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.