand to the object's location. Integration of visual information about the objects with kinaesthetic 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 frame of reference, a shoulder-centered frame of reference, and so on (Carrozzo et al. 1999, McIntyre et al. 1997, Flanders et al. 1992, Soechting et al. 1990, Soechting and Flanders 1989a). Such transformations are under adaptive control, as illustrated by the ability to generate appropriate motor behaviour 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 kinaesthetic perception of location. Adaptation is the process of re-aligning the two so that visual information is again transformed into appropriate motor commands.

The mechanisms by which adaptive re-alignment gives rise to new visuomotor relationships are not yet clear. Presumably, adaptation is a kind of 'best fit' re-alignment 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 kinaesthesia but will result in a generalised change in the responses of the subject. Wearing prisms could influence visuo-motor transformations at several or multiple levels (Wallace and Redding 1979, Welch et al. 1974). For instance, the adaptation induced by wearing prisms could involve changes in visual localisation (Foley 1974), mediated by changes in the perceived direction of gaze (Craske 1967, Kalil and Freedman 1966). It could also involve changes in proprioceptive localisation of the arm (Taub and Goldberg 1973, 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 kinaesthetic information, without changing visual and kinaesthetic localisation (Kitazawa et al. 1997, Redding and Wallace 1996, Rossetti et al. 1995).

The fact that the same type of 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 mismatches in visuo-kinaesthetic alignment. For example, providing continuous visual feedback during exposure, rather than at just the end of each movement, may alter the correction mechanisms (Redding and Wallace 1996, Choe and Welch 1974). The exact spatial characteristics of the perturbation may also affect what components will change. 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%). Mismatches induced by prisms could be interpreted as errors in judgements of either eye, or of head orientation or, of arm posture. Mismatches induced by concave lenses 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. The paradigm is to use 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 generalisation 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 generalised over different target positions. This generalisation 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. 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 hypothesise 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 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 generalise 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 visuo-kinaesthetic alignment would therefore 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 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 4.1). 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).

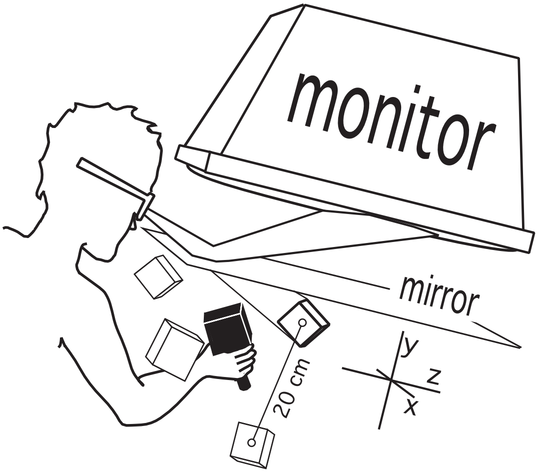


Figure 4.1 *Schematic view of the setup. Subjects stood in front of a monitor holding a cube attached to a rod. They were asked to align this cube's position and orientation with the position and orientation of a target cube (a simulated wire frame which they saw via the mirror). Four possible positions 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.*

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 sub-pixel 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 msec.

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 figure 4.1). 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 randomised 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 post-veridical test phase, a perturbed feedback phase and a post-perturbation 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 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 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 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.

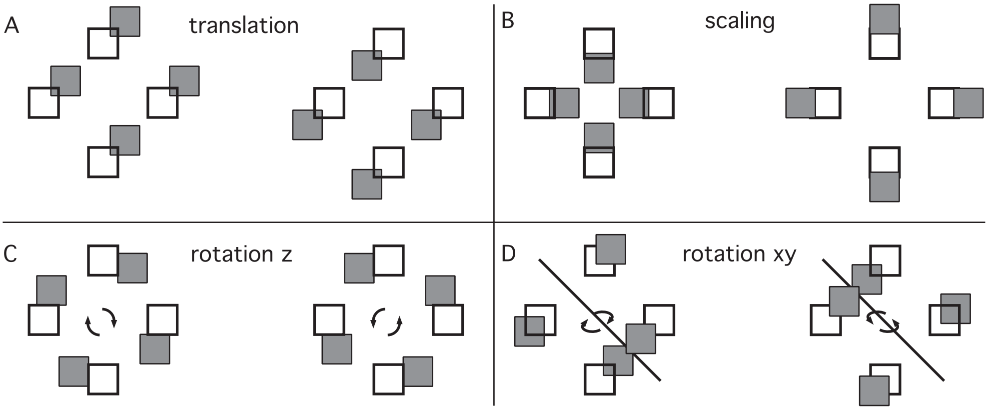


Figure 4.2 *Projections of the perturbations in the xy-plane (see figure 4.1). Open squares show the four target positions that were used in the test phases. Shaded squares indicate where the feedback cube would be if the real cube were aligned with the target cube. The 3D distance between the real cube and its feedback was always 5 cm in this situation.*

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 (2 of the 8 conditions), a scaling (2 conditions), and two types of rotation (4 conditions). All perturbations were defined within the Cartesian coordinate system within which we registered the positions of the active markers (see figure 4.1). Figure 4.2 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.

Panel A of figure 4.2 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.

Panel B 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 tetrahedron. 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 tetrahedron. 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.

Panel C 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 tetrahedron, 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. Panel C 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. Panel D 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.

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 post-veridical and post-perturbation 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 minutes per 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. 1999a, 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 randomising 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 post-veridical and post-perturbed 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 post-veridical or post-perturbed 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 post-veridical or post-perturbed 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 post-veridical and post-perturbed 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 post-veridical and post-perturbed test phases. These averages were each based on three movement endpoints. We calculated the adaptation vector ($\vec{a}$) between the average computed for the post-perturbed test phase and the average movement endpoint computed for the preceding post-veridical test phase. We did so for each perturbation, subject and target cube position We defined a compensation vector ($\vec{c}$) as the displacement of the movement endpoint that would re-align 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.

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

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 generalisation of the perturbation (e.g. a translation will be interpreted as an egocentric rotation). Such a generalisation does not exactly mimic the mismatches in visuo-kinaesthetic 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 ($\vec{u}$) we subtracted for each target position the explained adaptation ($\vec{e}$ = mean percentage adaptation × $\vec{c}$) from the adaptation vector ($\vec{a}$) averaged over all subjects. We interpret the length of this difference vector $\vec{u}$ 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 $|\vec{u}|/(|\vec{u}|+|\vec{e}|)$. A large value means that the systematic change in behaviour 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 both phases the target was visible until the hand stopped). Figure 4.3 shows the difference in movement endpoints between the post-veridical and post-perturbation test phase, expressed as percentage adaptation. This is shown for each type of perturbation, both for the session with randomised 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 ($F(3,39) = 66.0; p < .0001$) 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.

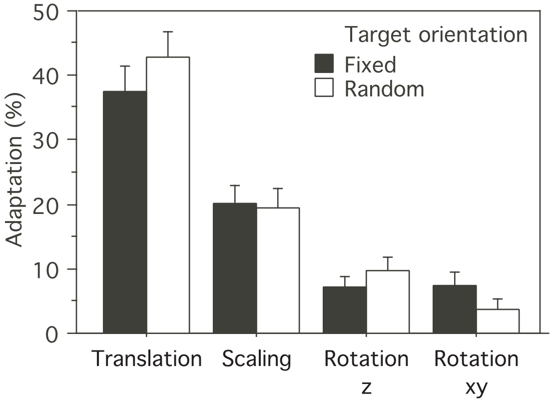


Figure 4.3 *Percentage of adaptation to the different types of perturbations for the two sessions in experiment 1. The error bars show the standard errors in this value across 14 subjects.*

Figure 4.4 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 perturbations 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 4.4 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 figure 4.5). A small relative unexplained response suggests that the way that subjects were interpreting the transformation was appropriate for generalising 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 ($F(3,28) = 39.2; p < .0001$). 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.

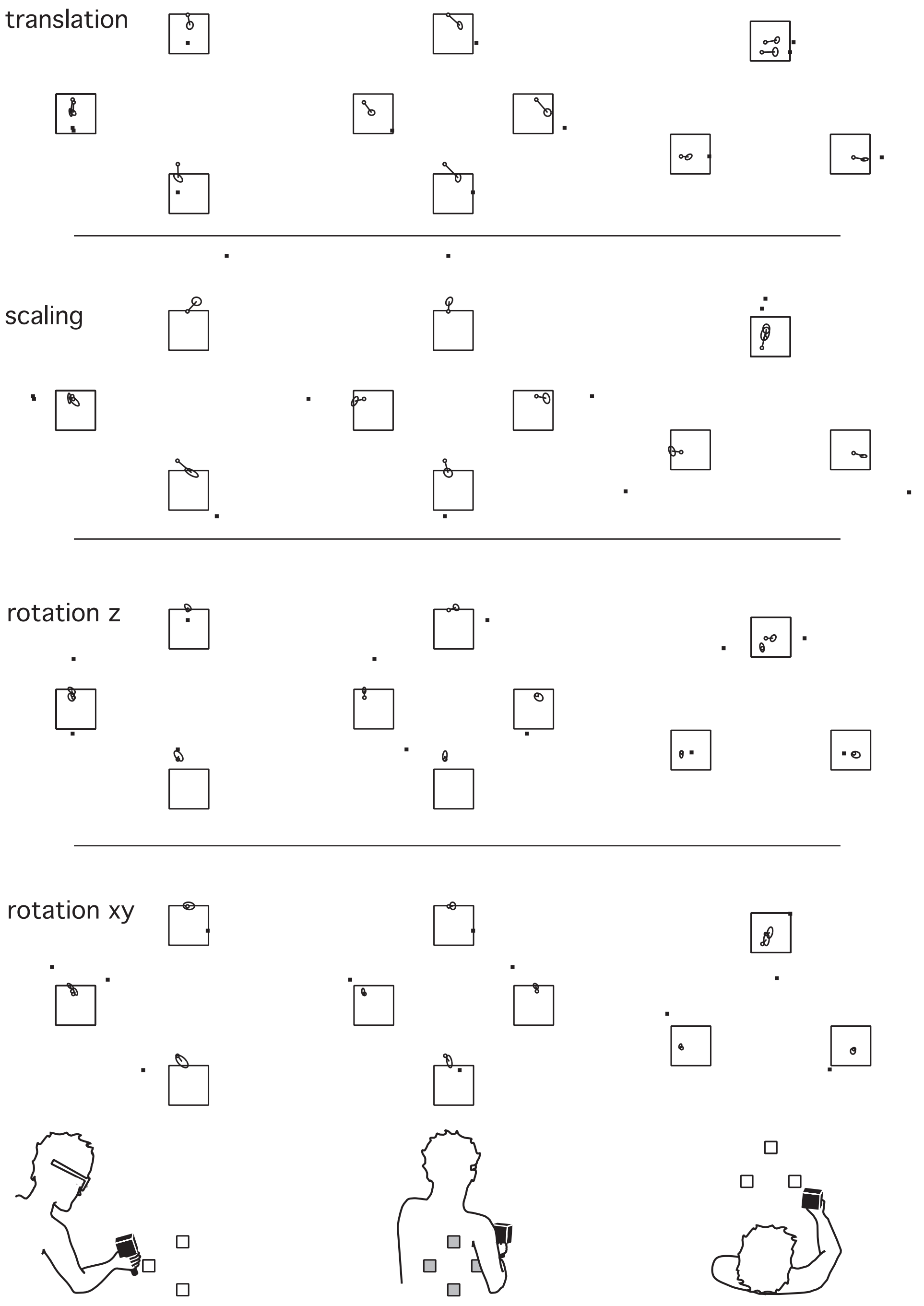
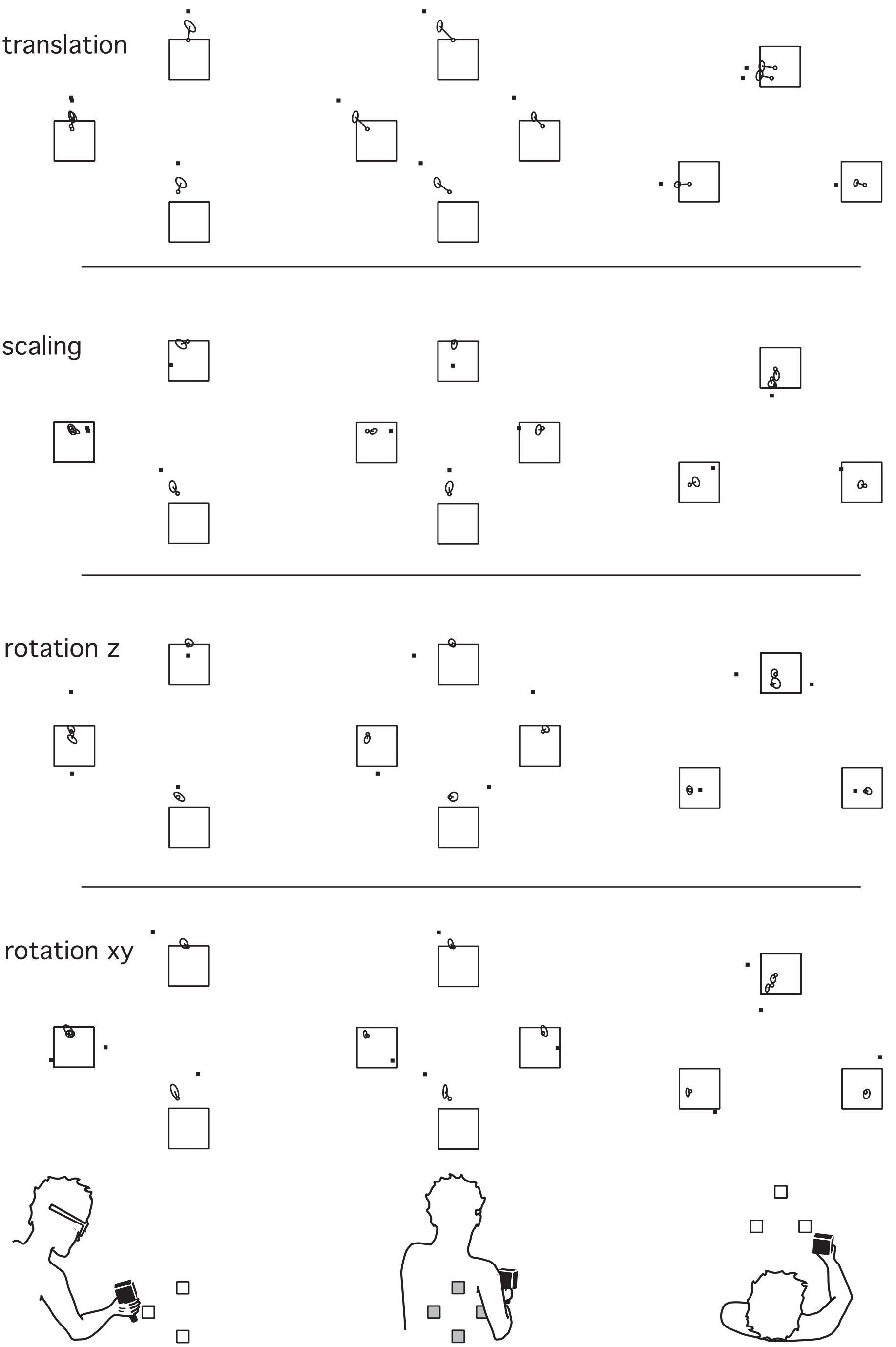


Figure 4.4 *Projections of the averaged movement endpoints in experiment 1 for each type of perturbation, direction of perturbation and target position. Open squares (size=5 cm) show the four targets that were used in the test phases. The small black squares show the position that would correspond to a percentage adaptation of 100%. Circles show the average*



endpoints during post veridical 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.

Figure 4.5 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.

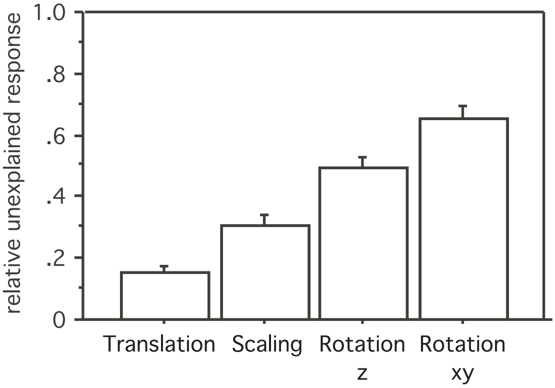


Figure 4.5 *Relative unexplained response for each type of perturbation. The error bars show the standard errors in this value across the direction of the perturbation and the target position.*

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.

Experiment 2

In figure 4.6 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 ($F(3,30) = 25.2; p < .0001$) and the arm that was tested (exposed vs. unexposed, $F(1,10) = 12.2; p < .0057$), as well as an interaction between these variables ($F(3,30) = 4.3; p < .0121$). Post-hoc testing revealed that the unexposed arm adapted significantly less than the exposed arm for translations and rotations, but not for scaling.

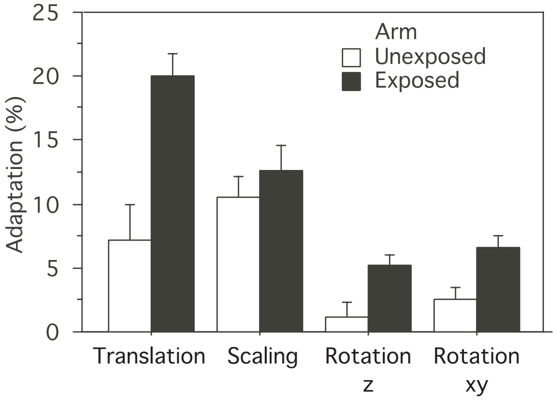


Figure 4.6 *Percentage of adaptation to the different types of perturbations in experiment 2. The white bars indicate the results obtained with the arm that was not used in the feedback phase. The black bars indicate the results that were subsequently obtained with the arm that was used in the feedback phase. The error bars show the standard errors in these values between subjects.*

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 kinaesthetic 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 reanalysed the data of the post-perturbation 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. Figure 4.7 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.

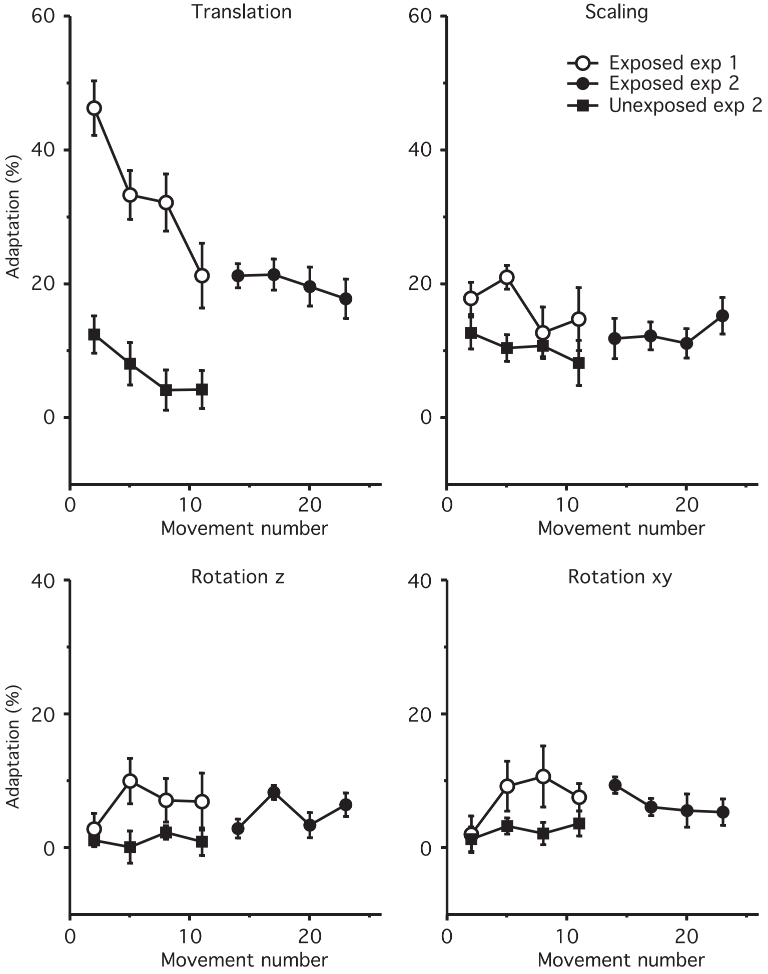


Figure 4.7 *The development of adaptation during the post-perturbation test phase. Results for the four different types of perturbations. Each symbol is the average of three consecutive settings for the 11 subjects who participated in both experiments 1 and 2. Open and filled symbols show the results 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.*

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 this 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 kinaesthesia could be interpreted as an error in the judged direction relative to 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 figure 4.7) suggests that the adaptation is partly a change in the interpretation of the kinaesthetic 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 kinaesthesia 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 figure 4.5). 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 post exposure measurements). Robust after-effects 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 generalisation 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 generalised 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. 2001), 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 figure 4.7). 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.

Re-alignment or context dependent adaptation

The decay of adaptation without exposure to veridical feedback shows that adaptation does not solely consist of re-aligning vision with proprioception (Cunningham and Welch 1994, Welch et al. 1993). If the two were re-aligned 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 re-aligning vision and kinaesthesia 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 post-perturbed test phase. Does exposure to the veridical feedback reset adaptation completely? If no re-aligning occurred during perturbed feedback phases one expects the settings to return to normal during testing after veridical feedback. However, if re-alignment 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 post-veridical test phases following the exposure to the translated feedback, with settings of post-veridical test phases that subjects made before being exposed to the translated feedback. The results are displayed in figure 4.8.

Figure 4.8 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 kinaesthesia 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

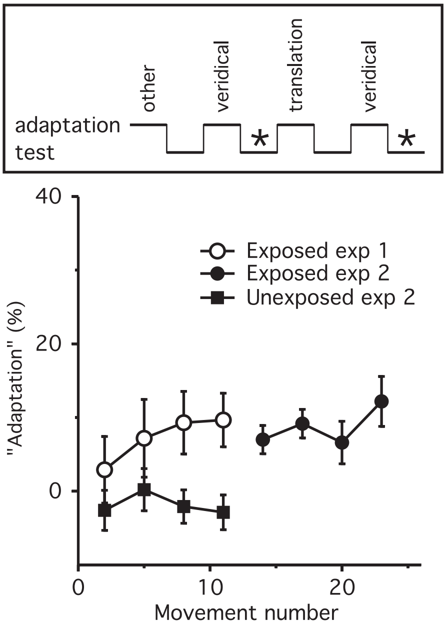


Figure 4.8 *Remnants of adaptation to translation during the post-veridical test phase. 'Adaptation' is the error in the movement endpoints after veridical feedback expressed as a percentage of the perturbation in the previous perturbed feedback phase. Stars in the top panel show which of the test phases 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.*

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 post-perturbation test phase (see figure 4.7). Thus, alignment does appear to take place.

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.

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.

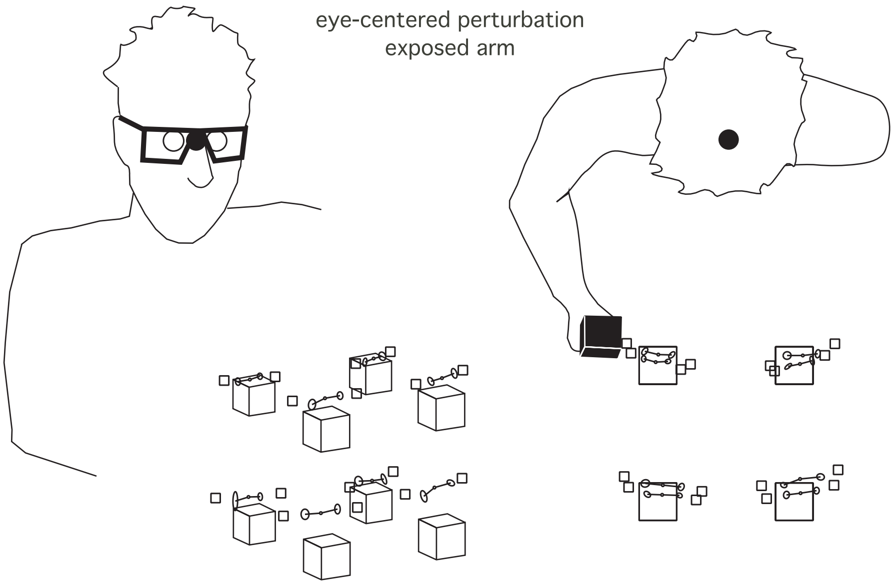
Perturbations

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

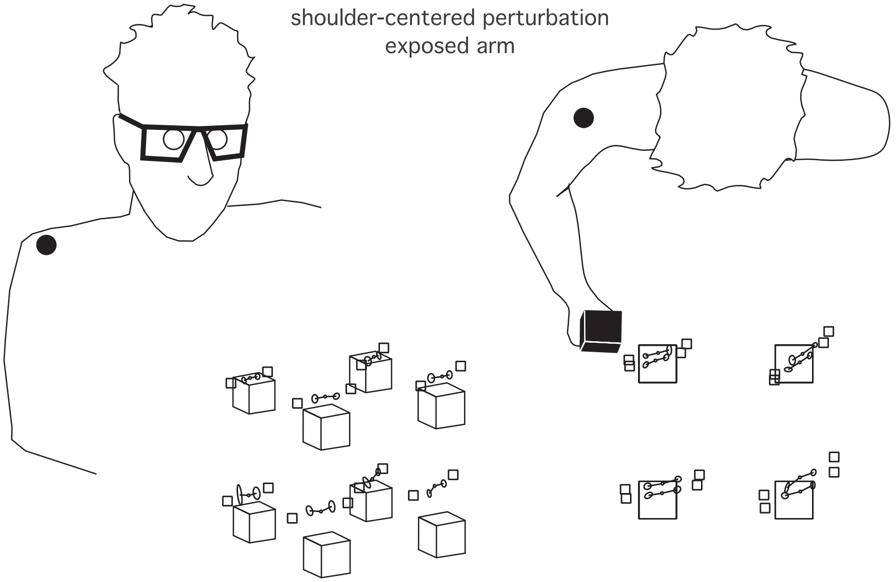

shoulder-centered perturbation
exposed arm

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

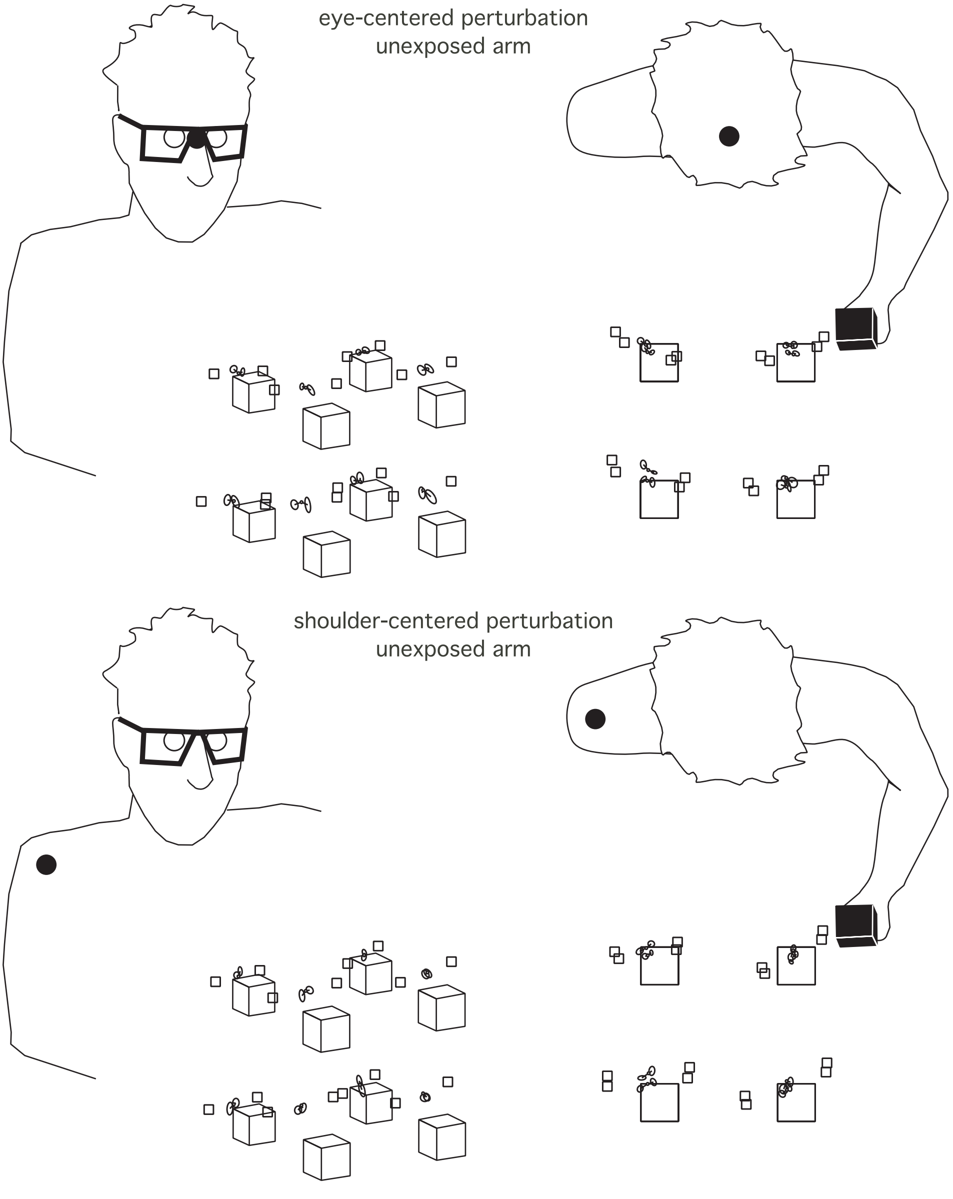


Figure 5.2 *Projections of the average movement endpoints of the unexposed arm. For details see the legend of figure 5.1. Note that the directions of the changes in endpoints after perturbed feedback (lines through ellipses) do not always point toward the small squares. This means that the direction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

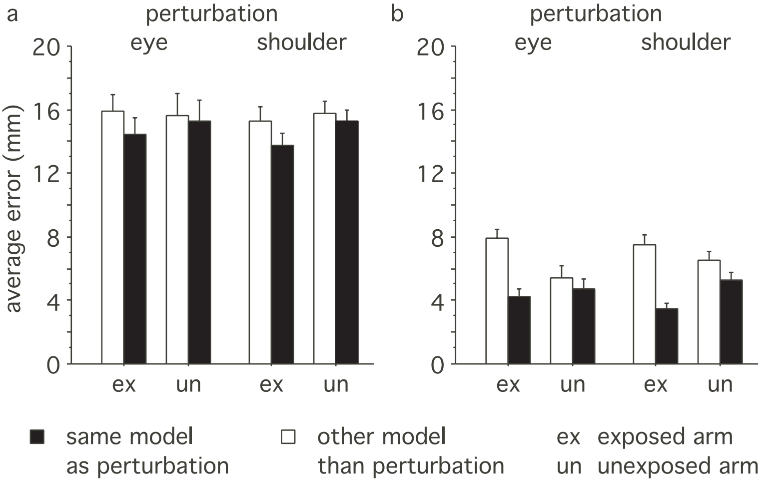


Figure 5.3 *Average errors: the changes in endpoint that cannot be accounted for by a single rotation around the eye or shoulder. Black bars show the results for the model that corresponds to the perturbation. White bars show the results for the model that does not. a) Average errors of individual subjects (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).

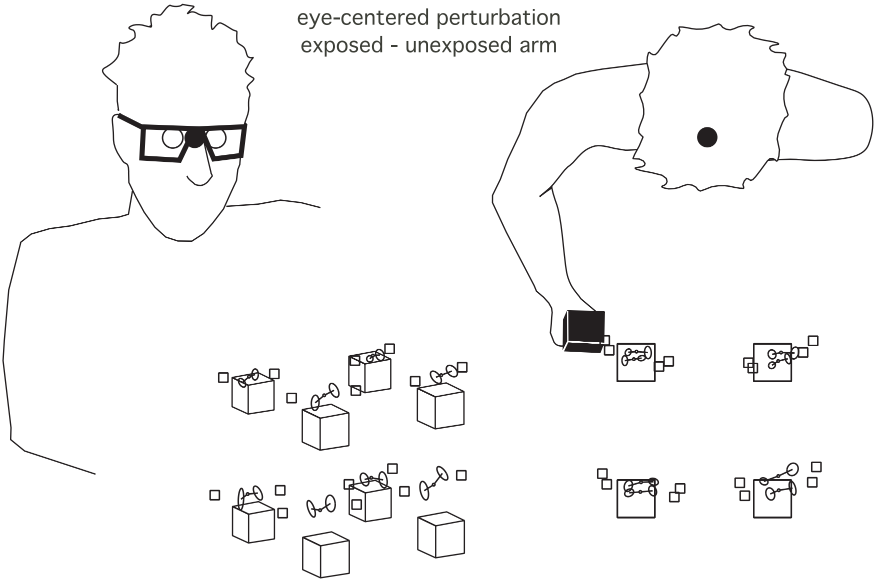
Vetter et al. (1999) proposed that the changes in subjects' pointing behaviour after laterally shifted feedback reflected adjustments within an eye-centered reference frame, because the pattern of generalisation was best captured by a rotation centered near the eyes. Consistent with the results of Vetter 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.

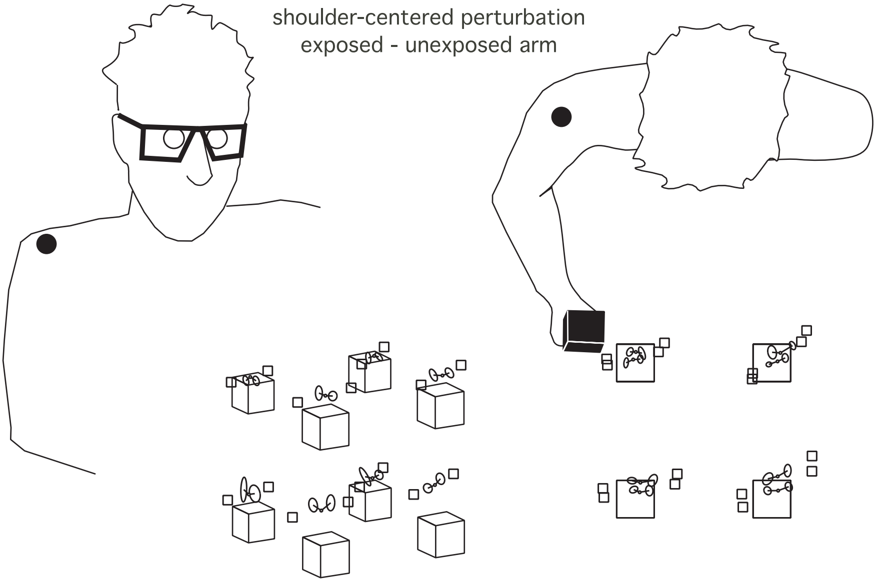
Our reasoning may appear to indicate that visuomotor adaptation simply involves changes within both eye-centered and shoulder-centered reference frames irrespective of the type of perturbation (eye- or shoulder-centered), and that only the eye-centered component of adaptation has transferred. However, 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.

Chapter 6

Summary and conclusions

We investigated the human ability to align visually and kinaesthetically perceived end positions of arm movements. We specifically looked at the spatial characteristics of movement endpoints and the responses of the visuomotor system to altered relationships between visual and kinaesthetic information. In one study we evaluated the variability in visual-kinaesthetic alignment, and in three adaptation studies we examined the re-alignment of vision and kinaesthesia in response to imposed mismatches between these sources of position information. In these studies we tried to determine what spatial information is incorporated in the motor commands generated by the visuomotor system and how this spatial information is represented. The main results and conclusions are summarised in this section.

Endpoint specification

Contradictory evidence has been provided during the last decades concerning the ability to plan the endpoints of arm movements without knowledge of the starting position of the hand. A simple movement could either be controlled in terms of the intended endpoint (position coding; Polit and Bizzi 1979) or in terms of the required displacement from the initial position (vector coding; Desmurget et al. 1998, Bock and Eckmiller 1986). Most studies into the parameters of the motor commands rely on the analysis of movement endpoints, assuming that the spatial characteristics of the distributions solely arise from noise in the planning of these parameters. This approach is, however, complicated by the fact that the distributions of endpoints are also affected by drift between visual and kinaesthetic position information that instantly occurs upon removal of the visual feedback of the hand. Chapter two describes a study in which we investigated whether the visuomotor system uses knowledge about the initial hand position to encode the intended final hand position with use of a method that accounted for possible effects of drift. In the experiment, subjects made sequential movements between visual targets with an unseen hand so that the endpoint of one movement was the initial position of the next. This ensured that vision and kinaesthesia were perceptually aligned prior to each movement (even though there is a lack of correspondence as shown by the presence of errors). Under these conditions, the vector coding hypothesis predicts that the variability of movement endpoints is the sum of the variability in initial positions and displacements while the position coding hypothesis predicts that the variability in the displacements is the sum of the variability in initial and final positions. A comparison of the variability in displacements and final positions showed that under these conditions movements to visual targets are position coded.

Visual-kinaesthetic re-alignment

For accurate reaching visual information about the target must be integrated with kinaesthetic information about the position and movements of the hand. Adaptation studies, in which a mismatch is introduced between vision and kinaesthesia, reveal the remarkable plasticity of these sources of position information and flexibility in the way they are integrated by the visuomotor system. This re-alignment requires that the sensory discrepancy is registered at some locus in the visuomotor system. However, neither vision nor kinaesthesia is perfect. Both are subject to constant and variable errors, each with their own anisotropies. These errors will affect whether and how a discrepancy is detected and therefore the compensatory processes that are required. Conscious detection of the mismatches may hamper adaptive processes because it could induce strategic compensation so that re-alignment is no longer necessary. The studies of chapter 3 investigate whether there is a relation between the amplitude and direction of a mismatch, its detectability and the magnitude of adaptation to these mismatches. In one experiment we determined the thresholds for detecting mismatches of a certain amplitude and direction and in another experiment we measured the extent to which subjects adapted to detectable and undetectable mismatches. The results show that mismatches in depth are less easily detected than lateral mismatches. The magnitude of adaptation was comparable for all mismatches showing that detection of the discrepancy did not counteract re-alignment.

Egocentric parameters for adaptation

The mechanisms by which visual-kinaesthetic re-alignment brings about new visuomotor relationships are not yet clear. Presumably, the adaptive responses are modifications of egocentrically specified parameters that link visual information about objects to kinaesthetic information about the hand. This may involve parameters related to the orientation of the eye in the head, the head on the trunk, the orientation of the shoulder and so on. The modification of these parameters is a kind of best fit to the perturbation so that the magnitude of the adaptation will depend on how well a perturbation of visual feedback can be compensated for, by altering these parameters. In the study of chapter 4 we investigate adaptation to translation of visual feedback, and scaling and rotation of feedback relative to a single position in front of the subject. These different types of perturbations differ in the extent to which they can be related to egocentric parameters. Lateral translation can be registered as an offset in eye, head or shoulder orientation, while scaling can approximately be described as an altered distance from the eyes or head. In contrast, rotations around an external position are much more difficult to interpret as such an internal error. Consistent with this hypothesis we found that adaptation to translations was more pronounced than adaptation to scaling, and much more pronounced than adaptation to rotations of visual feedback. In a second experiment we determined whether these adaptive responses were linked to parameters related to the eye or head, or to the arm by looking at the transfer of adaptation to the arm that was not exposed to the perturbation. The results show that intermanual transfer was incomplete for translation indicating that part of the adaptation was linked to the arm and part to the eye or head. In contrast, transfer was complete for adaptation to scaling suggesting that it was mainly linked to the eye or head.

Adaptation within specific egocentric reference frames

The incomplete intermanual transfer for translation that is described in chapter 4 suggests that humans may alter multiple parameters linked to different parts of the body. This could be due to the fact that no single parameter available to the visuomotor system for adjustment could compensate completely for a translation or that the visuomotor system preferentially alters parameters specified at the level of the eyes or head, or at the level of the arm. To investigate this we exposed subjects to perturbations relative to specific frames of reference. In one condition the visual feedback was rotated around a single position between the eyes and in another condition the feedback was rotated around the shoulder. The results are described in chapter 5 and show that subjects were able to register the imposed eye-centered and shoulder-centered perturbations and to adjust the parameters of the visuomotor system for appropriate compensation. However, for both types of perturbations the spatial characteristics of intermanual transfer indicate that the modified parameters do not correspond to the ones that were used to define the perturbation. This indicates 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 can mimic such adaptation.

General remarks

The studies presented in this thesis show that sensory information specified by multiple egocentric parameters is concurrently incorporated in the motor commands for goal-directed movements. The issues discussed have been debated for years, and our conclusions are contrasted by sound experimental facts presented in several other studies. How can we reconcile these discrepancies? The differences are probably due to differences in the experimental approaches used.

Reaching movements have been extensively studied while subjects pointed to objects on a computer monitor by controlling a cursor with a ‘mouse’ (Abeele and Bock 2001, Clower and Boussaoud 2000, Krakauer et al. 2000, Messier and Kalaska 1997, Pine et al. 1996, Ghilardi et al. 1995, Gordon et al. 1994, Ghez et al. 1993). In this case, the correspondence between the movement of the hand and the movements of the cursor is not direct. There are large discrepancies between the position of one’s hand and that of the cursor, the velocity of the hand can be different from that of the cursor and the movements are in differently oriented planes. This may force subjects to rely on other sensory information or make them use other movement strategies than they would do in more natural circumstances. Moreover, the movements are made along a constraining surface (e.g. a table) and this may generate forces that are not accounted for during the planning of the movement. These forces may, however, influence the outcome of the movement (Desmurget et al. 1997a). This also holds for studies in which subjects make two-dimensional movements to targets presented on a table (Vindras and Viviani 2002, 1998, Messier and Kalaska 1999, Vindras et al. 1998, Rossetti et al. 1994). Further, in most of these studies the starting position is in front and near the subjects so that movement direction is often confounding with visual direction and the final configuration of the arm. Finally, subjects are often instructed to make fast arm movements (Adamovich et al. 1999, 1994), preventing them from making corrective movements based on kinaesthetic feedback.

Three-dimensional movements are often investigated in tasks in which subjects point to virtual targets (Carrozzo et al. 1999, Vetter et al. 1999). Most of these virtual reality setups require that the head of the subjects is fixed (e.g. by way of a bite-board or chin rest). Orienting movements to visual targets usually involve concurrent movements of the eyes and head so that this may alter normal visuomotor behaviour. In addition, the use of single dots as targets prevents the use of most depth cues like disparity and perspective and this could affect visual localisation of the target.

The tasks and experimental setup in the present studies were designed to study three-dimensional arm movements with the above-mentioned factors in mind. With use of geometrical constructs we were able to identify part of the controlled parameters that generate arm movements to visual targets and to identify part of the parameters that are changed during visuomotor adaptation. Despite the usefulness of this approach for describing the data, our results also show that such constructs should be used with caution. The visuomotor system has a remarkable ability to (re-)align vision and kinaesthesia and adjusts numerous internal parameters to obtain suitable compensation for imposed mismatches between these sources of sensory information. The changes in endpoints that occur during adaptation may exhibit properties that are consistent with adjustments of certain parameters. However, combined adjustments of several parameters can lead to similar global changes. We were able to disentangle the relative contributions of adjustments at different levels of the visuomotor system by investigating intermanual transfer of adaptation. Such an approach will add to a further understanding of the control of goal-directed arm movements.

Applications

The main aim of the present research was to reveal the nature of visuomotor coordination. However, the paradigm used also serves to assess the adaptability of the visuomotor system. This may have implications for ’real-life’ situations in which humans are confronted with discrepant sensory information. Discrepancies between what we feel and what we see are present in nearly all man-machine interactions. For instance, in teleoperation, the consequences of the operator’s actions are artificially transmitted back to him by means of a camera-monitor system. Because of the inherent characteristics of such a system and the usually limited band-width between the remote site and the operator, these images are of degraded quality (e.g. a restricted field of view, a zoomed-in image, decreased information about the camera viewpoint and viewing direction, a time delay between the control input and the consequent feedback, and reduced spatial and temporal resolution). Depending on the circumstances and the task at hand this may impose major demands on the operator and may lead to serious accidents. One example of such a task is minimal invasive surgery. In traditional (open) surgery the direct contact with the patient leads to direct feedback about motor actions. In minimally invasive surgery, direct vision of the surgical field has been replaced by a video image and surgical instruments have replaced the fingers. This complicates the surgeon's depth perception and disorders the surgeon's eye-hand coordination. Normal visuomotor coordination is no longer appropriate, because the camera's line of sight is different from the surgeon's normal line of sight, so that the movements of the instruments do not correspond to the movements seen on the monitor. Hence endoscopic surgery is seen as complicated and difficult to learn.

It is at present uncertain whether one could generalise the obtained knowledge presented in this thesis to the visuomotor behaviour displayed in other tasks or when using other tools. We may use different transformations between visual and kinaesthetic information for different kinds of tools. However, even if this is so, we still need to adjust this information to account for variability in the tools use (e.g. the way it is held). The present studies give insight in the characteristics and limits of the processes that pertain to the body of the operator. Knowledge about the way the visuomotor system is organised and the processes by which adaptation occurs may help to identify the crucial difficulties encountered when using complex tools and contribute to the development of appropriate training programs.

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Samenvatting

Ons vermogen om gereedschappen te hanteren is een belangrijke stap in de evolutie geweest. Deze bedrevenheid wordt vaak toegeschreven aan de ontwikkeling van ons denkvermogen, maar ze komt evenzeer voort uit de ontwikkeling van visueel-motorische vaardigheden. Als je naar iets reikt komt hetgeen wat je je hand ziet doen overeen met hetgeen wat je je hand voelt doen (kinesthesie). Ons visueel-motorisch systeem integreert visuele en kinesthetische informatie om motor commando's te plannen voor de aansturing van de spieren. Gereedschappen veranderen de relatie tussen wat onze spieren doen en het effect van deze acties. Een manier om daar mee om te gaan is het veranderen van de koppeling tussen wat we zien en wat we voelen. Oftewel, we moeten adapteren aan de nieuwe ruimtelijke relatie tussen visuele en kinesthetische informatie. De wijze waarop dit gebeurt kan ons veel vertellen over de werking van visueel-motorisch handelen. De adaptatie aan een verstoring van de normale relatie tussen visus en kinesthesie wordt beperkt door de opbouw van het visueel-motorische systeem. De karakteristieken van de adaptatie reflecteren zodoende de eigenschappen van dit systeem.

In de studies die staan beschreven in dit proefschrift wordt onderzocht hoe het visueel-motorisch systeem visuele en kinesthetische informatie gebruikt om doelgerichte armbewegingen te plannen. In verschillende experimenten meten we hoe proefpersonen de kinesthetisch waargenomen positie van hun hand matchen met een visueel waargenomen positie door ze een echte kubus naar een gesimuleerde kubus te laten bewegen. Daarnaast wordt bekeken hoe dit verandert tijdens adaptatie aan een verstoring in de relatie tussen visuele en kinesthetische informatie. We bestuderen welke ruimtelijke informatie wordt gebruikt om het eindpunt van de armbeweging naar de gesimuleerde kubus te bepalen en hoe deze informatie is gerepresenteerd.

Eindpunt specificatie

Het eindpunt van een beweging kan in het motor commando worden beschreven als een positie ten opzichte van de persoon zelf; in egocentrische coördinaten (positiecodering), maar ook ten opzichte van de startpositie van de hand. In dit laatste geval beschrijft het motor commando de richting en afstand van de vereiste verplaatsing van de hand (vectorcodering). Vector codering impliceert dat het visueel-motorisch systeem informatie gebruikt over de startpositie van de hand bij de bepaling van het eindpunt. In het geval van positiecodering wordt informatie over de startpositie van de hand niet gebruikt.

Het bepalen van een eindpunt van een armbeweging gaat niet zonder het maken fouten. Deze fouten kunnen ontstaan door ruis in de geplande parameters en veroorzaken variabiliteit in de eindpunten. Afhankelijk van welke parameters gespecificeerd worden ontstaan karakteristieke patronen van eindpuntfouten. Door de fouten te analyseren kan men achterhalen welke parameters in het motor commando worden beschreven. In de studie van hoofdstuk 2 bewegen de proefpersonen een echte, voor de proefpersoon niet zichtbare kubus naar een visuele simulatie van een kubus. De gesimuleerde kubus wordt achtereenvolgens op verschillende posities aangeboden. Het eindpunt van één van deze bewegingen is dan het startpunt van een volgende beweging. Onder deze condities voorspelt het principe van vectorcodering dat de variabiliteit van eindpunten de som is van de variabiliteit in startposities en de variabiliteit in de planning van de verplaatsing. Positiecodering voorspelt dat de variabiliteit in verplaatsingen de som is van de variabiliteit in start- en eindposities. Uit de metingen blijkt dat onder de onderzochte omstandigheden de eindpunten van bewegingen positie gecodeerd zijn.

Mismatches tussen visuele en kinesthetische informatie

Om te kunnen adapteren aan veranderingen in de relatie tussen visuele en kinesthetische informatie moet de mismatch tussen deze bronnen van positie informatie goed worden geregistreerd door het visueel-motorisch systeem. Beide bronnen van informatie hebben hun eigen onnauwkeurigheden, welke bovendien richtingsafhankelijk zijn. Deze onnauwkeurigheden kunnen effect hebben op de detectie van mismatches en zodoende de adaptatie aan een mismatch beïnvloeden. In de studies van hoofdstuk 3 bepalen we hoe goed mismatches tussen visus en kinesthesie van verschillende groottes en in verschillende richtingen worden gedetecteerd. Vervolgens toetsen we de mate waarin proefpersonen adapteren aan deze mismatches. De resultaten laten zien dat mismatches in diepte minder snel worden waargenomen dan zijwaartse mismatches, maar dat de mate van adaptatie vergelijkbaar is voor deze verschillende verstoringen.

Egocentrische parameters voor adaptatie

De wijze waarop het visueel-motorisch systeem adapteert aan visueel-kinesthetische mismatches is afhankelijk van de parameters die gebruikt kunnen worden om de relatie tussen visus en kinesthesie te veranderen. De resultaten van hoofdstuk 2 laten zien dat eindpunten van armbewegingen in termen van egocentrische parameters worden gecodeerd. Mogelijk hangt adaptatie samen met de mate waarin de mismatch geïnterpreteerd kan worden als een verandering in deze egocentrische parameters. In hoofdstuk 4 onderzoeken we adaptatie aan translaties, rotaties en expansies van de visuele informatie over positie. Deze verstoringen verschillen in hoeverre ze aan egocentrische parameters gerelateerd kunnen worden. Laterale translaties lijken op veranderingen in de oriëntatie van de ogen, de oriëntatie van het hoofd, of de oriëntatie van de arm. Expansies kunnen benaderd worden als veranderingen in de afstand vanaf de ogen of het hoofd. Rotaties om een punt in de externe ruimte zijn veel moeilijker te relateren aan egocentrische parameters. De resultaten laten zien dat de proefpersonen meer adapteren aan translaties dan aan expansies en nauwelijks aan rotaties. In een volgend experiment is bekeken of de adaptatie meer gerelateerd is aan parameters die oog- of hoofd-, of armoriëntatie beschrijven. Als de adaptatie op het niveau van de ogen of het hoofd plaatsvindt, verwacht je een gelijk effect van de adaptatie voor beide armen (transfer van adaptatie). Wanneer de adaptatie vooral plaatsvindt op het niveau van de arm die is blootgesteld aan de verstoorde informatie, verwacht je verschillende effecten voor de twee armen. We vonden dat de mate van adaptatie aan expansies gelijk was voor beide armen en dat de adaptatie aan translaties vooral gekoppeld was aan de arm.

Adaptatie aan oogcentrische en schoudercentrische verstoringen

Uit de studies van hoofdstuk 4 bleek dat bij adaptatie aan een translatie de transfer van adaptatie naar de andere arm niet volledig was. Een deel van de adaptatie vindt dus plaats op het niveau van de ogen (of het hoofd) en een deel op het niveau van de arm. In hoofdstuk 5 bestuderen we of proefpersonen selectief kunnen adapteren op het niveau van de ogen of de arm. We onderzoeken de effecten van adaptatie aan rotaties van de visuele informatie om het oog (oogcentrisch) en om de schouder (schoudercentrisch). Mogelijk adapteren proefpersonen op het niveau van het oog aan oogcentrische verstoringen en op het niveau van de schouder aan schoudercentrische verstoringen. De proefpersonen blijken adequate te compenseren voor beide type verstoringen. Onderzoek naar de transfer van adaptatie laat echter zien dat proefpersonen niet selectief parameters veranderen op het niveau van de ogen of de schouder, maar dat de adaptatie op meerdere niveaus plaatsvindt.

Dankwoord

En nou dit nog. Ik heb nog even voordat dit boekje naar de drukker moet, ben het zat en zit er aardig doorheen, na de bekende stress die hoort bij de afronding van een proefschrift. Vlug dan. Wie moet ik nu waarvoor bedanken? Wie moet er zeker in en wie zou ik nog liever... Simpel houden is het beste, dus begin ik gewoon met Monique. Haar bedank ik natuurlijk omdat ze er altijd voor me was en veel meer.

Oké, en dan. Aio’s hebben genoeg om over te klagen en ik doe daar graag mee, maar met de begeleiding zat ik beter dan goed. Ik ben Eli en Jeroen zeer dankbaar, omdat ik altijd bij ze terecht kon en vooral voor de ruimte die ze me gaven om te prutsen. Dat heeft het afronden van het proefschrift niet echt versneld, maar zo kon ik me ontwikkelen van ‘knutselsmurf’ tot ‘qualified technician’ en dat is ook belangrijk in dit vak.

In deze laatste weken kwamen de bemoedigende woorden vooral van Jos. Hij heeft sowieso een streepje voor op mijn andere collega’s. Jos, bedankt voor de regelmatige rustpunten waarop ik stoom kon afblazen. Een heel andere uitlaatklep waren Jeroen Smale en Anne-Marie. Tegelijk begonnen en dat schept een band (of misschien een gezamenlijke vijand). Nog zo een gelijkgestemde vond ik in Editha. Ik bedank hen voor alle momenten die vooral niks met wetenschap te maken hadden.

Veel mensen hebben kleine dingen voor me gedaan, waardoor alles makkelijker of plezieriger verliep. Zo vervaardigde mijn vader onderdelen voor mijn opstelling en legde mijn moeder hem uit wat het moest zijn. Ria voorkwam financiële fiasco’s en smokkelde onmisbare apparatuur door de douane. Koen en Karel boden onderdak toen ik naar Rotterdam kwam. Via hen leerde ik ook Tim, Maurice en Nanne kennen, die voor de noodzakelijke ontspanning zorgden met een borrel, etentje of voetbalwedstrijd. Allemaal bedankt.

De laatste woorden van dank zijn voor Peter. Met hem schreef ik de procedure voor het plotten van de ellipsoïden, maar op een of andere manier is zijn bijdrage veel groter geweest. Hij had hier ook moeten zijn.

Curriculum vitae

John van den Dobbelsteen werd op 13 juni 1973 geboren in Geldrop. Zijn VWO-diploma behaalde hij aan het Strabrecht College te Geldrop in 1992. In september 1993 begon hij aan de opleiding Functieleer bij de vakgroep Experimentele en Arbeidspsychologie van de Rijksuniversiteit Groningen. Onder begeleiding van Wiebo Brouwer deed hij onderzoek naar de verwerking van optic flow informatie voor ruimtelijke oriëntatie bij neglect patiënten. Daarnaast liep hij stage bij TNO Technische Menskunde te Soesterberg onder begeleiding van Jan van Erp. Hier werkte hij onder meer mee aan onderzoek ten behoeve van het verbeteren van de mens-machine interface van onbemande vliegende platforms. Hij studeerde af in 1998 en begon in datzelfde jaar aan zijn promotieonderzoek bij Eli Brenner en Jeroen Smeets op de afdeling Fysiologie (nu Neurowetenschappen) in Rotterdam. De resultaten van dit onderzoek staan in dit proefschrift. Vanaf september 2002 is hij op de afdeling Neurowetenschappen werkzaam als postdoc.

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