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.

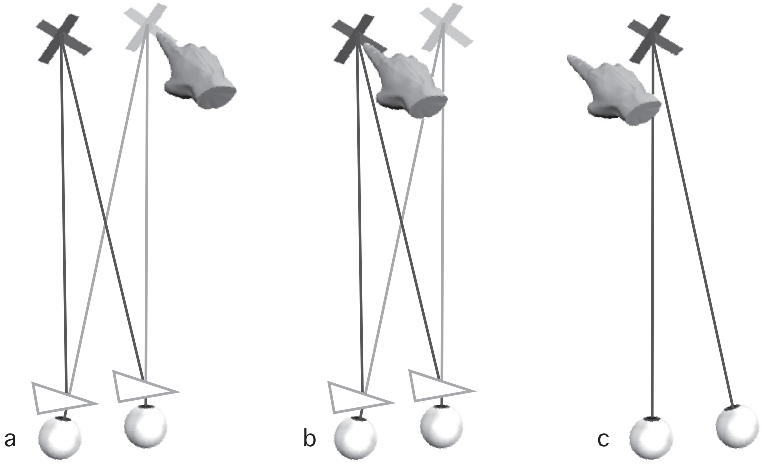

Figure 1.1 *A schematic representation of the principle of prism adaptation. a) Prisms placed in front of the eyes displace the visual image (grey cross) of a target (black cross) so that reaches initially deviate in the direction of the displacement. b) During prolonged exposure to the effects of the 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.