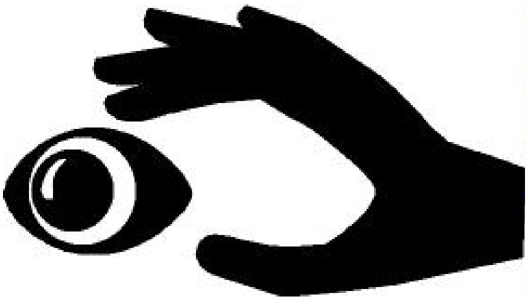
Eye-Hand Coordination in Time and Space



Uta Sailer

Aus der Neurologischen Klinik und Poliklinik der Ludwig-Maximilians-Universität München
Vorstand: Prof. Dr. med. Dr. h. c. Thomas Brandt FRCP

Thema der Dissertation:

Eye-Hand Coordination in Time and Space

Dissertation
zum Erwerb des Doktorgrades der Humanbiologie
an der Medizinischen Fakultät der
Ludwig-Maximilians-Universität zu München

vorgelegt von

Uta Sailer

aus

München

Jahr

2003

Mit Genehmigung der Medizinischen Fakultät
der Universität München

1. Berichterstatter:	Prof. Dr. A. Straube
2. Berichterstatter	Prof. Dr. F.P. Kolb
Mitberichterstatter:	Prof. Dr. R. Breul
	Prof. Dr. I. Rentschler
Mitbetreuung durch den promovierten Mitarbeiter:	Dr.-Ing. Thomas Eggert
Dekan:	Prof. Dr. med. Dr. h. c. K. Peter
Tag der mündlichen Prüfung:	08.04.2003

Contents

1 General Introduction

Every day of our lives starts with a succession of actions that require eye-hand coordination. From the time we try to turn off the alarm clock and get dressed, to putting toothpaste on the brush and preparing coffee: all these goal-directed hand movements need to be coordinated with information from the eye.

When performing such simultaneous goal-directed eye and hand movements, both the time and location at which eye and hand land on the object need to be harmonised. For better localising the alarm clock, we need to see it before we hit it. In order to use this visual information for an accurate hand movement, we need the eye to land at the same position, i.e. eye and hand both need to be on the alarm clock instead the water glass beside. These two aspects, temporal and spatial coordination, have encouraged a great deal of research. On the following pages, first a number of existent findings will be summarised on how this coordination could be achieved. Then the experiments performed within this thesis to extend the results in the literature will be described.

1.1 Temporal coupling

The term "temporal coupling" of eye and hand encompasses two aspects: one is the temporal organisation of eye and hand, i.e. the order in which eye and hand are executed or the point in time at which eye and hand movements are initiated relatively to each other. The second aspect of temporal coupling is the question whether there is one common start signal to initiate the movements, or two separate ones.

1.1.1 Order of movement execution

Historically, studies on eye-hand coordination first dealt with its temporal aspect. Typically, the eye is on target before the hand (e.g. Abrams et al. 1990, Carnahan & Marteniuk 1991). Foveating a target before manipulating an object has several advantages: information with higher resolution provided by the fovea may help in the initial phases of the hand movement, for example in preshaping the hand. Moreover, foveation of the target provides more detailed information to compare the target with the moving hand (e.g. about distance, grasp size). This information can be used to correct the ongoing hand movement's grasp component and trajectory. More specifically, it was shown that the primary saccade is completed around the time the hand achieves peak velocity (e.g. Helsen et al. 2000). In this way, important visual information for movement correction can be picked up and used for an online adjustment of hand movements. Indeed, it has repeatedly been shown that hand movement accuracy drops when foveation of the target is prevented (e.g., Abrams et al. 1990, Vercher et al. 1994).

Other results indicate that this temporal yoking of hand to eye is not a one-way street. Neggers and Bekkering (2000) found that saccade onset to a second target was delayed until an arm movement to the first target was completed. This finding shows that not only the hand is dependent on the eye, but also the eye is coupled to the hand.

Recently, the investigation of the temporal organisation of eye and hand has been extended to real-life situations. The behaviour induced by a restricted laboratory context may be different from that in the natural environment because the environments' spatial extent, involved dimensions and behavioural goals differ (Hayhoe et al. in press). The authors found that in natural contexts a large number of hand movements were directed to objects that had been fixated in the recent past. In these cases, the object may be fixated in order to acquire its spatial location for planning the hand movement towards it. The time difference for initiating an eye and hand movement towards the same target could be as much as a second. Thus, eye and hand movements seem to be planned a second ahead of time. Therefore, a visual representation or memory buffer lasting at least a second is required. As there may be several fixations in between the eye and hand movement to the target object, this representation has to be independent from eye position.

Based on the investigation of temporal order in natural tasks, Hayhoe et al. (in press) showed that motor planning is based on spatial representations of the scene, thus tapping into spatial coupling as the second main topic of eye-hand coordination.

Another study of combined eye and hand movements in the natural context investigated the relationship between directing eyes and hand to certain landmarks (Johansson et al. 2001). They showed that the subjects almost exclusively fixated certain landmarks that were important for controlling the task, e.g. actual and potential contact points. The change in gaze direction was anchored to kinematic events in the hand movement. This implies that the saliency of targets for the eye is determined by the requirements of the task. Thus, the eyes are not simply directed to perceptually salient characteristics in the environment. Instead, the importance of certain details in the environment for the hand determines where the eyes are directed to.

1.1.2 One command signal for movement initiation or two?

Early studies investigated the question of whether one common or two separate command signals initiate eye and hand movements. This question was suggested because there was evidence for eye and head being controlled by one common command. Because of the reduced amount of computation necessary, it would be handy if this command were used also to control hand movements (Fischer 1989). However, already the initial studies on this question showed that it cannot be answered as easily. For example, the high correlation (>.6) between eye and hand latencies reported by Herman et al. (1981) has later been attributed to methodological artefacts (Bekkering 1995). Other studies replicated these high correlations only in part (Frens & Erkelens 1991) or not at all (Biguer et al. 1982). Generally, the correlation of eye and hand latencies is higher with non-visual targets than with visual targets. This has been shown both for auditory (Mather &Fisk 1985) and kinesthetic (Neggers & Bekkering 1999) and will be shown for remembered and imagined targets in chapter 2 (Sailer et al. 2000). It is assumed that in these cases, eye and hand share more transformations or information, and that this accounts for the higher correlation observed.

Because of the inconsistency of latency correlation results, different methodologies have been developed to investigate temporal interactions between eye and hand. One alternative which is often applied is the dual-task methodology. The dual-task methodology involves measuring eye and hand movements both alone and when executed together. This allows to determine separate influences on the two motor systems and the interaction between them. Unfortunately, the results of studies using the dual-task methodology are also far from being consistent. It has been found that manual latencies decrease and saccadic latencies increase in the dual-task (Mather & Fisk 1985), that manual and saccadic latencies both increase (Bekkering et al. 1995a), and that saccadic latencies decrease and manual latencies remain unaltered (Lünenburger et al. 2000). Future studies will have to study to what extent these results are dependent on the specific conditions of the experiment. Nevertheless, this variability makes a common signal for movement initiation unlikely and suggest separate activation of the eye and hand motor systems.

Other data also speaking for such a separate activation are differential effects of prism exposure on the latencies of eye and hand movements (Rossetti et al. 1993).

Recently, Snyder et al. (2002) have shown that in the monkey, the main sequence of saccades was changed when they were accompanied by a hand movement towards the same target. The main sequence characterises the correlation between amplitude and peak velocity and is a stereotyped and robust feature of saccades in humans and nonhuman primates (Fuchs et al. 1985). Thus, hand movements seem to influence saccade generation on a very basic level.

1.2 Spatial coupling

One major question in the domain of spatial eye-hand coordination is whether eye and hand use the same spatial representation of the target or not. Initial studies on this question rather spoke for the use of a common target representation. For instance, Gielen et al. (1984) reported similar responses of eye and hand movements to double-step targets. Eye and hand also always moved towards the same target when there were two simultaneous targets. This led the authors to conclude that there is a common command signal for specifying the end position of eye and hand movements. This conclusion can be reformulated to the use of a shared target representation.

Similar conclusions were reached by changes of spatial parameters in one motor system being caused by changes in the other system. A popular paradigm used for this approach is the saccadic adaptation paradigm (e.g. McLaughlin 1967; Abrams et al. 1992). When the target is displaced during the saccade, subjects initially acquire the displaced target by means of a second, corrective saccade. After a number of trials, however, subjects land directly on the position of the displaced target. It is believed that this shift in end positions results from a gradual shift of the target representation towards the final position of the target (Gielen et al. 1984). Consequently, if eye and hand shared one target representation, the end positions of hand movements should also be gradually shifted towards the position of the displaced target. Such a result was indeed found by Bekkering et al. (1995b). When the target was displaced to a less eccentric position during the saccade, not only the eye adapted and went directly to the final target position, but the hand also showed similarly shortened amplitudes. Comparable results were found by de Graaf et al. (1995) using a similar paradigm. However, they put their results into perspective again in 1999, concluding that a transfer of saccadic adaptation to the hand motor system could not be proven consistently.

A different example of the effect of spatial information manipulated in one motor system on the responses of the other motor system was given by van Donkelaar (in press, 1997). Subjects had to look and point to the same targets while eye movements either started from the same position or from a position that required larger saccades than hand movements. It was found that saccadic amplitude and hand amplitude are not independent from each other, as hand amplitudes increased with saccadic amplitude. Thus, information about saccade amplitude is integrated into the response of hand movements.

But not only the saccadic signal influences hand movements, but hand movements also influence saccades. Eye trajectories towards a target in the presence of distracters was influenced by simultaneous reaches to the target (Tipper et al. 2001).

What all of these studies show is that at least some spatial target information is shared by eye and hand. However, we argue in chapter 3 that although eye and hand exchange spatial target information, evidence speaks against the use of a shared target representation. If a nearby distracter acted on the same target representations of eye and hand, the distracter would be expected to always influence eye and hand responses in a similar way. Instead, the differential effect of a nearby distracter on eye and hand movements in some conditions suggests that eye and hand are based on two separate target representations and selection mechanisms that exchange information (Sailer et al. in press a, b).

1.2.1 Sources of spatial information

If eye and hand are assumed to interact by an exchange of information, one should have a closer look on the nature of this information: What sources of spatial target information do eye and hand use and how does it influence the other motor system?

1.2.1.1 Retinal and extraretinal signals

A considerable number of studies have shown that prohibiting foveal vision of the target reduces the accuracy of hand movements (e.g. Vercher et al. 1994; Abrams et al. (1990) compared the behaviour of the hand in a condition where fixation of the target was allowed with a condition where it was not (subjects had to fixate a central fixation spot instead). Fixation of the target enabled larger error corrections of ongoing hand movements (Abrams et al. 1990). Similarly, extinguishing the target with hand movement onset resulted in decreased accuracy (e.g., Prablanc et al. 1986).

On the one hand, fixating the target provides retinal information about the target. There are a number of explanations why that leads to more accurate hand movements. The most obvious reason is that visual resolution is better on the fovea. The more accurate information taken in when the target is on the fovea can be used for a better modification of the ongoing hand movement.

On the other hand, fixating the target provides extraretinal information about eye position. It has been suggested that eye position (extraretinal gaze signals) serves as target for the hand. In other words: the hand points to where the eye is looking. According to this account, subjects try to match the end position of their hand movements to the end position of the eye. This so-called “final gaze hypothesis” (Adam et al. 1993) can be reformulated to whether the hand uses the target representation of the eye. Arguments in favour of this hypothesis come from a study of Soechting et al. (2001) who found that pointing errors and errors at the final gaze position were highly correlated, even when saccades had drifted to this final position. However, these findings are in strong contrast with that of several other authors who did not find a correlation of eye and hand end positions (Biguer et al. 1984; Delreux et al. 1991; Sailer et al. 2000). Thus, as Soechting et al. (2001) themselves remarked, a gaze signal serving as target for the hand is not obligatory. Thus, extraretinal signals can, but need not necessarily be integrated into the hand motor response.

Whether extraretinal signal are used efficiently by the hand motor system or not may depend on the presence of retinal stimulation. In completely dark environments, subjects are not so good in pointing in the direction of their gaze (Enright 1995, Blouin et al. 2002). Thus, extraretinal information appears to be used better by the hand motor system when retinal stimulation is present as well, particularly, if the amount of visual information is increased (Blouin et al. 2002).

1.2.1.2 Proprioceptive signals from the hand

Proprioception is an important source for accurate reaching movements. In pointing movements to visual targets, subjects without proprioception were found to have extensive directional errors compared to those with unaffected proprioception (Gordon et al. 1995). Moreover, these errors could not be detected by the subjects themselves when the lights were turned off.

Such proprioceptive information from the hand seems also to be used by the eye, particularly with tracking movements when more proprioceptive information is present. Already in 1969, it was found that tracking a target with the eyes was improved with concurrent hand movements (Steinbach 1969). This improvement was replicated with regard to the delay of the eye to the target, tracking velocity (Gauthier et al. 1988), and smoothness, i.e. the number of saccades during tracking (Koken &Erkelens 1992), although the improvement in the latter study was dependent on the predictability of the target.

However, like with simultaneous saccades and pointing movements, the parameters of eye and hand changed differently with changes in conditions. This applied both to the latencies in response to sudden target changes (Bock 1987) and the gain (Mather & Putchat 1983). These findings again support the idea that eye and hand are controlled by parallel but interacting mechanisms. Lazzari et al. (1997) proposed a model which assumes that both motor systems are completely independent but exchange information, mediated by sensory (vision, hand muscle proprioception) and hand motor signals. The model assumes that the characteristics of the hand are stored and considered by the eye. However, the findings of two deafferented subjects indicate that proprioception does not seem to be necessary for reducing the time between the onset of eye and hand tracking (Vercher et al. 1996). Instead, the role of proprioception may lie in the information it provides about the arm's inertia (Ghez et al. 1990). Thus, proprioception is necessary for building up a representation about the dynamical properties of the arm (Scarchilli & Vercher 1999).

1.2.2 Coordinates of spatial target representations

Several studies have analysed end point variability of hand movements to determine whether variable error patterns reveal the nature and origin of the coordinate system in which the movements were planned. In pointing to memorised targets, a gaze-centred reference frame was found when vision of the hand was available, whereas a hand-centred reference frame was found without vision of the hand (McIntyre et al. 1997). Similarly, using kinesthetic cues, Flanders et al. (1992) found evidence for a hand-centred reference frame.

Thus, hand movements are coded in a hand-centred frame of reference (Gordon et al. 1994; Vindras & Viviani 1998), but eye movements in an eye-centred frame of reference. This raises the question on how an exchange of information between the motor systems of eye and hand could take place. Investigating the nature of the visual representations in space, Henriques et al. (1998; in press) showed that open-loop pointing movements in near and far space are coded in an eye-centred coordinate frame. This means that the internal representations of visual targets are remapped for each eye movement. It is suggested that these representations apply to an early stage of hand movement control, i.e. initial perception. Only targets selected for action are thought to be transformed further into head- or hand-centred frames of reference. This suggests that the target representation in terms of a visual map of space consists only of those representations on which we choose to act. In fact, such a strategy seems attractive because of its economic efficiency.

In this sense, the visual representations independent of eye position assumed by Hayhoe et al. (in press) may be the result of such a more elaborate, later transformation process.

1.2.3 Clinical applicability of transformation accounts

Although such transformational accounts sound theoretically attractive, they also need to pass the empirical test of explaining clinical cases. This is what Buxbaum and Coslett (1997; 1998) have attempted to do with optic ataxia, a deficit in reaching under visual guidance and thus an intriguing clinical example of a breakdown of eye-hand coordination. Buxbaum and Coslett (1997; 1998) have attributed optic ataxia to failures in the transformation of retinal to hand-centred coordinates. More specifically, as parietal neurons could be responsible for this transformation (e.g., Ferraina et al. 2001; Batista et al. 1999), it has been proposed that optic ataxia can be explained by a failure of parietal neurons to combine directional eye and hand information (Battaglia-Mayer & Caminiti 2002).

However, it has been criticised that the transformational account fails to explain why some cases of optic ataxia are restricted to targets in the periphery (Carey et al. in press). Thus, this crucial condition of this phenomenon is simply not accounted for.

An alternative explanation for the deficits observed in optic ataxia is that it mainly represents a deficit in making fast on-line corrections (Pisella et al. 2000). Such on-line corrections are particularly important in peripheral vision, because then the movement is programmed on the basis of coarse peripheral visual information. In contrast, foveal vision provides enough precise visual information for an accurate programming of the movement and therefore, on-line correction is less important. Thus, this account can well explain why some patients display optic ataxia to peripheral targets only. The role of the posterior parietal cortex in movement correction has also be stressed elsewhere (Desmurget et al. 2001: Debowy et al. 2001). Using a saccadic adaptation paradigm, the brain areas responsible for a modification of eye and hand movements to the displaced targets were investigated using PET (Desmurget et al. 2001). Such updated movements were shown to be mediated by a network involving the posterior parietal cortex, cerebellum, and primary motor cortex.

A further example for a patient with impaired eye-hand coordination is “magnetic misreaching” (Carey et al. in press). This patient failed to reach to extrafoveal targets. However, the authors argue that magnetic misreaching cannot be subsumed under the term of optic ataxia, because in this patient reaching to proprioceptive and auditory targets was also impaired. They suggest that magnetic misreaching results from the disruption of sensorimotor loops in the posterior parietal cortex. Due to this disruption, foveation remains the only functioning route to goal-directed reaching.

1.3 Brain areas involved in eye-hand coordination

The question arises as to where in the brain such a transformation of eye-centred into hand-centred coordinates is performed. Neurophysiological studies have revealed the crucial role of the posterior parietal cortex in such a transformation. Reach-related activity in the posterior parietal area was found to be modulated by gaze direction in monkey (Batista et al. 1999) as well as in humans (Baker et al. 1999). However, activity during saccadic delay in the parietal reach region (PRR) in monkey posterior parietal cortex does not reflect the animal's plans to move the eye with the arm or the arm alone. Therefore, although PRR subserves visually guided reaching, there is no evidence for the direct coordination of eye and hand in PRR (Snyder et al. 2000). Saccade-related activity in PRR was seldom presaccadic. One interpretation of the authors holds that this activity reflects the maintenance of target position in an eye-centred frame of reference, if the eyes move after target appearance but before reaching.

Spatial locations for hand movements seem to be coded in an eye-centred frame of reference in the posterior parietal cortex (e.g., Colby et al. 1995), but in a hand-centred frame of reference in the premotor cortex (Graziano, 1999). Data of a recent transcranial magnetic stimulation study support the findings of these physiological studies (van Donkelaar et al. in press). TMS over the premotor cortex resulted in an increased influence of the saccadic signal on hand movements. In contrast, TMS over the posterior parietal cortex resulted in a decreased influence of saccades on hand movements. Thus, the two reference frames appear to compensate for each other, with TMS reducing the amount of compensation. However, the results of other studies hint on the distinction being less clear. Gaze signals have also been shown to influence the premotor areas (Boussaoud et al. 1998; Baker et al. 1999; Mushiake et al. 1997). Instead of a stage-wise transformation of coordinates from one frame into another, multiple reference frames may exist in parallel which are integrated in both the parietal and frontal cortex (Battaglia-Mayer et al. 1998; Graziano & Gross 1998). For example, the common coordinate frame in the posterior parietal lobe would allow the integration of different forms of spatial representations (Andersen 1998).

Another neural structure that has been proposed to play a role in coordinating eye and hand control signals is the superior colliculus (SC). Recently, activity in SC neurons has been reported not only in saccadic eye movements, but also in arm movements (Stuphorn et al. 2000), although the respective neuronal populations do not overlap. Forty percent of the reach cells in the SC were found to modulate their activity with gaze. As these cells provide a signal of the difference between the eye and hand target, they are well suitable for the on-line correction of hand movements. Stuphorn et al. (2000) further discuss that the SC in turn is inhibited by cortical structures, because lesions in the premotor cortex, frontal and supplementary eye field result in an inability to dissociate eye and hand targets, a condition similar to the magnetic misreaching case found in humans (see next paragraph and Carey et al. in press).

A further candidate area for eye-hand coordination is the cerebellum. Miall et al. (1998, 2001) report functional imaging data of subjects tracking targets with their eyes alone, their hand alone, or both. Compared to the single-task conditions, cerebellar areas were significantly more activated when the subjects performed a combined eye and hand movement. These findings speak for the involvement of the cerebellum in eye-hand coordination. Reciprocal interactions between the eye and hand motor systems have also been reported by van Donkelaar and Lee (1994). In this study, subjects with cerebellar lesions were slower in initiating eye and hand movements (see also Brown et al. 1993) and had considerably variabler hand movements than control subjects. Also, this variability could be reduced by restricting eye movements.

In monkeys, lesioning the cerebellar dentate nuclues and measuring the outcome on tracking task performance, the correlation between eye and hand movements decreased and the delay between target and eyes increased (Vercher & Gauthier 1988). Eye movements in the combined task were no longer different from those in the eye-alone task. Thus, after the lesion, the eye movement system could no longer use information from the hand motor system to enhance its performance. These results indicate the role of the cerebellum in coordinating eye and hand signals.

In the following, we will not further pursue the subject of the reference frames in which targets for eye and hand are coded. The focus of this thesis is rather on basic mechanisms coupling eye and hand movements and on the question of what kind of information is shared by eye and hand and up to which level of processing.

1.4 Short outline of chapters 2 to 6

In chapter 2, we tried to determine if the latencies as well as the coupling of eye and hand (in terms of latency correlations) depend on the paradigm. The paradigms used included reflexive tasks which required a fast reactive movement to the onset of a target, and intentional tasks. These intentional tasks required the suppression of a reactive movement to a sudden stimulus onset and/or a volitional movement to a remembered or imagined target. We found that the mean latencies of eye and hand movements were higher for intentional as compared to reflexive tasks. Moreover, temporal coupling of eye and hand movements was higher for intentional as compared to reflexive tasks. Relevant potential mechanisms for this result are being discussed.

In chapter 3, we examined temporal and spatial coupling of eye and hand by means of a distracter paradigm. It is known that when a target and a distracter are presented simultaneously and close to each other, saccades land in-between the two. The reason for this so-called "global effect" is thought to be that the saccade is triggered before fine visual processing or the separation of target and distracter are completed. This explanation is also supported by the finding that the global effect for saccades is strongest with short latencies and gradually disappears with longer latencies. Thus, the global effect occurs at the level of target selection only. This allows to draw conclusions on the processing level up to which target information is processed in common for both eye and hand. As the global effect was very similar for eye and hand in some conditions, but different in others, we concluded that eye and hand use separate target representations at the level of target selection. However, these representations are not independent from each other, but interact by exchanging information.

As the results of chapter 3 showed that hand movements influenced eye movements, we investigated in chapter 4 whether this influence extends to static hand position. Therefore, subjects were asked to either look away from the hand, towards the hand, or towards the initial position of the hand during presentation of the target. It turned out that eye movements were drawn towards the static position of the hand, both when the hand had been at the target location all the time and when it moved away from it during the memorisation period of the target. This suggests that information about hand position is integrated into the oculomotor command already at the time of target presentation.

Chapters 2 to 4 showed that eye and hand are coupled both during target selection and movement initiation. However, the processes for selecting a target for a movement vary in complexity, because the target can either be set externally or be internally generated (like in the antisaccade task of chapter 2). To investigate the influence of higher order strategies on eye-hand coupling, a task with an even more complex internally generated target was used in chapter 5. We probed how eye and hand predict the position of a moving target that has disappeared at the time of movement execution. The results show that eye and hand both do not use the target's velocity in the sense of an extrapolation to predict its position. Instead, they use a particular strategy which is not different for eye and hand.

As chapter 2 to 5 demonstrated temporal and spatial coupling of eye and hand, we analysed in chapter 6 whether this coupling is dependent on the attributes of the target. To this aim, we changed attributes of the target (and therefore, the target representation) which are relevant for the hand motor system only. This was done in order to find out if the effects on hand movements spread via coupling to eye movements. Results showed that hand movements showed altered kinematics to targets of different haptic texture, but this change was not reflected in eye movements. Thus, coupling is not only dependent on the task, but also on the characteristics of the stimulus and their relevance for each of the two motor systems.

1.5 References

Abrams R.A., Dobkin R.S., Helfrich M.K. (1992) Adaptive modification of saccadic eye movements, J. Exp. Psychol. Hum. Percept. Perform., 18: 922-933.

Abrams R.A., Meyer D.E., Kornblum S. (1990) Eye-hand coordination: oculomotor control in rapid aimed limb movements, *J Exp. Psychol. Hum. Percept. Perform.,* 16: 248-267.

Adam J.J., Ketelaars M., Kingma H., Hoek T. (1993) On the time course and accuracy of spatial localization: basic data and a two-process model, *Acta Psychol. Amst.,* 84: 135-159.

Andersen R.A., Snyder L.H., Batista A.P., Buneo C.A., Cohen Y.E. (1998) Posterior parietal areas specialized for eye movements (LIP) and reach (PRR) using a common coordinate frame, *Novartis Found. Symp.,* 218: 109-122.

Baker J.T., Donoghue J.P., Sanes J.N. (1999) Gaze direction modulates finger movement activation patterns in human cerebral cortex, *J Neurosci.,* 19: 10044-10052.

Batista A.P., Buneo C.A., Snyder L.H., Andersen R.A. (1999) Reach plans in eye-centered coordinates, *Science,* 285: 257-260.

Battaglia-Mayer A., Caminiti R. (2002) Optic ataxia as a result of the breakdown of the global tuning fields of parietal neurons, *Brain*, 125: 225-237.

Battaglia-Mayer A., Ferraina S., Marconi B., Bullis J.B., Lacquaniti F., Burnod Y., Baraduc P., Caminiti R. (1998) Early motor influences on visuomotor transformations for reaching: a positive image of optic ataxia, *Exp.Brain Res.,* 123: 172-189.

Bekkering H. (1995) *Eye-hand coordination: cooperative and competitive systems?* Unpublished doctoral dissertation, Rijksuniversiteit Limburg, Maastricht, Netherlands.

Bekkering H., Adam J.J., van den Aarssen A., Kingma H., Whiting H.T. (1995a) Interference between saccadic eye and goal-directed hand movements, *Exp. Brain Res.,* 106: 475-484.

Bekkering H., Abrams R.A., Pratt J. (1995b) Transfer of saccadic adaptation to the manual motor system, *Human Mov. Sci.,* 14: 155-164.

Biguer B., Jeannerod M., Prablanc C. (1982) The coordination of eye, head, and arm movements during reaching at a single visual target, *Exp. Brain Res.,* 46: 301-304.

Biguer B., Prablanc C., Jeannerod M. (1984) The contribution of coordinated eye and head movements in hand pointing accuracy, *Exp. Brain Res.,* 55: 462-469.

Blouin J., Amade N., Vercher J.L., Teasdale N., Gauthier G.M. (2002) Visual signals contribute to the coding of gaze direction, *Exp. Brain Res.,* 144: 281-292.

Bock O. (1987) Coordination of arm and eye movements in tracking of sinusoidally moving targets, *Behav. Brain Res.,* 24: 93-100.

Boussaoud D., Jouffrais C., Bremmer F. (1998) Eye position effects on the neuronal activity of dorsal premotor cortex in the macaque monkey, *J Neurophysiol.*, 80: 1132-1150.

Brown S.H., Kessler K.R., Hefter H., Cooke J.D., Freund H.J. (1993) Role of the cerebellum in visuomotor coordination. I. Delayed eye and arm initiation in patients with mild cerebellar ataxia, *Exp. Brain Res.,* 94: 478-488.

Buxbaum L.J., Coslett H.B. (1997) Subtypes of optic ataxia: Reframing the disconnection account, *Neurocase,* 3: 159-166.

Buxbaum L.J., Coslett H.B. (1998) Spatio-motor representations in reaching: Evidence for subtypes of optic ataxia, *Cogn. Neuropsychol.,* 15: 279-312.

Carnahan H., Marteniuk R.G. (1991) The temporal organization of hand, eye, and head movements during reaching and pointing, *Journal of Motor Behavior,* 23: 109-119.

Carey D.P., Della Sala S., Ietswaart M. (in press) Neuropsychological perspectives on eye-hand coordination in visually-guided reaching, *Prog. Brain Res.*

Colby C.L., Duhamel J.R., Goldberg M.E. (1995) Oculocentric spatial representation in parietal cortex, *Cereb. Cortex,* 5: 470-481.

de Graaf J.B., Pelisson D., Prablanc C., Goffart L. (1995) Modifications in end positions of arm movements following short-term saccadic adaptation, *Neuroreport,* 6: 1733-1736.

Debowy D.J., Ghosh S., Ro J.Y., Gardner E.P. (2001) Comparison of neuronal firing rates in somatosensory and posterior parietal cortex during prehension, *Exp. Brain Res.*, 137: 269-291.

Delreux V., Vanden-Abeele S., Crommelinck M., Roucoux A. (1991) Interactions between goal-directed eye and arm movements: Arguments for an interdependent motor control, *J Mot. Behav.,* 23: 147-151.

Desmurget M., Grea H., Grethe J.S., Prablanc C., Alexander G.E., Grafton S.T. (2001) Functional anatomy of nonvisual feedback loops during reaching: a positron emission tomography study, *J Neurosci.*, 21: 2919-2928.

Enright J.T. (1995) The nonvisual impact of eye orientation on eye-hand coordination, *Vis. Res.,* 35: 1611-1618.

Ferraina S., Battaglia M.A., Genovesio A., Marconi B., Onorati P., Caminiti R. (2001) Early coding of visuomanual coordination during reaching in parietal area Pec*, J Neurophysiol.,* 85: 462-467.

Fischer B. (1989) Visually guided eye and hand movements in man, *Brain Behav. Evol.,* 33: 109-112.

Flanders M., Helms Tillery S.I., Soechting J.F. (1992) Early stages in a sensorimotor transformation. *Behav. Brain Sci.,* 15: 309-362.

Frens M.A., Erkelens C.J. (1991) Coordination of hand movements and saccades: evidence for a common and a separate pathway, *Exp. Brain Res.,* 85: 682-690.

Fuchs A.F., Kaneko C.R., Scudder C.A. (1985) Brainstem control of saccadic eye movements, *Annu. Rev. Neurosci*, 8: 307-337.

Gauthier G.M., Vercher J.L., Mussa I.F., Marchetti E. (1988) Oculo-manual tracking of visual targets: control learning, coordination control and coordination model, *Exp. Brain Res.,* 73: 127-137.

Ghez C., Gordon J., Ghilardi M.F., Christakos C.N., Cooper S.E. (1990) Roles of proprioceptive input in the programming of arm trajectories, *Cold Spring Harbor Symp. Quant. Biol.*, 55: 837-847.

Gielen C., van den Heuvel P.J., van Gisbergen J.A. (1984) Coordination of fast eye and arm movements in a tracking task, *Exp. Brain Res.*, 56: 154-161.

Gordon J., Ghilardi M.F., Ghez C. (1994) Accuracy of planar reaching movements. I. Independence of direction and extent variability, *Exp. Brain Res.*, 99: 97-111.

Gordon, J., Ghilardi, M. F., Ghez, C. (1995). Impairments of reaching movements in patients without proprioception. I. Spatial errors, *J Neurophysiol,* 73, 347-360.

Graziano M.S. (1999) Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position, *Proc. Natl. Acad. Sci. USA*, 96: 10418-10421.

Graziano M.S., Gross C.G. (1998) Spatial maps for the control of movement, *Curr. Opin. Neurobiol.,* 8: 195-201.

Hayhoe M., Aivar P., Shrivastavah A., Mruczek R. (in press) Visual short-term memory and motor planning, *Prog. Brain Res.*

Helsen W.F., Elliott D., Starkes J.L., Ricker K.L. (2000) Coupling of eye, finger, elbow, and shoulder movements during manual aiming, *J Mot. Behav.,* 32: 241-248.

Henriques D.Y., Klier E.M., Smith M.A., Lowy D., Crawford J.D. (1998) Gaze-centered remapping of remembered visual space in an open-loop pointing task, *J. Neurosci.,* 18: 1583-1594.

Henriques D.Y.P., Medendorp W.P., Khan A.Z., Crawford J.D. (in press)_Visuomotor Transformations for Eye-Hand Coordination, *Prog. Brain Res.*

Herman R., Herman R., Maulucci R. (1981) Visually triggered eye-arm movements in man, *Exp. Brain Res.,* 42: 392-398.

Johansson R.S., Westling G., Backström A., Flanagan J.R. (2001) Eye-hand coordination in object manipulation. *J. Neurosci.,* 21: 6917-6932.

Koken P.W., Erkelens C.J. (1992) Influences of hand movements on eye movements in tracking tasks in man, *Exp. Brain Res.,* 88: 657-664.

Lazzari S., Vercher J.L., Buizza A. (1997) Manuo-ocular coordination in target tracking. I. A model simulating human performance, *Biol. Cybern.,* 77: 257-266.

Lünenburger L., Kutz D.F., Hoffmann K P. (2000) Influence of arm movements on saccades in humans, *Eur. J Neurosci.,* 12: 4107-4116.

Mather J.A., Fisk J.D. (1985) Orienting to targets by looking and pointing: Parallels and interactions in ocular and manual performance, *Q J Exp. Psychol.-A,* 37: 315-338.

Mather J.A., Putchat C. (1983) Parallel ocular and manual tracking responses to a continuously moving visual target, *J Mot. Behav.,* 15: 29-38.

McIntyre J., Stratta F., Lacquanti F. (1997) Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space [published errata appear in J. Neurophysiol. 1998, 79:preceding 1135 and 1998 Jun, 79:3301], *J. Neurophysiol.,* 78: 1601-1618.

McLaughlin S.C. (1967) Parametric adjustment in saccadic eye movements, *Perc. Psychophys.,* 2: 359-362.

Miall R.C. (1998) The cerebellum, predictive control and motor coordination, *Novartis Found. Symp.*, 218: 272-284.

Miall R.C., Reckess G.Z., Imamizu H. (2001) The cerebellum coordinates eye and hand tracking movements, *Nat. Neurosci.,* 4: 638-644.

Mushiake H., Tanatsugu Y., Tanji J. (1997) Neuronal activity in the ventral part of premotor cortex during target-reach movement is modulated by direction of gaze, *J. Neurophysiol.,* 78: 567-571.

Neggers S.F., Bekkering H. (1999) Integration of visual and somatosensory target information in goal-directed eye and arm movements, *Exp. Brain Res.,* 125: 97-107.

Neggers S.F., Bekkering H. (2000) Ocular gaze is anchored to the target of an ongoing pointing movement, *J Neurophysiol.,* 83: 639-651.

Pisella L., Grea H., Tilikete C., Vighetto A., Desmurget M., Rode G., Boisson D., Rossetti Y. (2000) An 'automatic pilot' for the hand in human posterior parietal cortex: Toward reinterpreting optic ataxia, *Nat. Neurosci.,* 3: 729-736.

Prablanc C., Pelisson D., Goodale M.A. (1986) Visual control of reaching movements without vision of the limb. I. Role of retinal feedback of target position in guiding the hand, *Exp. Brain Res.,* 62: 293-302.

Rossetti Y., Koga K., Mano T. (1993) Prismatic displacement of vision induces transient changes in the timing of eye-hand coordination, *Percept. Psychophys.,* 54: 355-364.

Sailer U., Eggert T., Straube A. (in press a) Implications of distractor effects for the organization of eye movements, hand movements, and perception, *Prog. Brain Res.*

Sailer U., Eggert T., Ditterich J., Straube A. (in press b) Global effect of a nearby distracter on targeting eye and hand movements, *J Exp. Psychol. Hum. Percept. Perform.*Sailer U., Eggert T., Ditterich J., Straube A. (2000) Spatial and temporal aspects of eye-hand coordination across different tasks, *Exp. Brain Res.,* 134: 163-173.

Scarchilli K., Vercher J.L. (1999) Oculo-manual coordination: taking into account the dynamical properties of the arm, *Exp. Brain Res.,* 124: 42-52

Snyder L.H., Batista A.P., Andersen R.A. (2000) Saccade-related activity in the parietal reach region, *J Neurophysiol.,* 83: 1099-1102.

Snyder L.H., Calton J.L., Dickinson A.R., Lawrence B.M. (2002) Eye-hand coordination: saccades are faster when accompanied by a coordinated arm movement, *J. Neurophysiol.,* 87: 2279-2286.

Soechting J.F., Engel K.C., Flanders M. (2001) The duncker illusion and eye-hand coordination, *J Neurophysiol.,* 85: 843-854.

Steinbach M.J. (1969) Eye tracking of self-moved targets: the role of efference, *J Exp. Psychol.,* 82: 366-76.

Stuphorn V., Bauswein E., Hoffmann K.P. (2000) Neurons in the primate superior colliculus coding for arm movements in gaze-related coordinates, *J Neurophysiol.,* 83: 1283-1299.

Tipper S.P., Howard L.A., Paul M.A. (2001). Reaching affects saccade trajectories, *Exp. Brain Res.,* 2: 241-249.

van Donkelaar P. (1997) Eye-hand interactions during goal-directed pointing movements, *Neuroreport,* 8: 2139-2142.

van Donkelaar P., Lee J.-H., Drew A.S. (in press) Cortical frames of reference for eye-hand coordination, *Prog. Brain Res.*

van Donkelaar P., Lee R.G. (1994) Interactions between the eye and hand motor systems: disruptions due to cerebellar dysfunction, *J. Neurophysiol.,* 72: 1674-1685.

Vercher J.L., Gauthier G.M. (1988) Cerebellar involvement in the coordination control of the oculo-manual tracking system: effects of cerebellar dentate nucleus lesion, *Exp. Brain Res.,* 73: 155-166.

Vercher J.L., Gauthier G.M., Guedon O., Blouin J., Cole J., Lamarre Y. (1996) Self-moved target eye tracking in control and deafferented subjects: roles of arm motor command and proprioception in arm-eye coordination, *J. Neurophysiol.,* 76: 1133-1144.

Vercher J.L., Magenes G., Prablanc C., Gauthier G.M. (1994) Eye-head-hand coordination in pointing at visual targets: spatial and temporal analysis. *Exp. Brain Res.*, 99: 507-523.

Vindras P., Viviani P. (1998) Frames of reference and control parameters in visuomanual pointing, *J Exp. Psychol. Hum. Percept. Perform.,* 24: 569-591.

2 Spatial and temporal aspects of eye-hand coordination across different tasks

2.1 Abstract

The way in which saccadic eye movements are elicited influences their latency and accuracy. Accordingly, different tasks elicit different types of saccades. Using such tasks, we analysed combined eye and hand movements to determine whether both motor systems share control strategies. Errors and latencies were measured to examine whether changes in eye motor behaviour are reflected in hand motor behaviour.

Directional and variable errors of eye and hand changed differently according to the tasks. Moreover, errors of the two systems did not correlate for any of the tasks investigated. Contrary to errors, mean latencies of eye and hand movements were organised in the same pattern. A correlation of latencies indicates that both motor systems rely on common information to initiate movement. Temporal coupling was stronger for intentional tasks than for reflexive tasks.

2.2 Introduction

Visual information is crucial for the accuracy of hand movements. As long as the motor reaction relies on visual information, it seems obvious to assume that the two motor systems of eye and hand are coordinated. How they are coordinated, however, is still a matter of debate.

Generally, two aspects of eye-hand coordination are discussed: temporal and spatial coupling. Temporal coupling implies that a common command signal initiates movement, whereas spatial coupling implies that there is a common representation of the target location. A common command signal is typically inferred from similarities in the response of both motor systems to changes in conditions. However, the literature on these two aspects of eye-hand coordination is inconsistent. Among the studies supporting the notion of spatial coupling, Gielen et al. (1984) found similar responses of eye and hand movements to double-step target displacements. Moreover, when presenting two targets simultaneously, eye and arm were always found to move towards the same target. On the basis of these results, the authors assume a common neural representation of target position for both motor systems. Conversely, other authors argue for a separate spatial representation. In a pointing task towards peripheral targets at different eccentricities, Prablanc et al. (1979) found that when cutting off the target at the onset of the saccade, there was no relationship between the errors of the saccade and the corresponding hand movement. The authors therefore suggested separate representations of target position for both motor systems. It is at present difficult to determine the reasons for these contradictory findings, but they may partly be explained by the use of fairly different tasks, and, in particular, different measures.

Likewise, studies on the notion of temporal coupling have yielded inconsistent results. For instance, Herman et al. (1981) found a strong association of ocular and manual reaction times (i.e., a correlation coefficient of .8) in a simple task in which the target had to be touched by a stylus. From the results of other studies, however, the respective authors have concluded that there are separate command signals to specify the initiation of movements. Likewise, Gielen et al. (1984) found more modest correlation coefficients of .6 for single-step stimuli and non-existent correlations for double-step targets in opposite directions after a certain time interval. Similarly, Biguer et al. (1982) found a correlation of only .4 for the initiation of a tracking task (Biguer et al. 1982). Again, it is difficult to find reasons for these divergent results. As pointed out by Gielen et al. (1984) in this context, modest correlations can result from shared perceptual input without necessarily common mechanisms being involved for movement initiation. However, correlations of .8 as found in the study by Herman et al. (1981) cannot be explained simply by shared perceptual input.

Discrepant results have also been reported under different conditions of the same experiment (e.g., Mather and Fisk 1985). In their study, a modest correlation of latencies was observed for orienting to auditory, but not to visual targets, and correlation of end positions was present for targets of short, but not of long duration. From these and other data, Mather and Fisk (1985) conclude that in the early stages of an orienting movement (i.e., the initial analysis of spatial information and movement planning) “the same neural substrates are involved in the processing of sensory information for the eye and limb movements”, whereas in later processing stages each system is controlled by distinct neural circuits.

Such general inconsistency suggests that eye-hand coordination possibly differs with the task employed. Therefore, we investigated combined eye and hand movements towards the same target in a number of different tasks to clarify the conditions under which reaction patterns of eye and hand movements are similar.

It is known that parameters of saccades, e.g., latency and accuracy, vary with the task.. Depending on the response required, saccades can be categorised into two main types:

reflexive (reactive) as opposed to intentional (voluntary) responses. Reflexive saccades are nonwilful and are triggered by a sudden external stimulus, which may be visual or auditory. Intentional saccades are wilful and are triggered internally by a visual stimulus that can be memorised or imagined.

The corresponding tasks provide an opportunity to determine whether changes in eye motor behaviour are reflected in hand motor behaviour. While there have been combined studies of eye and hand movements for the gap task explained below (e.g., Fischer and Rogal 1986; Bekkering et al. 1996), to the best of our knowledge the other tasks have not been investigated with concomitant hand movements.

Four tasks are commonly applied to elicit different types of eye movements: the gap task of reflexive saccades, the memory, scanning and antisaccade task of intentional saccades.

In the gap task, the fixation point is switched off before the lateral target appears; this leads to reduced latencies in saccadic eye movements (e.g., Saslow 1967; Fischer and Rogal 1986). A similar gap effect has been shown for manual movements (Bekkering et al. 1996). In the memory task saccades are made to remembered target locations. Memory-guided saccades require encoding and memorisation of the visual target position. In the scanning task, targets are continuously visible and do not change. Saccades made during scanning can be considered a rather automated process of breaking fixation and redirecting sight towards a feature of the visual scene which has captured the viewer's attention (Burman and Segraves 1994). In the antisaccade task a visual stimulus is presented on one side while the subject is asked to look towards the opposite side of the stimulus (Hallett 1978). This requires the subject to suppress a reflexive saccade towards the visual stimulus (prosaccade) and instead generate a voluntary saccade to the opposite side (Everling and Fischer 1998).

We investigated how parameters of manual and ocular movements vary depending on the task employed. If eye and hand are temporally coupled, i.e., they use common command signals to initiate movements, latencies of both systems should change in a similar way under these conditions in terms of a correlation. If eye and hand are spatially coupled, i.e., they use a common command signal for spatial localisation, we would expect a similar change of ocular and manual errors under these conditions. If hand and eye movements rely on a shared common final motor command to initiate movement and/or to represent the target, a high correlation should be observed independently of the task employed. Accordingly, the present study investigates the conditions under which a common command signal can be assumed.

2.3 Method

2.3.1 Subjects

Ten right-handed employees of the Ludwig-Maximilians University, ages 25 to 41 years, participated in the study. All had normal or corrected-to-normal vision and no history of a neurological disorder.

2.3.2 Apparatus

The target and fixation point was a red laser spot controlled by a mirror galvanometer (General Scanning G120D) and projected onto a screen at eye level and a distance of 138 cm. The target was presented to the subjects at horizontal eccentricities of –20°, -10°, 0°, 10° and 20°. The ongoing target step followed a pseudo-randomised sequence with a constant amplitude of 10°. A computer controlled the position and presentation time of the spot.

Each subject sat in a completely dark room with his right elbow resting on a firm support and the upper arm next to the body. A wooden shield between the chin and the arm prevented vision of the moving arm. The subject wore a plastic glove on the right hand to stabilise the wrist and keep the fingers extended. When pointing, the subject slightly flexed the elbow. A small wooden rod of 34 cm length was attached to the subject's hand by a Velcro ribbon. Two ultrasonic speakers 1 cm in diameter were attached to the rod so that they were 24 cm apart. One speaker was at the height of the first index finger joint and the other speaker in the middle of the forearm. The spatial 3-D location of these speakers was measured at a sampling rate of 100 Hz using an ultrasonic device (Zebris).

Calibration was performed at the beginning of each session and was based on a set of 4 markers with known 3-D coordinates. Over all sessions there was a mean accuracy of 3.6 mm. A laser pointer was fixed to one end of the rod. It projected a red laser spot onto the screen when switched on and its beam was collinear with the line connecting both speakers.

Eye movements were monitored with an infrared corneal reflection device (IRIS Skalar). Analogue output from the IRIS system was digitised at a rate of 1 kHz. The subject's head was stabilised by a chin rest. Each session began with a calibration performed by having the subject saccade to targets at known eccentricities.

Prior to each session 50 practice trials allowed the subjects to practice matching the position of the laser pointer with the target. In the antisaccade paradigm, the practice trial number was increased to up to 100 trials, if necessary, until subjects felt familiar with the task. Then 100 trials were performed in the testing phase of each condition. Each subject was tested under all 6 experimental conditions. The order of conditions was counter-balanced for the subjects.

2.3.3 Tasks

The different tasks employed are illustrated in Figure 1.

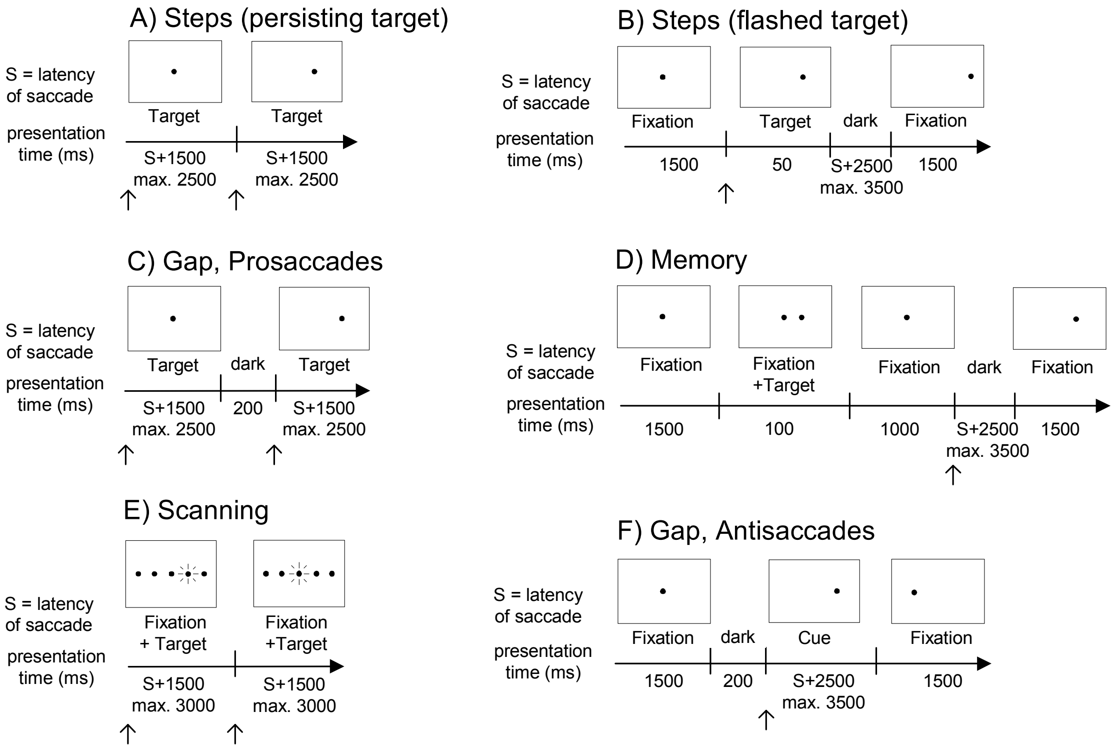


Figure 1 Experimental tasks employed; arrows indicate moments in time when an ocular and manual movement is required. Latencies are related to these moments in time.

For tasks A to C subjects were requested to saccade and point to the target with their eyes and right hand as quickly and accurately as possible. The fixation spot always appeared at the position of the target in the preceding trial.

2.3.3.1 A) Steps with persisting target

At each position, the target stayed on for 1500 ms after a saccade or maximally 2500 ms after target onset, if no saccade was detected. The target then jumped to a new position.

2.3.3.2 B) Steps with flashed target

Subjects looked at a fixation point that remained visible for 1500 ms. Immediately afterwards a target was flashed for 50 ms to the left or right of the previous fixation point. The next fixation spot appeared 2500 ms after a saccade to the target or maximally 3500 ms after target offset, if no saccade was detected.

2.3.3.3 C) Gap, Prosaccades ("proGap")

At each position, the target stayed visible for 1500 ms after a saccade or maximally 2500 ms after target onset, if no saccade was detected. After a darkness interval of 200 ms, the target jumped either to the left or right to a new position.

2.3.3.4 D) Memory

Each trial started with presentation of a fixation point. After 1500 ms, the target appeared for 100 ms to the left or right of the fixation point. Subjects were instructed to continue to fixate the fixation point until it disappeared, 1000 ms after target presentation. The disappearance of the fixation point was the signal for the subject to saccade and point to the remembered position of the target. During the saccade the subject was in complete darkness. The fixation point for the next trial appeared 2500 ms after a saccade or 3500 ms after disappearance of the fixation point if no saccade was detected. Anticipated or reflexive saccades starting before the fixation point disappeared were excluded from further analysis.

2.3.3.5 E) Scanning

Five red laser spots (the brightest indicated the target) were continuously presented. The next target to the left or right was lit up 1500 ms after a saccade or 3000 ms after brightening of the target, if no saccade was detected. Subjects were requested to saccade and point to the target. They were instructed to be on target before the next target lit up. No further time constraints for hand and eye movements were given.

2.3.3.6 F) Gap, Antisaccades ("antiGap")

The subjects looked at a fixation point that remained visible for 1500 ms. A stimulus (red laser spot) was presented to the left or right of the fixation point 200 ms after fixation point offset. The stimulus served as a cue to the location of the target. It appeared at –30°, -20°, -10°, 0°, +10°, +20°, or +30°. Target position was always diametrically opposite the stimulus with respect to the fixation point, at the same eccentricity. The subjects were requested to generate a saccade and make a pointing movement to the opposite side of the stimulus (antisaccade) as quickly and accurately as possible. The stimulus stayed on for 2500 ms after a saccade was detected or maximally for 3500 ms, if no saccade was detected. Subjects were urged to be on target before the fixation point appeared. Trials with manual movements that were completed only after onset of the next fixation point were excluded from further analysis. Only correct anti-movements of eye and hand were included in comparisons with other tasks.

2.3.4 Data acquisition and calibration

Data of hand and eye movements were stored and analysed offline. Eye movements were calibrated by means of a third-order polynominal calibration based on fixation data (for a more detailed description, see Eggert et al. 1999).

Pointing position was first defined as the horizontal coordinate of the point where the connecting line between the two markers and the screen intersected (P', see Figure 2). However, a first inspection of the hand movement data showed a systematic bias of pointing position to the left for all subjects and conditions. To compensate for this bias, we performed a mathematical correction procedure similar to the one suggested by Soechting et al (1990). Instead of using the connecting line between the index marker M1 and the forearm marker M2 to define the pointing direction, M2 was replaced by an imaginary reference point R fixed in space (see Figure 2). For each individual and each task, the coordinates of R(d1,d2) were fitted to minimise the root mean square distance (RMS (ε)) between the target position T and the pointing position P. This procedure was carried out with values of target T and pointing position P which were obtained during the fixation phase preceding each trial. Thus, the compensation was performed on a static error that is not specific for the task at hand. The end point of the connecting line of the index finger marker and the reference point R on the screen represents the pointing position P that is the basis for all further analyses. Pointing position P is expressed in terms of the angle α.

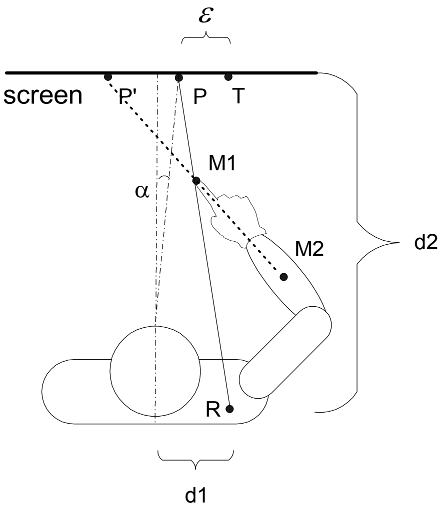


Figure 2 Mathematical fit performed on pointing data. A reference point R (d1,d2) is calculated such that the pointing error ε is minimised. The pointing position P is defined as the horizontal coordinate of the point where the connecting line between R and the index finger marker M1 intersects with the screen. Distance from the screen to the eyes was 138 cm. d2 was constrained to a maximum value of 148 cm.

Sample results of the fit performed on the pointing data of a typical subject under all conditions investigated are given in Table 5 (see Appendix). It is important to note that the coordinates of the reference point R remain constant over all conditions.

Ocular saccades and manual movements were detected automatically on the basis of velocity criteria. The beginning was defined as the moment at which the velocity of the eye or hand exceeded 10% of peak velocity. Minimum peak velocity for characterising a saccade was 150 deg/sec, for a hand movement 15 deg/sec. The end of the saccade or manual movement was defined as the moment at which the velocity of the eye or hand fell below 10% of peak velocity. Maximal latency for a saccade or manual movement to be marked was set at 600 ms. Trials with a binocular or manual latency below 80 ms were classified as anticipatory and discarded.

Only the parameters of the first saccade or manual movement were analysed.

2.3.5 Data analysis

The following parameters were calculated for eye and hand movements:

- latency: time between target onset (disappearance of the fixation point in the memory paradigm) and movement initiation
- directional error: distance of the movement endpoint (in degrees) from the target, signed positively when overshooting the target from the body axis and negatively when undershooting it
- normalised error: subtraction of mean directional errors for each combination of target position and movement direction per individual before pooling the data. In this way, position dependency of the directional error was eliminated.
- variable error: standard deviation of the normalised error, as a measure of endpoint variability

In a first step to organise the data, hierarchical cluster analysis was performed on the latencies and directional errors of eye and hand. Data of the single trials of eye and hand were entered separately. Cluster analysis organises data by abstracting the underlying structure (Jain and Dubes 1988) and identifying relatively homogeneous groups of conditions based on characteristics of similarity. Objects - in our case conditions - are grouped according to indices of proximity between pairs of objects. The proximities can be the distance between pairs of points, such as squared Euclidean distance used in the analysis below. For cluster linkage, Ward's method (Ward 1963), also called the minimum variance method, was employed. Because cluster analysis is explorative, it provides no statistical methods for testing differences between the clusters obtained. Therefore, we further examined the cluster memberships for latencies of eye and hand independently in a subsequent repeated-measurements analysis of variance (task as within-subjects factor) by using planned comparisons on the basis of the clusters identified. The results of cluster analysis for directional errors are not presented below, because almost as many clusters as conditions and no clear pattern of clustering emerged. Cluster analysis was not performed for the variable error as aggregate measure, because the corresponding data matrix would have been too small to allow valid clustering.

Directional and variable errors of eye and hand were each submitted to a 6x2, task x movement type (eye vs hand), repeated-measures analysis of variance. We further calculated the time interval between the end of the eye movement and the end of the hand movement (cf. Biguer et al. 1984). This measurement reflects the maximum time available after foveation for possibly correcting the hand motor output.

Pearson product moment correlations were calculated on a trial by trial basis between ocular and manual latencies as well as between ocular and manual errors. A first inspection of the data showed a systematic bias of errors. Errors were position dependent, which gave rise to spurious correlations. Therefore, to correlate errors we performed a normalisation procedure on the single trials to eliminate effects of systematic biases: for each subject the mean of hand and eye directional error for each combination of target amplitude and target position was calculated. This mean value was subtracted from the single trials. By this method of "mean centering", the data is shifted towards the mean. Thus, only the deviation from the "typical" response is evaluated. The resulting value will be referred to as "normalised error" in the following. It was the basis for calculating the correlations. By transformation to Fisher's Z scores, all the correlations were normalised and submitted to analyses of variance.

2.4 Results

2.4.1 Movement latency

2.4.1.1 Effect of task on mean latencies

Mean saccadic and manual latencies for eye and hand in the different tasks are given in Table 1.

Table 1 Mean eye and hand latencies and standard deviations between subjects for different tasks (each cell represents the mean of subject means, N=10)

Task	*eye*		*hand*	
	mean (ms)	*standard deviation (ms)*	*mean (ms)*	*standard deviation (ms)*
A steps (persisting target)	167	23	245	20
B steps (flashed target)	176	20	255	20
C proGap	160	39	254	48
D memory	318	64	382	99
E scanning	283	71	376	105
F antiGap	377	72	473	104

To determine the prevailing patterns for latencies, separate cluster analyses were performed on the single-trial data of eye and hand. Eye and hand latencies were found to be organised in the same two clusters: the steps conditions (persisting and flashed target) and condition proGap (A, B, C) formed one cluster, while conditions memory, scanning, and antiGap (D, E, F) formed the other cluster. The first cluster is characterised by lower latencies, the second by higher latencies. A plot of mean latencies shows these two clusters (cf. Figure 3).

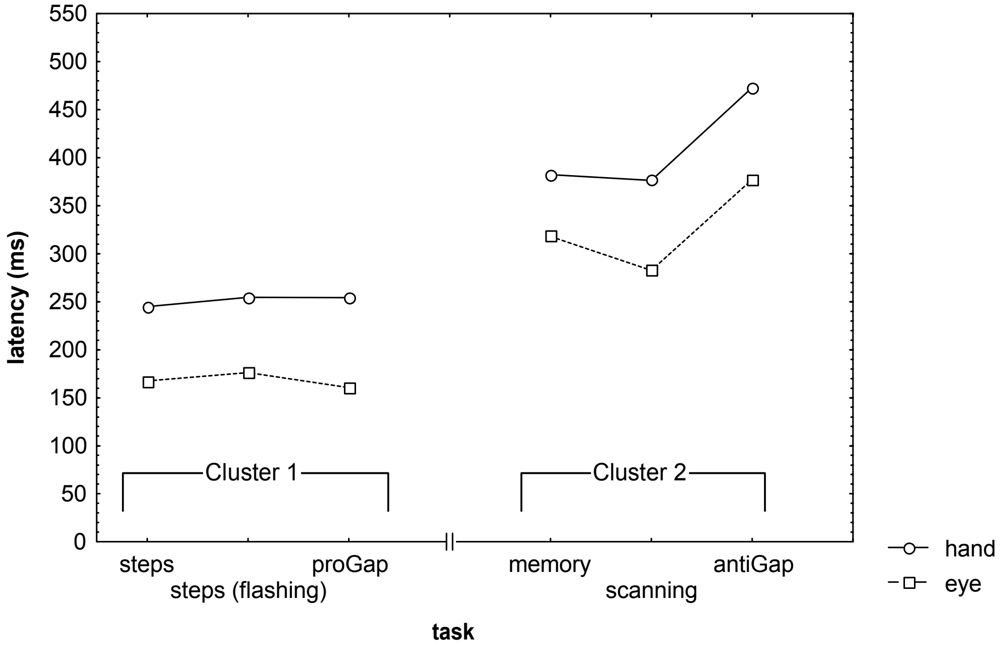


Figure 3 Mean latencies of eye and hand in different tasks

To determine whether the differences between clusters and between the different movement types are significant, an analysis of variance was required. To detect any differential effects of the task on eye or hand, mean latencies were submitted to a 6x2 analysis of variance with the factors *task* (conditions A, B, C, D, E, F) and *movement type* (eye versus hand). There was a highly significant main effect for task (*F*= 26.11, *df*=5, *p*<.001), showing that mean latencies differed over conditions. This was also true for movement type (*F*=62.16, *df*=1, *p*<.001), showing that hand latencies were longer than eye latencies. No interaction of task with movement type was observed. Therefore, eye and hand were not differentially affected by the tasks applied. Planned comparisons confirmed the two latency clusters for eye and hand movements (*F*=146.19, *df*=1, *p*<.001).

In general, the primary saccadic eye movement (*M*=247 ms, *sd*=92 ms) started 84 ms before initiation of the hand movement (*M*=331 ms, *sd*=94 ms). This mean value is slightly larger than that obtained by other authors for purely reflexive tasks, e.g., 70 ms in a speeded aiming task requiring button pressing (Helsen et al. 1998), or 73 ms when quickly pointing to perturbed targets at 15° eccentricity (Carnahan and Marteniuk 1994).

2.4.1.2 Time interval between the end of the eye movement and the end of the hand movement

The eye arrived at the target 386 ms (*sd*=106 ms) before the hand. This time interval is long enough to permit correction of the limb position by visual information about the target location (e.g., Jeannerod 1988; Elliott and Allard 1985).

To check whether this time interval varies with the task, an analysis of variance with the task as within-subjects factor and the time interval between the end of the eye movement and the end of the hand movement as dependent variable was performed. It revealed a significant main effect for the task (F=2.90, df=5, p<.05). This time interval was found to be significantly larger under condition proGap than under the step condition with flashed target and under condition memory (both p <.05), as shown by a post hoc analysis, Tukey's HSD. A closer inspection of the data revealed that this larger time interval was due to longer duration of the hand movement, which delayed the end of hand movement.

2.4.1.3 Correlation of ocular and manual latencies

To investigate temporal coupling of eye and hand, the correlations of eye and hand latencies were calculated on a trial by trial basis. Subsequently, the mean correlation for each task was calculated by averaging the z-transformed correlation coefficients of each subject. They were found to vary between the tasks from .32 to .74 (see Table 2).

Table 2 Mean trial to trial correlation and standard deviation between subjects of eye and hand latencies in different tasks (each cell represents the mean of the individual correlation coefficients, N=10)

Task		*pearson correlation*	*standard deviation*
A	steps (persisting target)	.49	.13
B	steps (flashed target)	.42	.30
C	proGap	.32	.19
D	memory	.68	.39
E	scanning	.59	.42
F	antiGap	.74	.34

(All correlations significantly different from 0 at the 1% level (two-tailed), according to a t-test performed on the z-transformed correlation coefficients of each subject)

The task clearly affected latency correlations of eye and hand. An analysis of variance of the z-transformed correlations of eye and hand latencies with task as within-subjects factor yielded a highly significant main effect for the task (*F*=5.18, *df*=5, *p*<.001). This effect can be specified according to the clusters obtained in the analysis of mean latencies. Planned comparisons of the step conditions (flashed and persisting target) and proGap with the conditions memory, scanning and antiGap confirmed the clusters obtained for mean eye and hand latencies (*F*=20.83, *df*=1, *p*<.01). Thus, eye and hand show closer temporal coupling for movements to remembered targets, scanning and anti- movements than for reactive movements.

In general, two different types of saccades can also be found within the antisaccade task, i.e., correct voluntary antisaccades and wrongly executed reflexive prosaccades. In the present study, this difference in movement types was also observed for hand movements. This provided an opportunity for analysing whether the differences found for different tasks also apply to different types of movements within the same task. Therefore, we performed a separate analysis of latency correlations for different types of movements within the antisaccade task. Eye-hand latency correlations for “wrong” prosaccades and hand movements oriented towards a physically present visual cue were compared with those obtained for correct antisaccades and hand movements towards the cognitively derived target. Trials in which hand and eye moved in different directions were excluded from this analysis.

This criterion was applied to 224 trials in which only the eye erroneously made a reflexive prosaccade, whereas trials with a wrong "pro"-movement only for the hand were absent.

Latency correlation for trials with wrong pro-movements was r=.50 (N=35, p<.01, two-tailed) as opposed to r=.74 (N=495, p<.001, two-tailed) for correct anti-movements. A comparison of the transformed correlation coefficients (Bortz 1993, p. 203; StatSoft 1999, paragraph "other significance tests") showed that correlations for wrong pro-movements were significantly lower (p<.05) than for correct anti-movements.

2.4.2 Movement accuracy

For all calculations involving errors, trials in which the normalised error (as described in the paragraph on data analysis) of eye or hand movements deviated more than 2 standard deviations from the mean over all subjects and conditions were excluded from the analysis.

2.4.2.1 Effect of task on mean errors

Mean directional errors for eye and hand in different tasks are listed in Table 3.

Table 3 Mean directional error in degrees of visual angle and standard deviations between subjects of eye and hand movements for different saccadic tasks (each cell represents the mean of the individual errors, N=10)

Task		*eye*		*hand*	
		mean (deg)	*SD (deg)*	*mean (deg)*	*SD (deg)*
A	steps (persisting target)	-0.18	0.48	1.38	1.96
B	steps (flashed target)	-0.34	0.47	1.25	1.29
C	proGap	-0.14	0.50	3.75	4.13
D	memory	-1.66	1.46	1.77	2.93
E	scanning	0.10	0.48	1.46	3.20
F	antiGap	-0.96	1.66	2.57	2.33

(positive values: overshoot; negative values: undershoot)

Over all conditions, mean directional error for ocular movements was -0.53 deg (*sd*=0.66 deg), and 2.03 deg (*sd*=0.97 deg) for hand movements. Thus, eye movements tend to undershoot the target, while hand movements generally overshoot the target (see Figure 4).

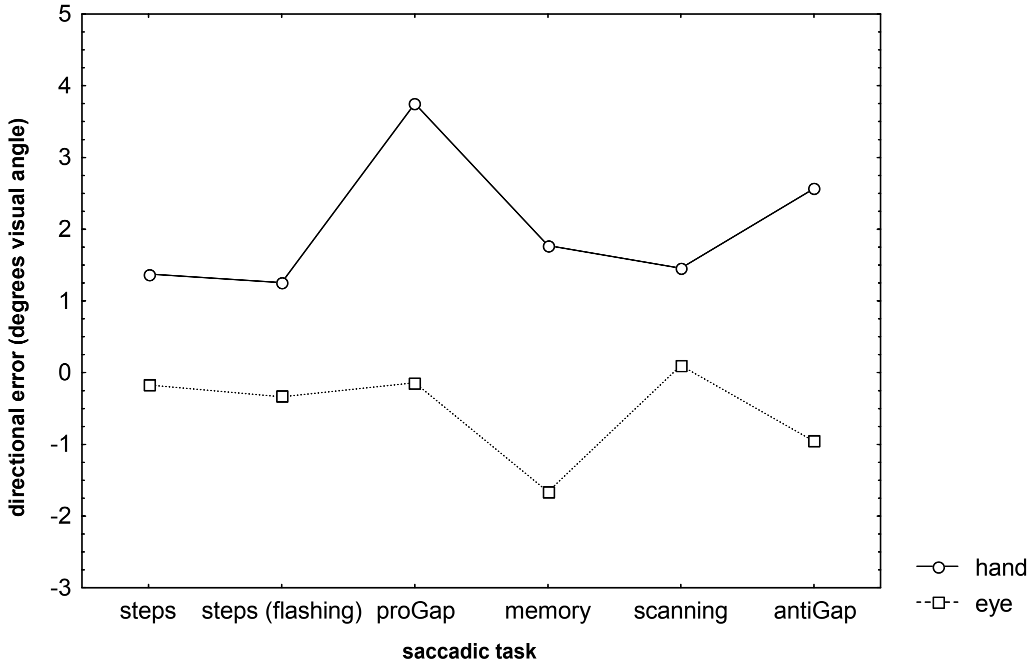


Figure 4 Mean directional error of eye and hand for different tasks

To assess whether errors of eye and hand were organised in a pattern, directional errors (i.e. single trials) were submitted to cluster analysis. As it yielded ambiguous results that were contrary to mean latencies, no hypotheses stemming from cluster analysis were tested for directional errors. Instead, both dependent measures were investigated by means of a separate analysis of variance.

Mean directional errors were affected by both the task and the type of movement. Analysis of directional errors revealed a significant main effect for task (*F*=2.76, *df*=5, *p*<.05) and movement type (*F*=15.58, *df*=1, *p*<.01), indicating that directional errors under all conditions were higher for hand movements than for eye movements. Directional error was also affected by a two-way interaction of the factors movement type x task (*F*=3.21, *df*=5, *p*<.05). The pattern of dependency of the directional error on the tasks was not identical for eye and hand movements. Whereas larger undershoot of the eye was observed in the memory and antiGap task, larger overshoot of the hand was found in both gap tasks.

Mean variable errors are plotted in Figure 5. Analysis of variable errors revealed a significant main effect only for movement type (*F*=59.26, *df*=1, *p*<.0001). Again, variable errors under all conditions were larger for hand movements than for eye movements. Moreover, a two-way interaction of the factors movement type x task (*F*=2.77, *df*=5, *p*<.05) was observed, indicating different patterns of variable error for eye and hand movements.

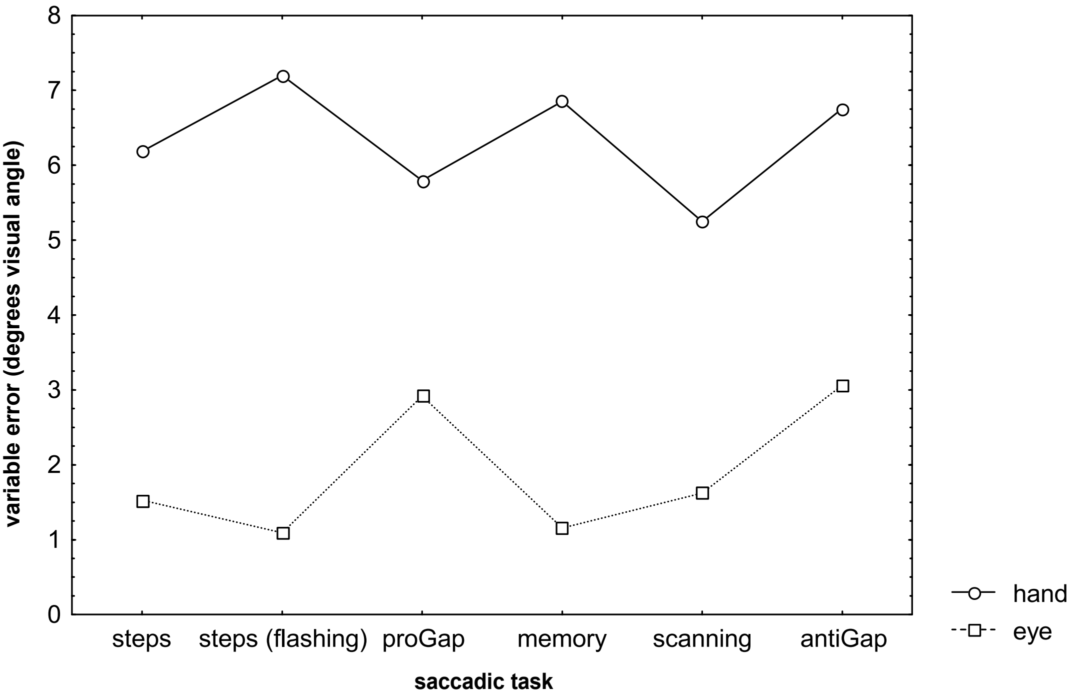


Figure 5 Mean variable error of eye and hand for different tasks

2.4.2.2 *Effect of target flashing on directional and variable errors*

As the eyes reached the target well before the hand, sufficient time was available for updating target position by vision and using it to adjust the hand's landing point. If such an online-correction occurs, variable errors of manual movements should increase under the steps condition, when visual target information is restricted by target flashing as opposed to steps with a persistently visible target .

To determine the effects of target flashing on accuracy of ocular and manual movements, the corresponding variable errors of the step conditions with persisting and flashed target were submitted to a 2x2 (visual target information x movement type) two-factor, within-subject analysis of variance. There was only a main effect for movement type (*F*=83.98, *df*=1, *p*<.0001), i.e., an overall larger variable error for hand movements. Flashing of targets had no influence on variable errors.

An analogous analysis of the directional error was performed, because other studies reported that restricted visual (foveal) target information affected the directional error (e.g., Prablanc et al. 1979; Delreux et al. 1991). Again, only a main effect for movement type was observed (*F*=13.15, *df*=1, *p*<.01), showing that manual directional errors were larger than ocular directional errors. Flashing of targets had no influence on directional errors.

2.4.2.3 Correlation of ocular and manual normalised errors

To investigate spatial coupling of eye and hand, mean correlations of the ocular and manual normalised errors on a trial by trial basis were calculated. Subsequently, the mean correlation for each task was calculated by averaging the z-transformed correlation coefficients of each subject. Mean correlations of eye and hand normalised errors on a trial by trial basis were not significant for any of the conditions tested (see Table 4).

Table 4 Mean trial to trial correlation and standard deviation between subjects of eye and hand normalised errors in different saccadic tasks (each cell represents the mean of the individual correlation coefficients, N=10)

Task	*pearson correlation*	*standard deviation*
A steps (persisting target)	0.09	0.26
B steps (flashed target)	0.16	0.31
C proGap	0.09	0.21
D memory	0.12	0.16
E scanning	-0.03	0.37
F antiGap	-0.02	0.14

(All correlations not significantly different from 0 (two-tailed), according to a t-test performed on the z-transformed correlation coefficients)

To check for effects of the task on correlations, an analysis of variance of the z-transformed correlations of ocular and manual normalised errors with task as within-subjects factor was carried out. There were no significant differences for tasks.

Contrary to latencies, correlations of normalised errors of eye and hand were not compared for correct intentional anti-movements and wrong reflexive pro-movements in the antisaccade paradigm, because there were too few trials for a valid calculation of the normalised error of wrong pro-movements.

2.4.2.4 Effect of target flashing on spatial coupling

Because restricted visual target information prevents updating, the manual movement might be executed purely on the basis of originally encoded information that is perhaps shared with the oculomotor system. We therefore determined whether the error correlation increases in tasks characterised by restricted availability of visual target information, i.e., steps with flashed target compared to steps with a persistently visible target.

The z-transformed error correlations of the step conditions with persistent and flashed target were submitted to a paired-samples t-test. No difference in error correlations was observed.

2.5 Discussion

The way in which saccadic eye movements are elicited is known to influence their latency and accuracy. We investigated eye-hand coordination with different tasks to determine whether there is a similar change in latency and accuracy for eye and hand movements. Such a finding would favour the view that both motor systems share a common command signal to initiate movement or to represent a target.

We found evidence for both common and separate motor commands. First, results of latencies and errors in different tasks are discussed for eye and hand separately, and then the issue of interaction of both motor systems is addressed.

2.5.1 Movement latency

Latencies of eye movements were organised in two clusters: the conditions memory, scanning, and antiGap formed a cluster of increased latencies as opposed to the steps conditions (flashed and persisting target) and proGap, which formed a cluster of lower latencies. These clusters parallel the distinction between reflexive and intentional saccades suggested by Pierrot-Deseilligny et al. (1991) (see Introduction). Reflexive and intentional saccades are commonly believed to be generated by different cortical circuits (Pierrot-Deseilligny et al. 1991). Reflexive saccades are thought to be mediated by pathways from the posterior parietal cortex to the superior colliculus. Intentional saccades are believed to be mediated by pathways from the frontal or supplementary eye field to the brain stem, partially via the superior colliculus (Pierrot-Deseilligny et al. 1991, 1995; Carter and Zee 1997). Interestingly, hand movements were also organised in the same clusters as eye movements. This finding suggests that the dissociation of reflexive versus intentional also characterises hand movements (Benecke et al. 1986). The availability of visual target information in terms of non-target versus on-target movements might not distinguish the two clusters, because under the condition of scanning a target is continuously provided. Instead, the crucial distinction seems to be the way that movements are elicited. Given that the change in latencies appears to occur in parallel for eye and hand movements over tasks, it seems likely that eye and hand movements draw upon the same information. Moreover, the time interval between the end of the eye and hand movement remained constant over most conditions. An exception was condition proGap, where a larger time interval was observed, probably due to a longer duration of the hand movement. This can be explained by the larger overshoot of the hand movement (as discussed in the paragraph “movement accuracy”), because hand movements of a larger amplitude typically take longer to be completed.

2.5.1.1 Correlation of latencies

The same cluster pattern was also found for the correlations of latencies. Correlation coefficients for ocular and manual latencies reported in the literature vary between .5 (Prablanc et al. 1979) and .8 (Herman et al. 1981). We found a correlation of r=.6 and higher for intentional conditions. If hand and eye movements rely on a shared common final motor command, a high correlation independent of the paradigm used would be expected. However, our results suggest that the temporal coupling of eye and hand movements is different for reflexive and intentional tasks.

This pattern is confirmed by an analysis of reflexive ocular and manual “pro”-movements (i.e., prosaccades and hand movements towards the physically present cue) versus intentional ocular and manual “anti”-movements (i.e. antisaccades and hand movements towards the imaginary target) occurring within the same antisaccade paradigm. Again, the correlation for correct anti-movements was significantly higher than for reflexive, wrong pro-movements obtained in the same condition. This implies that signals to initiate movement rely more on the same information for intentional movements than is the case for reflexive movements.

This interpretation agrees with a conclusion that Frens and Erkelens (1991) drew from temporal and spatial data in their study. They suggested that saccades can be generated by two different mechanisms: one relies only on visual information and is used exclusively to generate eye movements; the other relies on visual as well as cognitive information and is used to generate eye and hand movements. Our results suggest that the first mechanism is responsible for the generation of reflexive saccades, while the second operates in both intentional eye and hand movements.

Another observation in our data can be interpreted in terms of the above separation: in the antisaccade paradigm there was a considerably larger number of trials in which only the eye wrongly made a reflexive prosaccade (N=224) compared to trials in which this was the case for eye as well as hand movements (N=35). Trials with a wrong prosaccade only for the hand were absent. This fact might indicate that there is indeed a separate mechanism for the generation of reflexive eye movements.

As to the nature of a common mechanism for generating intentional eye and hand movements, there are at least two possible explanations. From a physiological perspective, the same structures may be involved in the generation of intentional eye and hand movements, e.g., the basal ganglia (as suggested by Frens and Erkelens 1991). The basal ganglia have been shown to play a role in the generation of intentional saccades, because this type of eye movement is impaired by basal ganglia disorders such as Parkinson’s syndrome (e.g., Crawford 1989). Equally, the role of the basal ganglia in the generation of internally triggered arm movements has been demonstrated in non-human primates (van Donkelaar et al. 1999) and in humans (e.g., Georgiou 1997). However, as the respective circuits within the basal ganglia are separate and work in parallel (Alexander et al. 1986), a higher correlation of latencies is difficult to explain. In a recent study comparing human brain areas active during anti-saccades and anti- hand movements a parietal network was found to be active during both eye and hand movements (Connolly et al. 2000). The authors suggest that these areas may be involved in the transformation of visual stimulus location into the location of the anti-target within a common frame of reference.

From a functional point of view, the generation of both intentional eye and hand movements may involve a synchronising process. Intentional tasks require delaying of movement initiation. Given that the delay is large enough so that motor planning is already completed for eye and hand, both systems remain in a kind of “standby mode”. The go-signal then initiates the movements, thereby synchronising both motor systems.

Alternatively, both motor systems may have been already initiated, but the actual execution may depend on common information not yet available, e.g. about target location retrieved from working memory. Thus, waiting for the common information to be available would necessarily result in a synchronising effect.

2.5.1.2 Movement accuracy

While ocular and manual latencies were organised in the same pattern, errors of both systems were not. An interaction of movement type with task demonstrated that directional and variable errors of eye and hand change differently with the task. Ocular directional error was largest (undershoot) under the conditions memory and antiGap. This might be due to the reduced availability of visual target information. A visual target does not exist for antisaccades, while visual information about target location has already started to fade when the reaction is made for memory saccades. For hand movements, however, the directional error was largest (overshoot) under the conditions proGap and antiGap. This finding cannot be explained by the absence of visual target information, as this is not the case for the condition proGap. Probably it can be attributed to the existence of a temporal gap. A closer inspection of the data revealed that the increased directional error under the condition proGap was mainly due to two subjects who consistently showed a systematic overshoot under this condition.

2.5.1.3 Correlation of errors

In accordance with the findings of most studies that examined correlations of ocular and manual errors (e.g., Biguer et al. 1984; Prablanc et al. 1979; Delreux et al. 1991), we found that normalised errors were not correlated for all conditions investigated. This might be attributed to the two motor systems not sharing common information to specify target localisation, although this conflicts with results of Gielen et al. (1984), who suggested that there are common command signals for specifying *where* a target is. It must be kept in mind, however, that the directional error is the result of both movement planning and execution. It is difficult to determine whether a correlation of errors is lacking due to the absence of spatial coupling or due to processes that interfere with movement execution of each effector.

One explanation of the influences during execution holds that errors might not be correlated because an online correction of hand movements was possible. While eye movements are ballistic and probably completely predetermined, this is true only for the first part of a pointing movement (i.e. during acceleration). The second part (deceleration), however, is controlled online and is closed-loop (e.g. Prablanc and Martin 1992; Blouin et al. 1995), so that an ongoing pointing response can be influenced by retinal input after the saccade. Typically, the eye arrives at the target before the hand (e.g., Abrams et al. 1990; Biguer et al. 1982; Carnahan and Marteniuk 1991). In our experiment the eyes were on target 386 ms before the hand, a value similar to the findings of other authors (e.g., Carnahan and Marteniuk 1991; Helsen et al. 1998; Binsted and Elliott 1999). Therefore, visual information about the target can still be gathered before the hand movement is completed, allowing recomputation of target location and adjustment of the ongoing movement on the basis of the updated visual signal (e.g., Prablanc et al. 1986; Vercher et al. 1994). This process might also explain why, based on the analysis of initial movement direction, Frens and Erkelens (1991) found evidence for a common mechanism for generating eye and hand movements with the involvement of cognitive information. Contrary to measures of error, initial movement direction mostly relies on information before the saccade or hand movement. Hence, processes of movement execution like the correction of an ongoing response probably do not interfere to a high degree with this measure.

If visual target information is restricted by target flashing, an online correction of the manual movement might be prevented. If so, mean manual variable error should increase under conditions of such restricted visual information. However, this was not the case. We found that increased visual target information did not contribute to increased accuracy. On first sight, this finding seems to conflict with the results of Prablanc et al. (1979), who reported decreased pointing accuracy when the target was turned off at the onset of the saccade. However, this effect was more pronounced for closed-loop conditions, whereas we prevented visual feedback of the moving hand throughout all conditions.

Because visual target information was restricted and updating was thus prevented, the manual movement might be executed purely on the basis of originally encoded information that may be shared with the oculomotor system. However, error correlations under conditions of restricted visual information, i.e., conditions with flashed targets, memory and antisaccade, were not increased. This finding does not necessarily contradict the view that both systems rely on a common spatial representation, because even with shared information, the hand movement might simply not be executed purely on the basis of the originally visually encoded information. Hence, it seems more logical to assume that a potential spatial coupling is masked by a high rate of motor noise which occurs independently in both motor systems during movement execution. In other words, relatively larger independent noise sources might be interposed between a common spatial representation and the effectors.

Moreover, one cannot rule out the possibility that the amount of motor noise is still higher for pointing in far space than for pointing in near space. This potentially large proportion of unnecessary variance may mask small effects, so that the absent error correlation in our study may to some extent be due to the apparatus used. Therefore, the present experiment should be replicated for pointing movements in near space. Although promising for the analysis of the temporal coupling of eye and hand movements, the use of the tasks employed to clarify the question of spatial coupling seems less helpful. A different, perhaps better approach may be to dissociate both spatial representations.

2.5.2 Conclusion

Our results allowed two basic conclusions:

1. Latencies of ocular and manual movements change in a similar way during different tasks. The higher correlation of latencies under conditions requiring intentional movements compared to reflexive movements indicates that eye and hand movements are based more on shared information when they are intentional, i.e., when cognitive processing is involved.
2. Errors for the two motor systems seem to change differently for all conditions, and correlations are low for all conditions. This cannot be attributed to an on-line correction of the hand movement by visual information alone, because mean variable errors as well as error correlations were not larger under conditions with restricted visual information (flashed target). We suggest that independent noise appearing at a hierarchically lower level during motor generation interferes with a potential coupling of both motor systems.

2.6 Appendix

Table 5 shows data of the mathematical fit performed on pointing data of one subject under all experimental conditions. Exemplary for condition steps with flashed target, single trials for the same subject are plotted in Figure 6. The quality of the fit is obvious from the small deviation of the mean values of fitted pointing positions from the unity slope line.

Table 5 Fit of pointing positions for subject JD in condition steps (flashed target)

task		*d1* (cm)*	*d2* (cm)*	*RMS (cm) (ε)**
steps (persisting target)	fitted solution	17.83	139.90	6.92
	two-marker solution	-	-	37.58
steps (flashed target)	fitted solution	19.24	131.69	5.39
	two-marker solution	-	-	33.88
proGap	fitted solution	13.05	134.49	4.41
	two-marker solution	-	-	36.47
memory	fitted solution	15.65	131.29	6.64
	two-marker solution	-		32.44
scanning	fitted solution	19.85	133.87	5.93
	two-marker solution	-	-	22.48
antiGap	fitted solution	16.79	140.39	7.39
	two-marker solution	-	-	31.92

(* as defined in Figure 2)

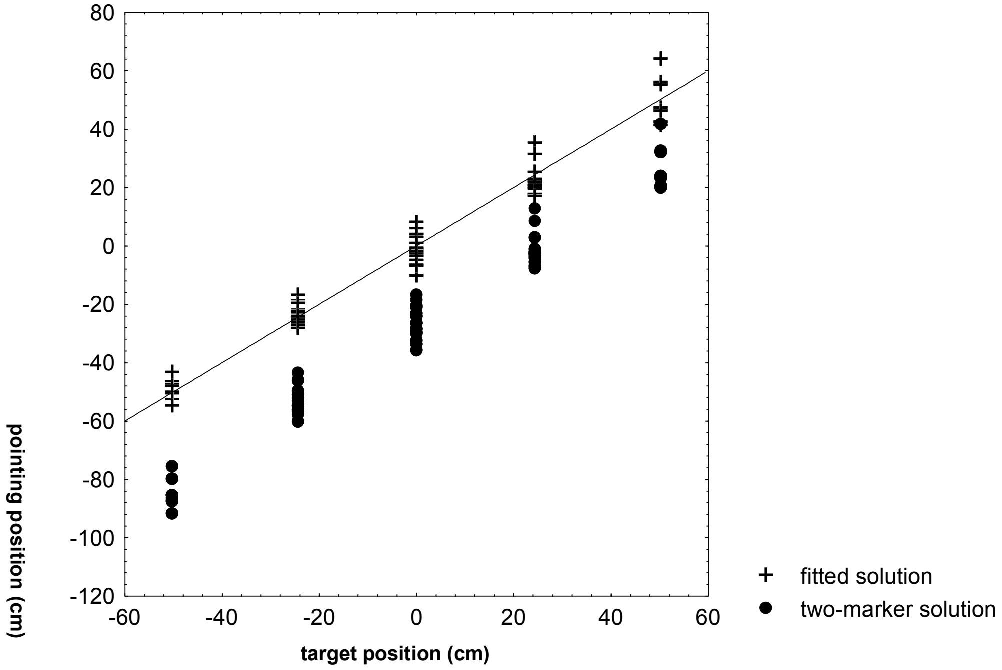


Figure 6 Pointing positions as defined by connecting two markers and by performing a fit on the one-marker solution of subject JD under the condition steps with flashed target. The line represents a unity slope line.

2.7 Acknowledgements

We are indebted to Marc Hassenzahl for preliminarily reviewing the manuscript and to Thomas Schenk for useful comments on the Discussion.

2.8 References

Abrams RA, Meyer DE, and Kornblum S (1990) Eye-hand coordination: oculomotor control in rapid aimed limb movements. J Exp Psychol Hum Percept Perform. 16: 248-267

Alexander GE, DeLong MR, Strick PL (1986) Parallel organization of functionally segregated circuits linking basal ganglia and cortex. Annu.Rev.Neurosci. 9: 357-381Bekkering H, Pratt J, and Abrams RA (1996) The gap effect for eye and hand movements. Percept Psychophys 58: 628-635

Benecke R, Rothwell JC, Dick JP, Day BL, and Marsden CD (1986) Performance of simultaneous movements in patients with Parkinson's disease. Brain 109: 739-757

Biguer B, Jeannerod M, and Prablanc C (1982) The coordination of eye, head, and arm movements during reaching at a single visual target. Exp Brain Res 46: 301-304

Biguer B, Prablanc C, and Jeannerod M (1984) The contribution of coordinated eye and head movements in hand pointing accuracy. Exp Brain Res 55: 462-469

Binsted G, and Elliott D (1999) Ocular perturbations and retinal/extraretinal information: the coordination of saccadic and manual movements. Exp Brain Res 127: 193-206

Blouin J, Bridgeman B, Teasdale N, Bard C, Fleury M (1995) Visual stability with goal-directed eye and arm movements towards a target displaced during saccadic suppression. Psychol.Res. 58: 169-176Bortz J (1993) Statistik für Sozialwissenschaftler. Springer, Berlin

Burman DD, and Segraves MA (1994) Primate frontal eye field activity during natural scanning eye movements. J Neurophysiol 71: 1266-1271

Carnahan H, and Marteniuk RG (1991) The temporal organization of hand, eye, and head movements during reaching and pointing. J Mot Behav 23: 109-119

Carnahan H, and Marteniuk RG (1994) Hand, eye, and head coordination while pointing to perturbed targets. J Mot Behav 26: 135-146

Carter N, and Zee DS (1997) The anatomical localization of saccades using functional imaging studies and transcranial magnetic stimulation. Curr Opin Neurol 10: 10-17

Connolly JD, Goodale MA, Desouza JF, Menon RS, Vilis T (2000) A comparison of frontoparietal fMRI activation during anti-saccades and anti-pointing. J Neurophysiol. 84: 1645-1655

Crawford TJ, Henderson L, Kennard C (1989) Abnormalities of nonvisually-guided eye movements in Parkinson's disease. Brain 112: 1573-1586Delreux V, Vanden-Abeele S, Crommelinck M, and Roucoux A (1991) Interactions between goal-directed eye and arm movements: Arguments for an interdependent motor control. J Mot Behav 23: 147-151

Eggert T, Mezger F, Robinson F, and Straube A (1999) Orbital position dependency is different for the gain of externally and internally triggered saccades. Neuroreport 10: 2665-2670

Elliott D, and Allard F (1985) The utilization of visual feedback information during rapid pointing movements. Q J Exp Psychol A Hum Exp Psychol 37A: 407-425

Everling S, and Fischer B (1998) The antisaccade: a review of basic research and clinical studies. Neuropsychologia 36: 885-899

Fischer B, and Rogal L (1986) Eye-hand-coordination in man: a reaction time study. Biol Cybern 55: 253-261

Frens MA, and Erkelens CJ (1991) Coordination of hand movements and saccades: evidence for a common and a separate pathway. Exp Brain Res 85: 682-690

Georgiou N, Phillips JG, Bradshaw JL, Cunnington R, Chiu E (1997) Impairments of movement kinematics in patients with Huntington's disease: a comparison with and without a concurrent task. Mov Disord 12: 386-396

Gielen C, van den Heuvel PJ, and van Gisbergen JA. (1984) Coordination of fast eye and arm movements in a tracking task. Exp Brain Res 56: 154-161

Hallett PE (1978) Primary and secondary saccades to goals defined by instructions. Vision Res 18: 1279-1296

Helsen WF, Elliott D, Starkes JL, and Ricker KL (1998) Temporal and spatial coupling of point of gaze and hand movements in aiming. J Mot Behav 30: 249-259

Herman R, Herman R and Maulucci R (1981) Visually triggered eye-arm movements in man. Exp Brain Res 42: 392-398

Jain AK, Dubes RC (1988) Algorithms for Clustering Data. Prentice Hall, Englewood Cliffs, New Jersey

Jeannerod M (1988) The neural and behavioural organization of goal-directed movements. Clarendon Press/Oxford University Press, Oxford, England UK

Mather JA, and Fisk JD (1985) Orienting to targets by looking and pointing: Parallels and interactions in ocular and manual performance. Q J Exp Psychol A Hum Exp Psychol 37A: 315-338

Pierrot-Deseilligny C, Rivaud S, Gaymard B, and Agid Y (1991) Cortical control of memory-guided saccades in man. Exp Brain Res 83: 607-617

Pierrot-Deseilligny C, Rivaud S, Gaymard B, Muri R, and Vermersch AI (1995) Cortical control of saccades. Ann Neurol 37: 557-567

Prablanc C, Echallier JF, Komilis E, and Jeannerod M (1979) Optimal response of eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. Biol Cybern 35: 113-124

Prablanc C, Martin O (1992) Automatic control during hand reaching at undetected two-dimensional target displacements. J.Neurophysiol. 67: 455-469

Prablanc C, Pelisson D, and Goodale MA (1986) Visual control of reaching movements without vision of the limb. I. Role of retinal feedback of target position in guiding the hand. Exp Brain Res 62: 293-302

Saslow MG (1967). Latency for saccadic eye movement. J Opt Soc Am 57: 1030-1033

Soechting JF, Tillery SIH, and Flanders M (1990). Transformation from head- to shoulder-centered representation of target direction in arm movements. J Cognit Neurosci 2: 32-43

StatSoft (1999). Electronic Statistics Textbook. Tulsa, Oklahomavan-Donkelaar P, Stein JF, Passingham RE, Miall RC (1999) Neuronal activity in the primate motor thalamus during visually triggered and internally generated limb movements. J.Neurophysiol. 82: 934-945

Vercher JL, Magenes G, Prablanc C, and Gauthier GM (1994) Eye-head-hand coordination in pointing at visual targets: spatial and temporal analysis. Exp Brain Res 99: 507-523

Ward JH Jr (1963) Hierarchical grouping to optimize an objective function. J Am Stat Assoc 58: 236-244

3 Global effect of a nearby distracter on targeting eye and hand movements

3.1 Abstract

Eye-hand coordination was investigated with the “global-effect paradigm”, a task that presents a target close to a distracter. Saccades typically land at an intermediate position, the “centre of gravity” of the configuration. This so-called global effect or spatial averaging is attributed to incomplete target selection.

Four experiments showed that the global effect also exists for hand movements. As the global effect was mostly similar for eye and hand, both are coupled at the level of target selection. However, under some conditions the global effect was different for eye and hand. This suggests that their coupling is not achieved via a shared target representation. Instead, eye and hand seem to use two separate target representations that exchange information. This interpretation is supported by the convergent amplitudes of eye and hand with simultaneous execution. The same was true for latencies.

3.2 Introduction

A great number of daily activities require the coordinated action of eye and hand. Whether reaching for a coffee cup or playing tennis, it is necessary to couple motor information with visual information for these actions to be successful. Since the hand motor system relies on visual information, it seems likely that the motor systems of eye and hand are closely coupled. Coupling can be studied with respect to the time of movement initiation and the representation of target position of both eye and hand.

It is generally assumed that the information used for *movement initiation* differs for hand and eye movements (e.g., Gielen, van den Heuvel, & van Gisbergen, 1984), at least in the case of reactive movements (Sailer, Eggert, Ditterich, & Straube, 2000). This assumption is supported by the rather weak correlations found between eye and hand movement latencies towards visual targets (e.g., Frens & Erkelens, 1991; Neggers & Bekkering, 1999). Movement initiation is thus probably based on two parallel motor commands generated after the arrival of visual information rather than on a single common motor command.

Whereas coupling of movement initiation (temporal coupling) has been thoroughly investigated, less is known about the coupling of *target position representation* (spatial coupling). There is, however, increasing evidence that this information is shared by eye and hand (e.g., Gielen et al., 1984; Mather, 1985). Several studies have demonstrated that retinal and extra-retinal signals obtained during a saccade influence reaching movements. For example, hand amplitude was found to increase systematically with saccade amplitude (van Donkelaar, 1997, 1998). Moreover, even a change of saccadic amplitude during saccadic adaptation transfers to the hand motor system (Bekkering, Abrams, & Pratt, 1995; de Graaf, Pélisson, Prablanc, & Goffart, 1995). It has also been proposed that eye position itself may provide the target for the hand motor system (Adam, Ketelaars, Kingma, & Hoek, 1993; Soechting, Engel, & Flanders, 2001). Other studies, on the contrary, raise doubts about a close spatial coupling of eye and hand. Several studies that have correlated the end positions of eye and hand reported only weak correlations (Biguer, Prablanc, & Jeannerod, 1984; Delreux, Vanden-Abeele, Crommelinck, & Roucoux, 1991; Sailer et al., 2000).

These discrepancies and the difficulties of interpreting them may result from the use of different tasks that address coupling at different stages of target processing or movement generation. Table 1 shows how the different stages of movement generation could be conceptualised and to which stage the dependent variables used to measure coupling by some example studies could be attributed. Accordingly, whether coupling occurs or not may depend on the stage of movement generation studied. However, it is not always clear which stage of movement generation was addressed by the studies. For example, it is unclear whether adaptation takes place at the stage of early sensory perception or upon movement execution (Bekkering 1995).

These different stages of movement generation can be measured by various dependent variables. For example, the coupling of movement directions (Frens & Erkelens 1991) deals with coordination at a point right after movement programming. Kinematic parameters, such as initial hand acceleration (found to be affected by saccadic programming by van Donkelaar, 1998), are a measure of coupling at a somewhat later point in time during movement programming than directions. End position correlations investigate coupling at the last possible moment, i.e., after movement programming, potential on-line correction of the hand, and execution have been completed. Coupling at this stage would suggest common information or processing stages at least at the end of the movement generation process.

Table 1 Examples for studies investigating spatial coupling of eye and hand at different stages during the process of movement generation, their dependent variables and conclusions about coupling

Stage of movement generation	*Dependent variable*	*Coupling?*	*Example study*
Visual input (early sensory perception)	Degree of adaptation of amplitude or end position[a]	High	Bekkering (1995), De Graaf et al. (1995)
Movement programming	Movement direction	High	Frens and Erkelens (1991)
	Initial hand acceleration	High	Van Donkelaar (1998)
Target selection	Changes in eye trajectory	High	Tipper et al. (2001)
Movement execution	End position correlation	Low	Biguer et al. (1984); Delreux et al. (1991); Sailer et al. (2000).

[a] This dependent variable and the respective studies could also be assigned to the stage of movement execution

Generally, coupling is found at all stages except for movement execution, which is measured by the correlation of end positions. An exception was recently reported by Soechting et al. (2001), who found that pointing errors and errors at the final gaze position were highly correlated, even when saccades had drifted to this final position. A possible explanation for this discrepancy is that Soechting et al. used a visual illusion. Under conditions of ambiguous visual stimulation eye position information may be more important for guiding hand movements. In the case of an illusion, eye-hand coupling may be affected already at a very early stage, e.g., the level of early sensory perception.

The coupling of eye and hand seems to be greater at the initial stages of movement generation (Mather & Fisk, 1985), when the same neural structures may be involved in information processing. Likewise, it has been suggested that concurrent saccades can influence hand motor control only during a limited time frame (van Donkelaar, 1998). In brief, to better understand eye-hand coupling, we believe it is necessary to specify the stage at which coupling is studied. This requires a paradigm that uses the observed effects to determine the stage of movement generation. One such paradigm is the “global effect paradigm”, a task requiring saccades to a target in the proximity of a distracter. Under this condition, saccades land at a position intermediate between target and distracter. Apparently, target and distracter are not completely resolved spatially by the saccadic system. This effect is referred to as “spatial averaging” or “centre of gravity” effect (Coren & Hoenig, 1972), or more generally, the “global effect” of the target distracter configuration (Findlay, 1981, 1982). According to the classification in Table 1, the global effect would occur on the level of target selection only.

More specifically, the global effect is assumed to arise from the limited time available for processing information about target position prior to a saccade. This temporal limit may lead to the global effect in two ways. First, visual processing initially uses a coarse spatial scale that is followed by finer spatial scales (Coeffé & O'Regan, 1987; Watt, 1987). If saccades are triggered after only a coarse stage of visual processing is completed, the discrimination of peripheral targets is poor and results in saccadic averaging. Second, the global effect may be the consequence of saccadic response selection, i.e., of the saccade being initiated before the target has been discriminated from the distracter (Aitsebaomo & Bedell, 2000; Coeffé & O'Regan, 1987; Ottes, van Gisbergen, & Eggermont, 1985). Both explanations place the "global effect" at an early stage of processing.

Indeed, averaging saccades are typically saccades with relatively short latencies. The averaging effect is diminished or even disappears with increasing latencies. This applies both to long-latency saccades within the natural variation of latencies (Ottes et al. 1985) and to responses delayed by instruction (Coeffé & O'Regan, 1987; Findlay, 1983; Ottes et al., 1985). It is currently under debate whether the increased saccadic accuracy is due to the fact that visual information about the configuration is more detailed, or whether the target separation process has been completed (Aitsebaomo & Bedell, 2000; Eggert, Sailer, Ditterich, & Straube, submitted).

To use the "global effect paradigm" to study eye-hand coordination, it is necessary to know whether the effect also pertains to hand movements. To our knowledge this has not been investigated so far. One result that suggests that hand movements have a similar effect stems from a study that measured the direction of reaching movements towards a target appearing after - not simultaneously with - a peripheral distracter was presented (Lee, 1999). Hand movements with latencies below 200 ms were mostly initiated towards the distracter, whereas movements with latencies above 300 ms were mostly initiated towards the target. At latencies between 200 and 300 ms, movements were often initially directed between the distracter and the target. Initial movement direction gradually changed from the distracter to the target as the latency increased.

The goal of the present study was to investigate spatial eye-hand coordination by the "global effect paradigm", a target-distracter configuration. This paradigm allows us to specify the level during the movement generation process at which coupling takes place, namely target selection. If the hand motor system accesses eye movement information at a later point in time, i.e., when target separation is already completed, then no global effect should be observed for hand movements. If, in contrast, hand movements are based on the same initial information (target representation) as eye movements, hand movements should not only show a global effect, but also one of comparable magnitude.

To this aim, eye and hand movements towards targets with and without a distracter were investigated when performed alone (single-task conditions), as well as concurrently (dual-task condition). Consequently, it was possible to determine potential effects of the target-distracter configuration on hand and eye movements separately. Moreover, we determined whether this effect is mediated by the influence of one motor system on the other. If the global effect is specific to eye movements, then no such effect should be observed for hand movements alone. However, it could spread to the hand movement system in the dual-task condition if both are tightly coupled.

3.3 Experiment 1

Experiment 1 used a distracter less eccentric than the target. Therefore, a global effect would be manifest in a reduced movement amplitude in the presence of a distracter. Classically, eye and hand should land in-between the target and the distracter.

3.3.1 Method

3.3.1.1 Subjects

Nine research workers from the neurology department, three women and six men (age 27-42 years), participated in the experiment. Five of them were naïve with respect to the hypotheses and the purpose of the experiment, four of them (the authors) were not. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). All subjects were right-handed, except for one subject who was ambidextrous.

3.3.1.2 Apparatus

The subjects viewed a 15-inch flat screen color monitor (NEC MultiSync LCD 1525S) with a frame frequency of 72 Hz and a spatial resolution of 1280*1024 pixels. The screen was reinforced by an additional pane of perspex. It was firmly screwed to a table at an angle of 50 deg. The subjects were seated in front of the table at a distance of approximately 35 cm from the screen with their right elbow resting on a padded support and their head stabilised by a chin rest. A personal computer was used for experimental control, visual presentation, control of video signals (via a TIGA (Texas Instruments Graphics Adapter) interface), and data collection. The stimuli appeared on a dark grey background.

3.3.1.3 Measurement of hand and eye movements

To measure hand movements, one ultrasonic speaker, 1 cm in diameter, was attached to the tip of the subject's right index finger. This speaker's spatial 3-D location was sampled at 200 Hz by an ultrasonic device (Zebris, Isny, Germany). Pointing position was defined as the horizontal coordinate of this speaker. A calibration of the system was performed at the beginning of each session based on a set of four markers with known 3-D coordinates. This yielded a mean accuracy of 3.6 mm over all sessions. Hand movements were calibrated by having the subjects point to targets at known eccentricities.

Horizontal eye movements were measured with an infrared corneal reflection device (IRIS, Skalar, Delft, Netherlands), sampled at 1 kHz. Eye movements were calibrated by having the subject fixate targets at known eccentricities.

All data were stored for later off-line analysis. Raw eye and hand movement data were calibrated by means of a third-order polynomial based on fixation data or pointing data, respectively. For a hand movement to be marked as a pointing movement, its peak velocity had to exceed 10 deg/sec and its amplitude 5 deg. For an eye movement to be marked as a saccade, its peak velocity had to exceed 50 deg/sec and its amplitude 5 deg. The moment at which velocity exceeded or fell below 10% of peak velocity determined the beginning or end of a hand or eye movement.

Trials in which eye movements were required were discarded if saccade latency exceeded 1000 ms. Trials with eye or hand movement latencies below 80 ms were excluded because they were considered anticipatory. During the hand-alone condition, trials were discarded in which a saccade occurred before completion of the pointing movement. Outliers were defined separately for each condition and for trials with and without distracters to be trials in which the gain of the eye or hand movement (ratio eye or hand amplitude to target amplitude) deviated more than 2 standard deviations from the mean gain across all subjects.

3.3.1.4 Stimuli and task

The paradigm is shown in Figure 1. A red fixation spot was presented for 1500 ms. 100 ms after it was extinguished, a peripheral white target spot was flashed for 50 ms. This target appeared at a random position between 8 and 10 deg of visual angle to the right or left of the fixation spot. In 50% of the trials, a white distracter spot was flashed for 50 ms together with the target. It was located at a distance of 4 deg from the target and was always closer to the fixation spot than the target. The vertical coordinate of target and distracter was always 0. The subjects could not distinguish target and distracter by appearance, they had to be told.

When the target disappeared, the background illumination of the monitor was turned off, leaving the subject in complete darkness. The fixation spot of the next trial appeared at the previous target position 1500 ms after a saccade was detected, or 2000 ms after the target disappeared, if no saccade was detected within 500 ms after target disappearance.

The subject's task was to move towards the target as quickly as possible. When two white spots appeared, they were told to "move towards the more eccentric one, i.e., the one further away from the fixation spot". The task entailed three conditions: (a) saccade to the target (single-task condition, eye), (b) saccade and point to the target (dual-task condition), and (c) point to the target while keeping the eyes fixated at the location of the (now extinguished) fixation spot (single-task condition, hand). To facilitate fixation under the latter condition, the subject was told to not make any eye movement before the monitor was switched on again. The subjects were further instructed to realign their eye and/or hand with the fixation spot at the beginning of the next trial.

Practice trials were performed both during the subjects' first session and the hand-alone condition (single-task condition, hand) until they felt familiar with the task. Each condition consisted of 200 trials, 100 with distracter and 100 without distracter. Subjects performed all three experimental conditions, each on a different day. The order of the conditions was counter-balanced.

3.3.1.5 Dependent variables and offline analysis

Two dependent variables were calculated for both eye and hand movements, latency and the signed amplitude error.

Latency was defined as the time interval between target onset and movement initiation.

The signed amplitude error was defined as the difference between primary eye or hand amplitude and target amplitude. The amplitude of eye, hand, and target was defined as the difference between the respective start and end position. Positive amplitudes denote movements to the right, negative amplitudes movements to the left.

The sign of the amplitude error was adjusted to reflect the movement direction, so that negative error values indicated an undershoot and positive values an overshoot. Consequently, with identical target amplitudes, the smaller the error was, the smaller the movement amplitude. Compared to the measure of amplitude, the signed amplitude error has the advantage of eliminating the variations in target amplitude (distance of the target from the fixation spot), because the distance of the target from the distracter does not change. It is important to keep in mind that a smaller signed amplitude error does not mean increased accuracy but increased undershoot or reduced overshoot. Subsequently the term “amplitude” will sometimes be used for better understanding.

First, each dependent variable was analysed separately for eye and hand by means of a repeated-measurements ANOVA with the factors *task condition* (single/dual) and *distracter status* (present/absent).

Second, to determine whether the effect of the distracter was similar on eye and hand movements, eye and hand data were entered into one common analysis, introducing the factor *movement type* (eye/hand). One problem of such an analysis is that potential differences between eye and hand may reflect a latency difference between eye and hand instead of a direct influence on the target representations. This is because manual latencies are typically much higher than saccadic latencies, and the amplitudes of eye and hand depend on latency (e.g., Findlay, 1983; Prablanc, Echallier, Komilis, & Jeannerod, 1979). To distinguish an influence of the distracter on target representations from mere latency differences, latency was introduced as a changing covariate in a repeated-measurements ANOVA with the factors *movement type* (eye/hand), *task condition* (single/dual), and *distracter status* (present/absent). This compensates for the effect of latency on the signed amplitude error, but only if there is a linear relationship between latency and signed amplitude error, which is homogeneous across the factor levels involved. Therefore, this analysis is only a first approach to separate direct effects of the distracter on the target representation from indirect effects mediated by latency.

Further analyses are necessary to examine more complicated latency-mediated effects, e.g., a latency dependence of the signed amplitude error that is different across factor levels, i.e., for trials with and without distracter. Such an effect is suggested by findings in the literature, because, typically, the global effect is most likely when the response is fast, prior to efficient target selection. Therefore, we investigated in a further analysis whether the dependence of the global effect on latency was similar for eye and hand movements. First, latencies were broken down into four bins. The latencies were sorted separately for eye and hand movements from fastest to slowest across all subjects and conditions and then were split into four equally large groups. Univariate analyses of variance confirmed that these groups were in all experiments different from each other. These groups formed the factor *latency group* for the later analysis of variance. Then the mean signed amplitude errors of eye and hand movements were calculated for each group level and separately for each distracter status (present/absent). Data were collapsed across single and dual task conditions in order to ensure a sufficient number of data values for the analysis. The signed amplitude errors of eye and hand were then submitted to a 2x4x2 repeated-measures ANOVA with the factors movement type (eye/hand), latency group (1/2/3/4), and distracter status (present/absent). Larger distracter effects with faster latencies would become evident if distracter status and latency group interacted. The Mauchly test was applied to determine sphericity of the data. If the data were not spherical, the Huynh-Feldt correction was applied. In this case, the corrected degrees of freedom and significances are reported. Post-hoc comparisons were always based on the Scheffé test.

3.3.2 Results

3.3.2.1 Eye movements

3.3.2.1.1 Saccadic latencies

The mean saccadic latencies for each subject are presented in Table 2.

Table 2 Mean eye and hand latencies and signed amplitude errors (standard deviation in parentheses) in exp. 1 and 2

	exp. 1 (distracter less eccentric than target)				*exp. 2 (distracter more eccentric than target)*			
dependent variable	*single-task*		*dual-task*		*single-task*		*dual-task*	
	distracter absent	*distracter present*	*distracter absent*	*distracter present*	*distracter absent*	*distracter present*	*distracter absent*	*distracter present*
latency eye (ms)	276 (72)	288 (80)	298 (74)	315 (71)	257 (91)	269 (270)	288 (291)	299 (302)
latency hand (ms)	582 (243)	600 (253)	391 (87)	395 (88)	442 (216)	449 (227)	350 (68)	360 (90)
signed eye amplitude error (deg)	-0.42 (0.95)	-0.99 (0.92)	-0.98 (1.01)	-1.45 (1.08)	-0.50 (1.32)	0.37 (1.44)	-0.86 (1.21)	-0.22 (1.46)
signed hand amplitude error (deg)	0.70 (0.75)	0.55 (0.77)	-0.08 (0.62)	-0.30 (0.74)	0.76 (0.80)	1.46 (1.03)	-0.18 (0.60)	0.38 (0.71)

There was a main effect of distracter status ($F_{1,8} = 14.34$, $p<.01$). Saccadic latencies were significantly higher when the distracter was present than when the distracter was absent. There was also a main effect of task condition ($F_{1,8} = 9.11$, $p<.05$). Saccadic latency was higher in the dual-task condition than in the single-task condition. Thus, it took longer to initiate an eye movement with concomitant hand movements. There were no significant interactions.

3.3.2.1.2 Signed eye amplitude error

The mean signed eye amplitude error for each subject is presented in Table 2. There was a main effect of distracter status ($F_{1,8} = 8.78$, $p<.05$). The signed eye amplitude error was significantly smaller, i.e., movement amplitude was smaller, when the distracter was present than when it was absent (see Figure 2). Thus, eye movements landed in-between the target and the less eccentric distracter. No other effects were significant.

3.3.2.2 Hand movements

3.3.2.2.1 Manual latencies

The mean manual latencies for each subject are presented in Table 2. There was a main effect of task condition ($F_{1,8} = 9.35$, $p<.05$). Manual latency was higher in the single-task condition than in the dual-task condition. Contrary to eye movements, hand movements were initiated faster with concomitant eye movements. There was also a marginally significant main effect for distracter status ($F_{1,8} = 4.26$, $p=.07$). Manual latency was higher when the distracter was present (*M*=486 ms, *SD*=156 ms, *N*=9) than when absent (*M*=497 ms, *SD*=160 ms, *N*=9). Thus, the distracter seemed to interfere with planning and initiating a hand movement towards the target.

3.3.2.2.2 Signed hand amplitude error

The mean signed hand amplitude error for each subject is presented in Table 2. There was a main effect of distracter status ($F_{1,8} = 8.57$, $p<.05$). The signed hand amplitude error was significantly smaller, i.e., movement amplitude was smaller when the distracter was present than when it was absent (see Figure 2). Hand movements always landed outside the target-distracter configuration, but in the presence of a distracter this overshoot was reduced. There was also a main effect of task condition ($F_{1,8} = 16.85$, $p<.01$). The hand amplitude was larger in the single-task condition than in the dual-task condition. Moreover, there was also a change in the direction of the error. Whereas the hand overshot in the single-task condition, it undershot in the dual-task condition, thus approaching the landing position of the eye. No other effect was significant.

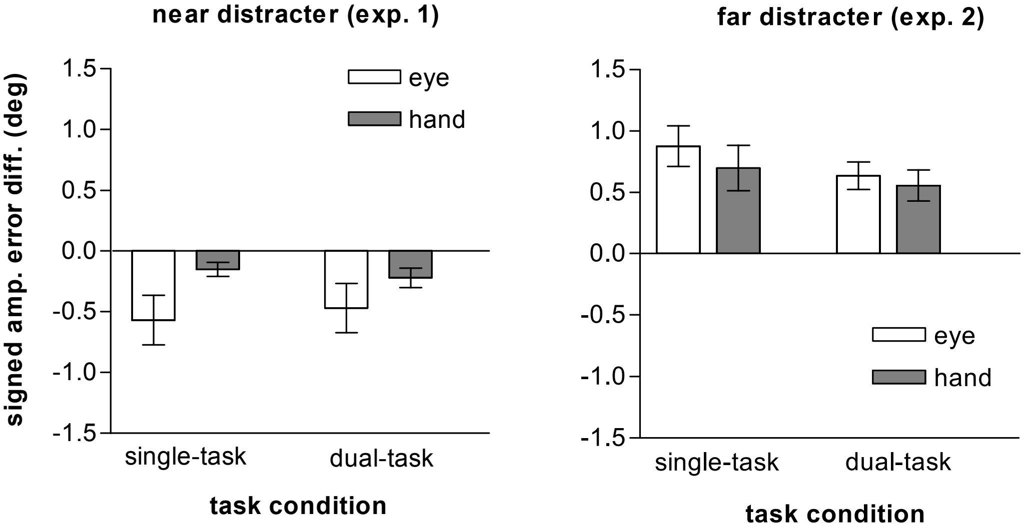


Figure 2 Difference in eye and hand signed amplitude errors between trials with and without distracter, (i.e., size of the global effect), and standard error of the mean (N=9) across single and dual-task conditions in experiment 1 (near distracter, i.e., distracter less eccentric than target) and experiment 2 (far distracter, i.e., distracter more eccentric than target)

3.3.2.3 Eye and hand movements

3.3.2.3.1 Signed amplitude error with latency effects partialed out

The separate analyses of eye and hand movements revealed that the distracter affected the amplitudes of both eye and hand movements. After the effects of latency were partialed out in a joint analysis, two main effects remained.

A main effect of movement type showed that the amplitude was smaller for eye movements than for hand movements ($F_{1,7}$=11.42, p<.05). The regression analyses performed as part of this covariance analysis showed that this effect was moderately influenced by latency (β =- .51). A main effect of distracter status ($F_{1,7}$=9.92, p<.05) showed that the amplitude was smaller when the distracter was present than when it was absent. Thus, both eye and hand were drawn towards the distracter. This effect was also found to be moderately influenced by latency (β= .53). No interactions were observed. The absence of an interaction of movement type and distracter status indicates that the distracter similarly affects eye and hand movements (after compensating for latency effects).

3.3.2.3.2 Effect of latency on the signed amplitude error (bin analysis)

For eye movements, levels of the factor latency group comprised the values 82-230 ms (group 1), 231-282 ms (group 2), 283-342 ms (group3), and 343-958 ms (group 4). For hand movements, levels of the factor latency group comprised the values 174-336 ms (group 1), 337-407 ms (group 2), 408-536 ms (group3), and 537-1758 ms (group 4).

There was a main effect of latency group ($F_{2.6,15.9} = 6.44$, $p<.01$), indicating that movement amplitude increased with increasing latency. There was also a main effect of distracter status ($F_{1,6}=7.14$, $p<.05$), indicating that movement amplitude was smaller when a distracter was present. This effect paralleled that in the covariance analysis, i.e., both eye and hand landed further away from the target and closer to the distracter.

Moreover, three interactions involving the factor latency group were observed. First, latency group interacted with movement type ($F_{3,18}=4.30$, $p<.05$). Only within the first latency group was eye amplitude significantly smaller than hand amplitude ($p<.05$). Eye and hand amplitude did not differ within the latency groups 2 to 4. At the longest latencies eye movement amplitude began to decrease again. Second, latency group interacted with distracter status ($F_{3,18}=6.49$, $p<.01$). This interaction was, however, not due to a difference in the global effect depending on latency groups. Finally, latency group interacted with movement type and distracter status ($F_{3,18}=4.25$, $p<.05$). For both movement types, amplitude tended to increase with latency. The distracter affected eye movement amplitude particularly at short latencies (difference between present and absent distracter $p<.05$). Thus, for eye movements the distracter effect was largest when the movements were fast. This dependency of the distracter effect on movement latency was less pronounced for hand movements.

3.3.3 Discussion

Experiment 1 showed that the presence of a distracter less eccentric than the target resulted in reduced eye and hand amplitudes. Direction and magnitude of the effect were similar for eye and hand movements.

This similarity of the distracter effect on movement amplitudes points to a coupling of eye and hand in the spatial domain. A coupling also in the temporal domain is suggested by the finding that the latencies of eye and hand approached each other in the dual task condition.

Eye and hand differed, however, in the dependence of the distracter effect on movement latency. For short-latency eye movements the tendency to land in-between the target and the distracter was particularly obvious, whereas hand movements did not show a dependency of the distracter effect on movement latency. Moreover, for trials both with and without distracter, hand movement amplitude always increased with latency, whereas eye movement amplitude first increased and then started to decrease again with higher latencies (latency group 3 and 4). These results show that the target representations of eye and hand are not equally affected in all respects by the presence of a distracter.

Whereas eye movements showed a classic global effect in this experiment, i.e., they landed at a position between the target and the distracter, hand movements showed a reduced overshoot when a distracter was present. As a result, hand movements actually became more accurate. Since manual latencies were also somewhat increased in the presence of a distracter, it cannot be ruled out that the reduced overshoot of hand movements in trials with a distracter was due to an improvement of movement accuracy related to the longer latency. Thus, the results could simply be the effect of a speed-accuracy trade off.

Therefore, experiment 2 was conducted to distinguish a distracter effect from the effect of increased accuracy. If the distracter is more eccentric than the target, a distracter effect should be evident in increased overshoot, whereas increased accuracy should result in reduced overshoot (see Figure 1).

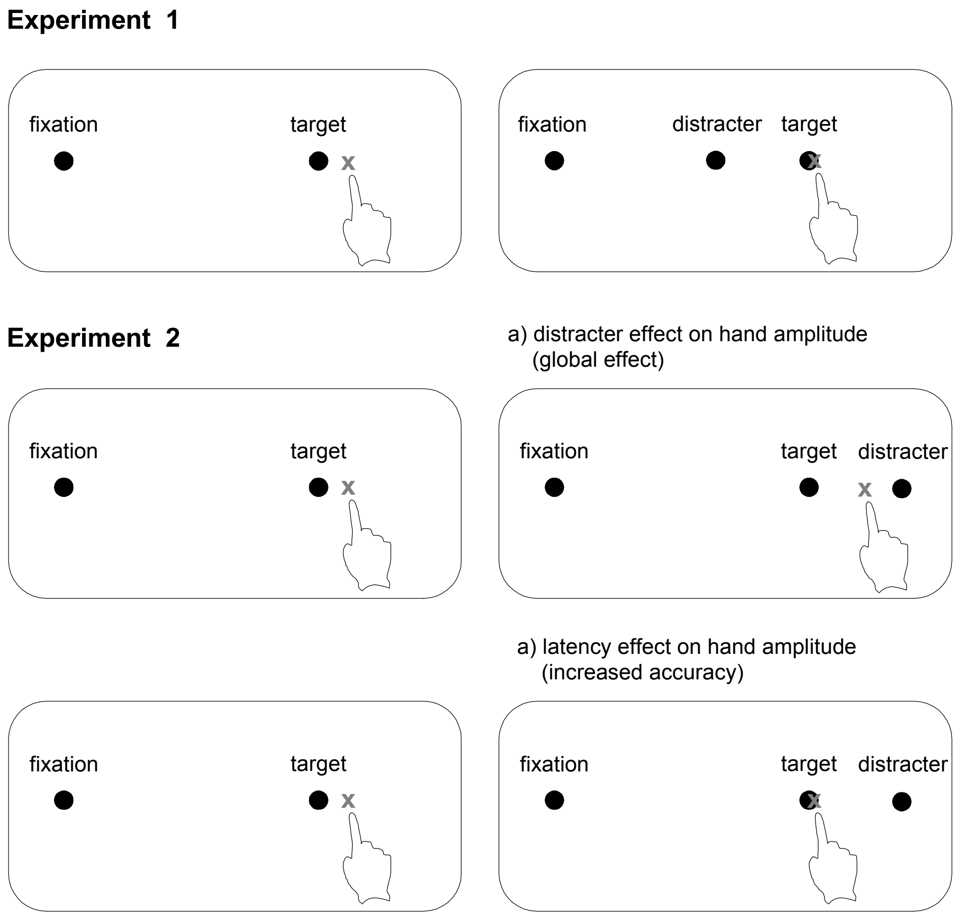


Figure 1 Graphical illustration of results of experiments 1 and hypotheses derived for experiment 2 ("x" denotes observed landing position for exp. 1 and expected landing position for exp. 2). The left column shows trials without distracter, the right trials with distracter.

3.4 Experiment 2

Experiment 2 used a distracter more eccentric than the target. Consequently, a global effect should be manifest in an increased movement amplitude in the presence of a distracter.

3.4.1 Method

Subjects, stimuli, apparatus, measured variables, and procedures were the same as in experiment 1, except for the location of the distracter and the subject's instructions. In contrast to experiment 1, the distracter was located 4 deg more eccentric than the target. Thus, the target was always closer to the fixation than the distracter. Accordingly, when two white spots appeared, the subjects were instructed to "move towards the less eccentric one, i.e., the one closer to the fixation spot".

3.4.2 Results

3.4.2.1 Eye movements

3.4.2.1.1 Saccadic latencies

The mean saccadic latencies for each subject are presented in Table 2. There was a main effect of task condition ($F_{1,8} = 20.86$, $p<.01$). As in experiment 1, saccadic latencies were higher in the dual-task condition than in the single-task condition. No other effect was significant.

3.4.2.1.2 Signed eye amplitude error

The mean signed eye amplitude error for each subject is presented in Table 2. There was a main effect of distracter status ($F_{1,8} = 36.94$, $p<.001$). The eye amplitude was larger when a distracter was present than when it was absent (see Figure 2). This means that eye movements landed in-between the target and the more eccentric distracter. No other effects were significant.

3.4.2.2 Hand movements

3.4.2.2.1 Manual latencies

The mean manual latencies for each subject are presented in Table 2. As in experiment 1, there was a tendency for the latency of hand movements to increase in the single-task condition. No significant effects or interactions were observed.

3.4.2.2.2 Signed hand amplitude error

The mean signed hand amplitude error for each subject is presented in Table 2. There was a main effect of distracter status ($F_{1,8} = 19.45$, $p<.01$). The signed hand amplitude error was significantly larger, i.e., the movement amplitude was larger with a present distracter than with an absent distracter (see Figure 2). Thus, hand movements, like eye movements, landed in-between the target and the more eccentric distracter. There was also a main effect of task condition ($F_{1,8} = 18.15$, $p<.01$). Analogous to experiment 1, the hand amplitude was larger in the single-task condition than in the dual-task condition. Thus, hand movements were more accurate when accompanied by eye movements. The hand was even found to slightly undershoot in the dual-task for trials without a distracter. No other effect was significant.

3.4.2.3 Eye and hand movements

3.4.2.3.1 Signed amplitude error with latency effects partialed out

The joint analysis of signed eye and hand amplitude errors revealed a main effect of movement type ($F_{1,7} = 26.23$, $p<.01$). As in experiment 1, the amplitude was smaller for eye movements than for hand movements. This indicates a general tendency of the hand to make larger movements than the eye. The regression analyses performed as part of this covariance analysis showed that this effect was strongly influenced by latency ($\beta =- .79$). There was also a main effect of task condition ($F_{1,7} = 6.24$, $p<.05$) which was strongly influenced by latency ($\beta =- .67$). Movement amplitude was larger in the single-task than in the dual-task condition. Thus, both movement types were more accurate when they were executed concurrently. This effect is paralleled by an interaction of the factors task condition and distracter status ($F = 10.93$, $p<05$). Thus, the distracter had a larger effect in the single-task condition, and this effect was strongly influenced by latency ($\beta =- .76$).

There was also a main effect of distracter status ($F_{1,7} = 23.08$, $p<.01$), which was only weakly mediated by latency ($\beta =- .17$). The negative sign of this regression coefficient indicates that the amplitude decreases with latency, as would be expected with a more eccentric distracter. In contrast, in experiment 1 with a less eccentric distracter, the sign was positive, indicating that amplitude increased with latency. The main effect of distracter status was a larger amplitude with a present than with an absent distracter, i.e., both eye and hand movements were drawn towards the distracter. Importantly, there was no interaction of movement type and distracter status. Therefore, the distracter did not differentially affect eye and hand amplitudes. No other interactions were significant.

3.4.2.3.2 Effect of latency on the signed amplitude error (bin analysis)

For eye movements, levels of the factor latency group comprised the values 83-152 ms (group 1), 153-261 ms (group 2), 262-330 ms (group3), and 331-996 ms (group 4). For hand movements, levels of the factor latency group comprised the values 117-287 ms (group 1), 288-337 ms (group 2), 338-418 ms (group3), and 419-1632 ms (group 4).

Analogous to the covariance analysis, there was a main effect of distracter status ($F_{1,6}$=26.71, $p<.01$), indicating that movement amplitude was larger when a distracter was present. Similar to experiment 1, latency group interacted with movement type ($F_{3,18}=8.64$, $p<.01$). Whereas hand movement amplitude increased with increasing latency, eye movement amplitude first increased before again decreasing. At the longest latencies, hand movement amplitude was significantly larger than eye movement amplitude ($p<.01$). Thus, the tendency of hand movements towards larger amplitudes seems to be increased with longer latencies. There was no interaction of latency group and distracter status, indicating that the global effect was not larger with shorter latencies for either movement type. No other effects or interactions were significant.

3.4.3 Discussion

Experiment 2 was conducted to distinguish a distracter effect on hand movements from the effect of increased accuracy. This distinction was necessary because in experiment 1 the reduced hand amplitude in the presence of a distracter implied greater accuracy, coinciding with increased manual latencies.

With a target less eccentric than the distracter, a distracter effect should be evident in increased overshoot, whereas increased accuracy should result in reduced overshoot. Indeed, hand movement overshoot increased in the presence of a more eccentric distracter. Therefore, hand movements in the presence of a distracter were not closer to the target (i.e., not more accurate), but clearly showed spatial averaging between the target and the distracter. Thus, the distracter directly affects the target representation for hand movements.

The same was true for eye movements. Eye movement amplitude also increased in the presence of a distracter. Again, the distracter effect was similar for eye and hand movements.

The dependency of movement amplitude on latency was again different for eye and hand movements. As in experiment 1, hand movement amplitude consistently increased with increasing latency. Eye movement amplitude first increased more steeply before again decreasing with longer latencies. Contrary to experiment 1, the global effect for eye movements was independent of latency. The global effect for hand movements was also independent of latency.

In the dual-task condition, the amplitudes of both eye and hand were smaller and more accurate. Moreover, the influence of the distracter was reduced when both movements were executed concurrently.

3.5 Experiment 3

Experiments 1 and 2 showed that the global effect exists also for hand movements. However, whereas the global effect for eye movements has been demonstrated both for targets of longer duration and for flashed targets (Eggert et al., submitted), the global effect for hand movements has not been demonstrated yet. To determine if the global effect for hand movements is also present with longer target presentation times, experiment 3 was performed.

In this experiment, target presentation time was varied in order to determine if the global effect for eye and hand movement is affected by the presentation time of the visual target. We thought that if more visual information about target position is available, the global effect might disappear. Three different times were chosen: 50 ms, to replicate the results of experiments 1 and 2; 350 ms as an approximate time after the hand has started to move but not yet arrived; and 850 ms when the hand movement is completed in most of the cases as the target disappears.

In contrast to experiments 1 and 2, no dual-task condition was included in experiment 3. This is because lengthened target presentation times in the dual-task condition have the consequence that in some trials, the eye is on target before the target is extinguished. Since hand movement accuracy profits from fixation of the target (e.g., Abrams, Meyer, & Kornblum, 1990; Vercher, Magenes, Prablanc, & Gauthier, 1994), the effect of target foveation would be confounded with the effect of increased target presentation time. A further confounder could result from information about eye position, which has also been shown to increase hand movement accuracy (Pélisson, Prablanc, Goodale, & Jeannerod, 1986). As it would have been difficult to control the amount of information about eye position and foveation of the target, no dual task condition was performed.

The distracter status was the same as in experiment 2, i.e., it was always more eccentric than the target.

3.5.1 Method

3.5.1.1 Subjects

Nine research workers from the neurology department, two women and seven men (age 29-43 years), participated in the experiment. Six of them were naïve with respect to the hypotheses and the purpose of the experiment, three of them (the authors) were not. Five subjects had already participated in the experiments 1 and 2. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). All subjects were right-handed, except for one subject who was ambidextrous.

3.5.1.2 Apparatus

The apparatus was the same as in experiments 1 and 2. In the hand-alone condition, an additional cardboard shield was attached to the chin rest. It was adjusted individually for each subject, so that the lower part of the screen approximately 3 cm below the target was no longer visible.

3.5.1.3 Stimuli and task

A red fixation spot was presented for 1500 ms in the single-task eye, and for 3500 ms in the single-task hand. 100 ms after the fixation spot was extinguished, a peripheral white target spot appeared. The target spot was presented for 50 ms, 350 ms, or 850 ms. The target appeared at a random position between 8 and 10 deg of visual angle to the right or left of the fixation spot. In 50% of the trials, a white distracter spot was flashed together with the target for the same duration. It was located at a distance of 4 deg from the target and was always more eccentric than the target. The fixation spot of the next trial appeared at the previous target position 2000 ms after the target had disappeared.

The subject's task was to move towards the target as fast as possible. When two white spots appeared, subjects were told to "move towards the less eccentric one, i.e., the one closer to the fixation spot". The task consisted of two conditions: (a) saccade to the target (single-task condition, eye), and (b) point to the target while keeping the eyes fixated at the location of the (now extinguished) fixation spot (single-task condition, hand).

As the LCD display did not allow target presentation without background illumination of the monitor, for target duration lasting 350 and 850 ms, sight of the moving hand could not be avoided by turning off the background illumination. In contrast to experiments 1, 2, and 4, the background illumination always stayed on. At the beginning of the hand-alone session, subjects were asked to indicate the exact position at which they no longer saw their fingertip on the screen because it was hidden by the shield. They were then instructed to put their finger on the fixation spot at the beginning of a trial, and subsequently move their finger vertically downwards on the screen into this region. Pointing towards the target was also performed within this region, i.e., at the same horizontal but lower vertical position. The instruction given the subjects emphasised that when pointing towards the target their finger should never be visible. During the experiment, the experimenter continuously checked that the subjects complied with this instruction.

Practice trials were performed in both conditions until the subjects felt familiar with the task. In the hand-alone condition, the experimenter first demonstrated the task before the practice trials started. Each condition consisted of 240 trials, 40 with distracter and 40 without distracter for each of the three presentation times. Subjects performed all two experimental conditions, each on a different day. The order of conditions was counter-balanced.

3.5.1.4 Measurement of hand and eye movements

Measurement of hand and eye movements was the same as in experiments 1 and 2. An additional outlier criterion was required in the eye-alone condition, excluding trials in which the position of the eye at the beginning of a movement deviated more than 5° from the target position.

Calibration of the ultrasonic device yielded a mean accuracy of 3.58 mm. Hand movements were calibrated by having the subjects point to targets at known eccentricities with full view of the hand.

3.5.1.5 Dependent variables and offline analysis

Dependent variables were the same as in experiments 1 and 2, i.e., latency and signed amplitude error. The dependent variables were each analysed by means of a 2x3x2 repeated-measurements ANOVA with the factors movement type (eye/hand), target duration (50ms/350ms/850ms), and distracter status (present/absent). For better comparability with experiments 1 and 2, analysis of the signed amplitude error was again performed with latency as changing covariate.

3.5.2 Results

3.5.2.1 Eye and hand movements

3.5.2.1.1 Latencies

Mean saccadic and manual latencies for each subject are presented in Table 3.

Table 3 Mean eye and hand latencies and signed amplitude errors (standard deviation in parentheses) for different target presentation times (exp. 3, distracter more eccentric than target)

	50 ms presentation		*350 ms presentation*		*850 ms presentation*	
dependent variable	*distracter absent*	*distracter present*	*distracter absent*	*distracter present*	*distracter absent*	*distracter present*
latency eye (ms)	203 (41)	207 (46)	190 (39)	192 (27)	186 (34)	197 (36)
latency hand (ms)	496 (132)	467 (128)	512 (159)	511 (144)	541 (242)	534 (238)
signed eye amplitude error (deg)	-0.12 (0.50)	0.86 (0.61)	0.11 (0.63)	0.93 (0.92)	0.17 (0.59)	0.82 (0.75)
signed hand amplitude error (deg)	0.67 (0.83)	1.32 (1.12)	0.38 (0.69)	0.88 (0.71)	0.56 (0.68)	0.71 (0.84)

Not surprisingly, there was a main effect of movement type ($F_{1,8} = 33.00$, $p<.001$), indicating that latencies of hand movements were larger than those of eye movements. No other significant effects or interactions were observed. The latencies of both eye and hand were thus independent of target duration.

3.5.2.1.2 Signed amplitude error with latency effects partialed out

Mean signed eye amplitude errors for each subject are presented in Table 3, mean signed hand amplitude errors in Table 3.

There was a main effect of distracter status ($F_{1,7} = 21.98$, $p<.01$). This effect was not influenced by latency ($\beta = .07$). Movement amplitude was larger when a distracter was present than when it was absent. Thus, as in experiment 2 eye and hand landed in-between the target and the distracter. However, this global effect was larger for eye than for hand movements, as shown by an interaction of movement type and distracter status (_$F_{1,7} = 13.64$, $p<.01$). This effect was slightly mediated by latency ($\beta = .36$). Target duration had only a marginally significant main effect (_$F_{2,14} = 3.64$, $p=.05$). This effect was in part (depending on the factor level) mediated by latency (β-coefficients ranging from -.46 to .83). Both eye and hand amplitude tended to decrease with increasing target duration, i.e., movements became more accurate (see Figure 3). The failure of distracter status to interact with target duration showed that the global effect did not depend on the duration of the target. No other effects or interactions were observed.

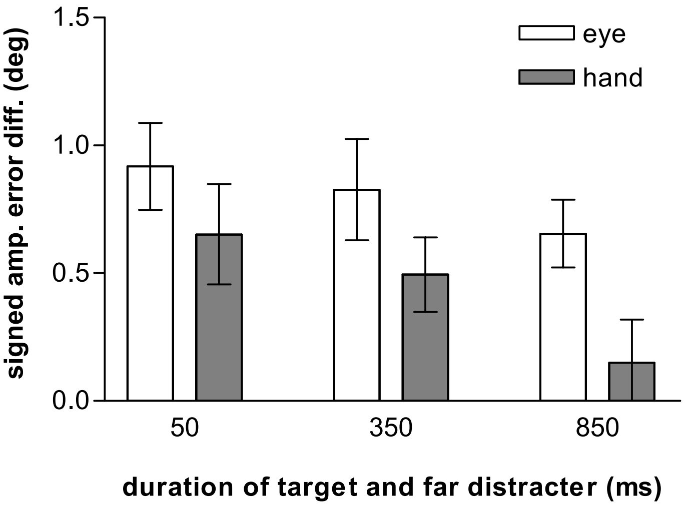


Figure 3 Difference in eye and hand signed amplitude errors between trials with and without distracter, (i.e., size of the global effect) and standard error of the mean (N=9) for different durations of target and far distracter

3.5.3 Discussion

The results of experiment 3 help to determine at what point in time target information is accessed by eye and hand. To this aim, the presentation time of the target was varied.

At least two strategies are conceivable. First, eye and hand make use of as much information as possible for movement programming before movement initiation. This would be reflected in longer latencies and decreased global effect with increasing presentation time. Second, the movement is initiated as quickly as possible, irrespective of differences in the amount of available information. The information provided may rather be used for feedback correction – online correction of the hand and corrective saccades of the eye - than for movement programming. This would be reflected by an independence of the latencies and the global effect from presentation time.

There was a global effect both for eye and hand movements, but contrary to experiments 1 and 2, the effect was larger for the eye than for the hand. For neither movement type was this global effect dependent on the presentation time of target and distracter. Although movements generally became more accurate with increasing target duration (see Figure 3), the global effect was not abolished, not even when target and distracter remained present until almost the end of the trial. Latencies of eye and hand movements did not vary with presentation time. These findings favour the second strategy: subjects first aim at the centre of the target-distracter configuration as rapidly as possible, from where the target can be reached or searched for more easily (Jacobs, 1987).

3.6 Experiment 4

In experiments 1, 2, and 3 the distracter was always either less eccentric or more eccentric than the target. Thus, subjects knew beforehand approximately where the target would occur. This may have reduced the interference of distracter and target. Therefore, we conducted an experiment in which the relative positions of target and distracter were varied. If eye and hand use the same target representation, such changed information about the target should affect them both in the same way.

We hypothesized that the eye and hand would be "pulled about" towards the distracter from trial to trial, depending on the location of the distracter.

3.6.1 Method

3.6.1.1 Subjects

Nine research workers from the neurology department, five women and four men (age 24-43 years), participated in the experiment. Six of them were naïve with respect to the hypotheses and the purpose of the experiment, three of them (the authors) were not. Five subjects had already participated in experiments 1, 2, 3. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). Seven subjects were right-handed, one subject was ambidextrous and one left-handed. The results of both these subjects did not differ from those of the right-handed subjects (handedness was introduced as a between-subjects factor in all following analyses).

3.6.1.2 Apparatus

The apparatus was the same as in experiments 1 and 2.

3.6.1.3 Stimuli and task

The fixation spot was a magenta cross, the target a white cross, and the distracter a white circle, each of the same diameter. The presentation time of target and distracter was set at 50 ms. The fixation cross was presented for 1500 ms. 100 ms after the fixation cross was extinguished, the peripheral target was flashed. The target appeared at a random position between 8 and 10 deg of visual angle to the right or left of the fixation spot. The distracter was located at a distance of 4 deg from the target. In 33% of the trials, the target was presented alone, in 33% the distracter circle was flashed at a position more eccentric that the target, and in 33% at a position less eccentric than the target. The distracter was always presented at the same time as the target. When the target disappeared, the background illumination of the monitor was turned off, leaving the subject in complete darkness. The fixation spot of the next trial appeared at the previous target position 1500 ms after a saccade was detected, or 2000 ms after the target disappeared, if no saccade was detected within 500 ms after it disappeared.

The subject's task was to move towards the white cross as quickly as possible. When the white cross and the white circle appeared simultaneously, they were told to "ignore the circle and move towards the cross". The task entailed three conditions: (a) saccade to the target (single-task condition, eye), (b) saccade and point to the target (dual-task condition), and (c) point to the target while keeping the eyes fixated at the location of the (now extinguished) fixation spot (single-task condition, hand). To facilitate fixation in the latter condition, subjects were told not to make any eye movement before the monitor was switched on again. The subjects were further instructed to realign their eye and/or hand with the fixation spot at the beginning of the next trial.

Practice trials were performed in both conditions until the subjects felt familiar with the task. Each condition consisted of 240 trials, 80 without distracter, 80 with a distracter more eccentric than the target, and 80 with a distracter less eccentric than the target. Subjects performed all three experimental conditions (i.e., single-task eye, single-task hand, dual-task), each on a different day. The order of conditions was counter-balanced.

3.6.1.4 Measurement of hand and eye movements

Hand and eye movements were measured as in experiments 1 and 2. An additional outlier criterion was applied to eye movements, excluding trials in which the position of the eye at the beginning of a movement deviated more than 5° from the target position.

Calibration of the ultrasonic device yielded a mean accuracy of 3.88 mm.

3.6.1.5 Dependent variables and offline analysis

Dependent variables were the same as in experiments 1 and 2, i.e., signed amplitude error and latency. Each dependent variable was analysed separately for eye and hand by means of a repeated-measurements ANOVA with the factors task condition (single/dual), and distracter status (near distracter/far distracter/target only). Near distracter means less eccentric than the target, and far distracter more eccentric than the target.

The comparison of signed eye and hand amplitude errors and the analysis of the latency dependence of the global effect were performed as in experiment 1 and 2, except that the factor distracter status consisted of three levels (near distracter/far distracter/ target only) instead of two (present/absent).

In the analyses without covariate, separate a priori planned comparisons were performed to assess the difference in signed amplitude error between the factor levels near distracter and target only, far distracter and target only, and near distracter and far distracter. All other comparisons were performed post-hoc by means of the Scheffé test.

3.6.2 Results

3.6.2.1 *Eye movements*

3.6.2.1.1 *Saccadic latencies*

The mean saccadic latencies for each subject are presented in Table 4.

Table 4 Mean eye and hand latencies and signed amplitude errors (standard deviation in parentheses) for different distracter statuses (exp. 4)

	single-task			*dual-task*		
dependent variable	*far distracter*	*near distracter*	*target only*	*far distracter*	*near distracter*	*target only*
latency eye (ms)	248 (58)	264 (69)	242 (62)	287 (55)	305 (54)	278 (40)
latency hand (ms)	404 (128)	411 (123)	396 (127)	324 (69)	314 (67)	312 (55)
signed eye amplitude error (deg)	1.51 (0.80)	-0.45 (1.03)	0.32 (0.86)	1.28 (1.43)	-0.34 (1.48)	0.56 (1.51)
signed hand amplitude error (deg)	1.80 (1.10)	0.38 (0.74)	0.38 (1.01)	0.98 (1.19)	-0.20 (0.82)	-0.22 (0.83)

There was a main effect of distracter status ($F_{2,16} = 10.26$, $p<.01$). Saccadic latencies were larger when a distracter was present, significantly so for the near distracter ($p<.05$). This effect parallels the one found in experiment 1, where the distracter was also less eccentric than the target. It seems as if distracters along the movement path interfere more with saccadic programming than distracters that appear beyond the target (Pratt & Abrams, 1994). There was also a main effect of task condition ($F_{1,8} = 8.56$, $p<.05$). As in experiment 1 and 2, saccadic latencies were larger in the dual-task condition than in the single-task condition. There was no significant interaction.

3.6.2.1.2 Signed eye amplitude error

The mean signed eye amplitude error for each subject is presented in Table 4. There was a main effect of distracter status ($F_{2,16} = 46.19$, $p<.0001$). Compared to the presentation of the target only, the eye amplitude was smaller with the near distracter ($F_{1,8} = 20.58$, $p<.01$) and larger with the far distracter ($F_{1,8} = 44{,}10$, $p<.001$). This means that the eye always landed in-between the target and the distracter, irrespective of their relative positions. Amplitude towards the far distracter was also significantly larger than for the near distracter ($F_{1,8} = 64.55$, $p<.0001$). No other effects were significant.

3.6.2.2 Hand movements

3.6.2.2.1 Manual latencies

The mean manual latencies for each subject are presented in Table 4. There was a main effect of task condition ($F_{1,8} = 11.02$, $p<.05$). In contrast to saccadic latencies, which were higher in the dual-task condition than in the single-task condition, manual latencies showed the opposite result. Manual latencies were lower in the dual-task condition than in the single-task condition. This is again the same effect as in experiments 1 and 2. No other effects or interactions were significant.

3.6.2.2.2 Signed hand amplitude error

The mean signed hand amplitude error for each subject is presented in Table 4. There was a main effect of distracter status ($F_{2,16} = 61.30$, $p<.0001$). Compared to the presentation of the target only, the hand amplitude was larger with the far distracter ($F_{1,8} = 95.13$, $p<.0001$). This means that the hand landed in-between the target and the far distracter. Hand amplitude towards the far distracter was also significantly larger than for the near distracter ($F_{1,8} = 64.55$, $p<.0001$). In contrast to eye movements, however, amplitude was not different for the near distracter than without distracter. Thus, for hand movements there was only a global effect for the far distracter, not for the near distracter.

As in experiments 1 and 2 there was also a main effect of task condition ($F_{1,8} = 11.91$, $p<.01$). Generally, the hand amplitude was larger, i.e., overshoot was larger, in the single-task condition than in the dual-task condition. This was independent of the presence of a distracter. No other effect was significant.

3.6.2.3 Eye and hand movements

Figure 4 shows the signed amplitude errors of eye and hand for different distracter statuses in the single- and dual-task condition.

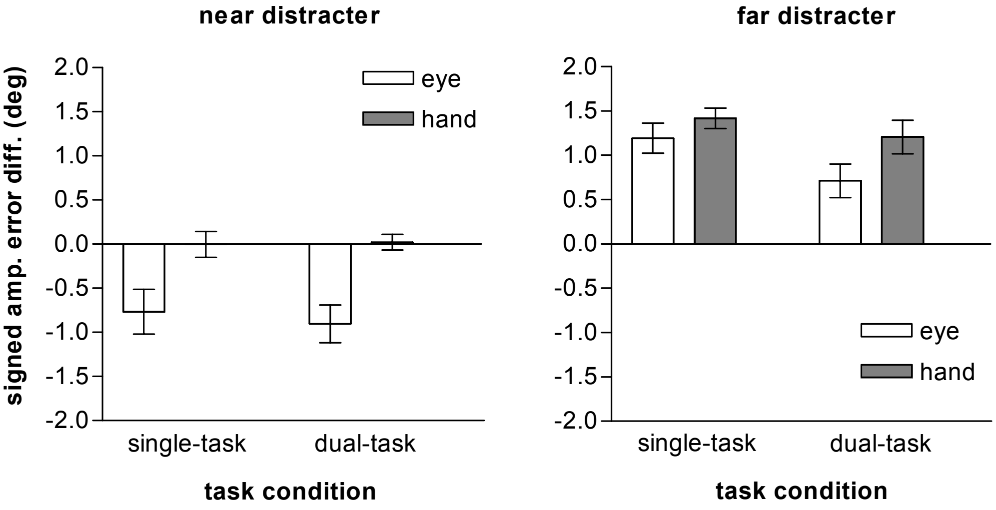


Figure 4 Difference in eye and hand signed amplitude errors between trials with and without distracter, (i.e., size of the global effect) and standard error of the mean (N=9) across single and dual-task conditions for different distracter statuses

3.6.2.3.1 Signed amplitude error with latency effects partialed out

The separate effect of the distracter on the signed amplitude error of eye and hand movements was confirmed in the joint analysis of eye and hand. There was a main effect of distracter status ($F_{2,14}=39.41$, $p<.0001$). The regression analyses performed as part of this covariance analysis showed that this effect was in part (depending on the factor level) influenced by latency (ß-coefficients ranging from -.30 to .56). Compared to the presentation of the target only, amplitudes were smaller with the near distracter ($p<.001$) and larger with the far distracter ($p<.0001$). Amplitude towards the far distracter was also significantly larger than for the near distracter (p<.0001). Thus, overall both eye and hand movements showed a global effect, i.e., both landed in-between the target and the distracter. This main effect was, however, mainly due to eye movements, as indicated by an interaction of movement type and distracter status ($F_{2,14}$=9.18, p<.01). The influence of latency on this interaction was rather high (β-coefficients depending on the factor level ranging from -.74 to .51). Whereas for eye movements, the amplitude towards the near distracter was smaller than towards the target only (p<.01), there was no difference for hand movements. This effect parallels the findings of the separate analyses of eye and hand. This means that eye movements showed a global effect both for the near and the far distracter, whereas hand movements showed a global effect only for the far distracter.

One reason for the differential global effect for hand movements with the near and far distracter could be differences in processing during movement execution. In this sense, a more elaborate information processing during the ongoing movement in the case of the near distracter should be reflected in longer hand movement times. To determine this, hand movement time was calculated as the time between the onset and the end of the movement and subject to a repeated-measures ANOVA with the factors task condition (single/dual), and distracter status (near distracter/far distracter/target only). Hand movement time for the far distracter was longer than for the near distracter or the target only, thus reflecting the findings of amplitudes. Movement time for the near distracter and the target only was not different. Thus, the differential global effect of hand movements with near and far distracters is not due to different amounts of processing during movement execution.

There was also an interaction of task condition and distracter status ($F_{2,14}$=4.58, p<.05). This interaction was moderately influenced by latency (β -coefficients ranging from -.25 to .65). The amplitudes were larger in the single- than in the dual-task condition (p<.01) only for the far distracter, not for the near distracter or the target only. This means that the global effect of the far distracter was larger when both movements were executed alone than when they were executed concurrently. Likewise, a larger global effect in the single-task condition was found in experiment 2 with a far distracter, but not in experiment 1 with a near distracter. Thus, only with a far distracter, movements towards the target in the presence of a distracter are more accurate when eye and hand movements are executed simultaneously.

3.6.2.3.2 Effect of latency on the signed amplitude error (bin analysis)

For eye movements, levels of the factor latency group comprised the values 84-162 ms (group 1), 163-277 ms (group 2), 278-333 ms (group3), and 334-920 ms (group 4). Signed eye amplitude errors for these different latency groups are plotted in figure 5.

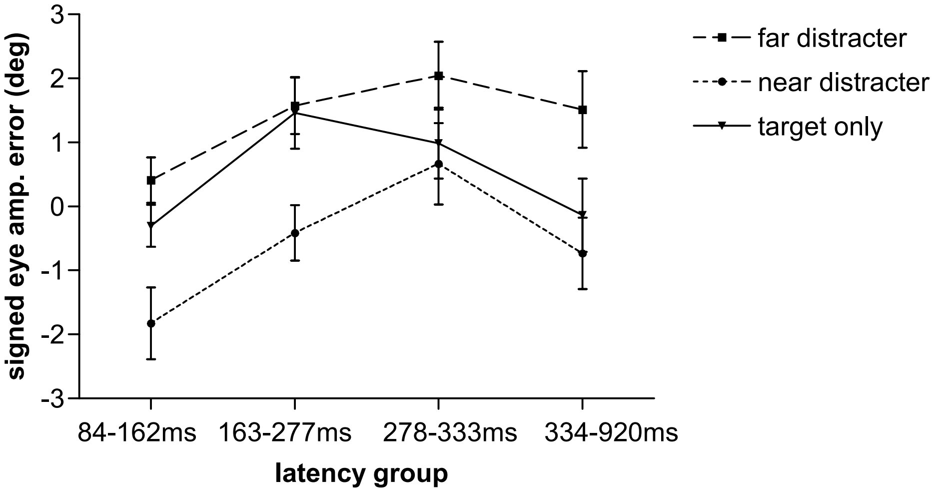


Figure 5 Mean signed eye amplitude error and standard error of the mean (N=9) per distracter status across different latency groups

For hand movements, levels of the factor latency group comprised the values 88-270 ms (group 1), 271-331 ms (group 2), 332-419 ms (group3), and 420-1255 ms (group 4). Signed hand amplitude errors for these different latency groups are plotted in figure 6.

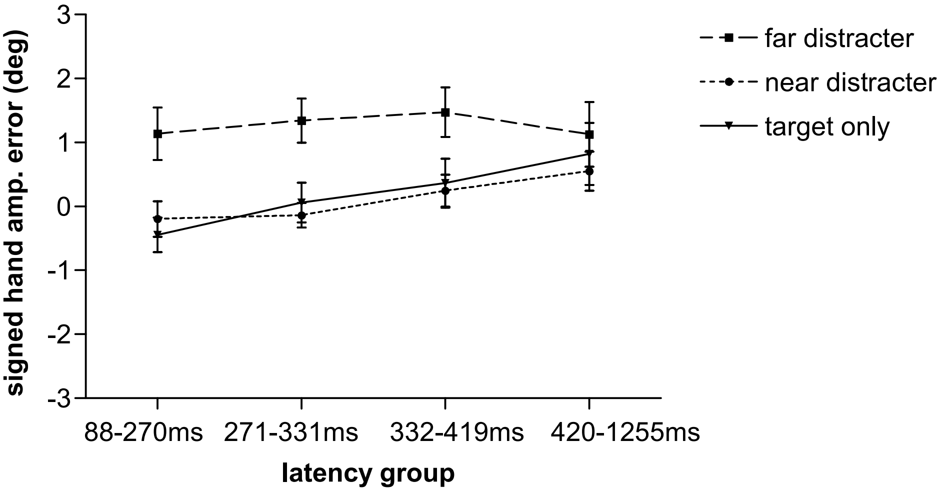


Figure 6 Mean signed hand amplitude error and standard error of the mean (N=9) per distracter status across different latency groups

There was again a main effect of distracter status ($F_{2,10}$=51.98, p<.0001). Compared to the presentation of the target only, the amplitude was larger with the far distracter ($F_{1,5}$=38.77, p<.01), and smaller with the near distracter ($F_{1,5}$=7.82, p<.05). Amplitude towards the far distracter was also significantly larger than for the near distracter ($F_{1,5}$=163.04, p<.0001). There was also a main effect of latency group ($F_{3,15}$=5.09, p<.05). The amplitude tended to increase with higher latencies. There was no interaction of distracter status and latency group. Thus, the distracter effect was not larger with smaller latencies. Instead, increasing latencies generally led to larger amplitudes, independent of the presence or location of a distracter. This finding paralleled the effect observed in experiment 1. The effect was more consistent for hand movements than for eye movements, as indicated by an interaction of movement type and latency group ($F_{3,15}$=4.09, p<.05). At the longest latencies, eye amplitude again decreased.

3.6.3 Discussion

Experiment 4 showed that the amplitude of eye and hand movements changed with the position of a distracter. When the distracter was more eccentric than the target (far distracter), amplitudes became larger in the presence of a distracter; when the distracter was less eccentric (near distracter), amplitudes became smaller. Generally, the effect of the far distracter was larger than that of the near distracter. This finding suggests similar processes of eye and hand for specifying target position. However, in the presence of the near distracter only eye movements showed a global effect, whereas hand movements did not. This suggests that the interaction between eye and hand is dependent on the task. Under the conditions of the present experiment, the interaction seems to have been higher with the far than with the near distracter. This interpretation is supported by the finding that with the far distracter, the global effect for both eye and hand was reduced when they were executed simultaneously, an effect also found in experiment 2, which also used a far distracter.

Another difference of eye and hand movements was in the development of movement amplitude with latency. Generally, movements became larger with increasing latency, independently of the presence of a distracter. As in experiments 1 and 2, this increase was more consistent for hand movements.

Again, an interaction in the temporal domain is suggested by the finding that the latencies of eye and hand approached each other when executed concurrently.

3.7 General discussion

The present study investigated the coordination of eye and hand by using the "global-effect paradigm". The global effect which is typically observed for eye movements is the tendency to land in-between a target and a distracter that are presented simultaneously and close to each other.

3.7.1 Global effect of eye and hand movements – nature of spatial coupling at the stage of target selection

Our findings showed a global also for hand movements, even in the single-task condition in the absence of eye movements. Thus, the global effect is not specific to the oculomotor system, but also occurs in the limb motor system. Moreover, the global effect was mostly similar for eye and hand movements. It is known that the global effect occurs on the level of target selection, i.e., before the process of separating the target from the distracter has been completed. Thus, eye and hand are coupled at this early stage. To achieve this coupling, eye and hand at least have to exchange information, or, even more, share one target representation. However, it is unclear, which alternative may be the case. Importantly, the term "shared target representation" as used here also implies an identical point in time when information about the target is read out. If either the target representation itself or the point in time when it is accessed are different for eye and hand, we speak of separate target representations.

In experiment 1 and 2 the global effect of hand movements was of the same direction and magnitude as that of eye movements. This similarity requires at least an exchange of information. The fact that with increasing eye latencies the global effect was reduced for the eye, but not the hand, raises doubt on the idea of a shared target representation. If the distracter affected a shared target representation, then the dependence of the global effect on latency should be the same for eye and hand. Thus, this finding speaks for two separate target representations. For the hand, the absence dependence of the global effect on latency suggests that the target representation is not updated, but "frozen" on an early stage.

However, this difference in the latency dependence of the global effect between eye and hand was not observed in experiments 2 and 4, because the global effect for the eye was no longer latency dependent. This seems unusual compared to the findings of other authors (e.g. Findlay, 1982; Ottes, van Gisbergen, & Eggermont, 1985). It may be due to the response in the present experiment being typically executed late in the target selection process, i.e., when separation of the target from the distracter is nearly finished. This explanation is supported by the finding that in all experiments the global effect was not very large, i.e., movements did not land exactly in-between the target and the distracter, but closer to the target. Thus, the fact that eye and hand showed a similar behaviour in experiments 2 and 4 with regard to latency dependence does not necessarily speak for a shared target representation.

In experiments 1, 2 and 4, the dependence of amplitude on latency – irrespective of the presence of a distracter - differed for eye and hand movements. Hand movement amplitude always increased with latency, and eye movement amplitude first increased before again decreasing. This difference could be induced by variations in processes *after* target selection, like the continuous integration of information about the target and the actual status of the effector (eye or hand). Therefore, this result cannot be interpreted as evidence for or against separate target representations of eye and hand.

Summing up, the results of experiment 1 and 2 represent only weak evidence for separate target representations. With truly separate target representations, the global effect for eye and hand should be different under certain conditions. Such a difference was observed in experiment 3, where the global effect was in the same direction but larger for eye than for hand movements. A global effect different in magnitude for eye and hand can not be explained by the distracter acting on a shared target representation.

The strongest argument against the hypothesis of shared target representations results from the different behaviour of eye and hand towards the "near" distracter in experiment 4. Whereas the global effect for the eye was the same as in experiments 1, 2 and 3, there was no global effect for the hand with a distracter less eccentric than the target. Hence, the global effect is less stable for hand movements than for eye movements, but seems to depend more on the features of the target-distracter configuration. This difference between eye and hand speaks against a shared target representation.

The remaining question is why there was a global effect for the hand in experiment 1 with the near distracter, but not in experiment 4. One major difference between experiment 1 and 4 was the degree of predictability of target position. Whereas in experiment 1 the distracter was always more eccentric than the target and in experiment 2 it was always less eccentric, in experiment 4 it could occur either more or less eccentric than the target. To explain the different behaviour of eye and hand towards the near distracter in experiment 4, the concepts of distracter saliency and inhibition have to be introduced.

According to Tipper and colleagues (e.g., Tipper, Howard, & Jackson, 1997; Tipper, Howard, & Houghton, 2000), selection is performed by inhibiting the activation caused by the distracter. With the right amount of inhibition, eye and hand land exactly on the target. With too little or too much inhibition, they do not, i.e., an error occurs. With too little inhibition, the error is in the direction of the distracter. Movements land in-between the target and the distracter, as found both for the eye (global effect) and the hand (e.g., Tipper et al. 2000; Welsh, Elliott, & Weeks, 1999). With too much inhibition, the error is in the direction opposite to the distracter, i.e., eye (e.g., Doyle & Walker, 2001; Sheliga, Riggio, & Rizzolatti, 1995) and hand movements (Fischer & Adam, 2001; Tipper et al., 1997) veer away from the distracter. The amount of inhibition is believed to increase with the salience of the distracter. Salience may be expressed in properties of brightness or contrast, and for hand movements also in distance from the hand (Tipper et al., 1997). Thus, the near distracter generally has differential salience for eye and hand. Assuming that the near distracter was inhibited more strongly for hand movements, the global effect persisted for eye movements, but disappeared for hand movements.

However, the same should apply to experiment 1, as there was also a near distracter involved. In contrast, a global effect for the hand was observed. In experiment 1 subjects knew that the distracter was always the nearer stimulus, so the direction in which the would occur was known in advance. We can only speculate that this higher degree of predictability reduced the saliency of the distracter and therefore, also the amount of inhibition necessary to act on the distracter. This would account for the observed global effect for the hand. In addition to the differences in predictability, experiments 1 and 4 differed also with regard to the features defining the target, the spatial distribution of distracter positions, and the complexity of visual processing required to select the target. The differences in hand movement responses towards the near distracter in experiments 1 and 4 could also be due to any of these factors.

On the basis of the results discussed so far, it seems unlikely that the target representation affected by the distracter is the same for eye and hand. Instead, we assume that parallel processes of response selection and inhibition influence the separate target representations of eye and hand. However, an interaction in the sense of an exchange of information between these processes seems to be necessary to achieve a global effect as similar for eye and hand as in experiment 1 and 2. These somewhat mixed findings may be explained by the amount of information exchanged being dependent on the conditions of the task. The difference in the global effect for eye and hand in experiment 4 with the near distracter suggests that in this case, less information is exchanged.

One possibility to gain further insight into this exchange of information is the application of the dual-task methodology. Although comparing the single- with the dual-task condition irrespective of the global effect does not provide the advantage of specifying the stage at which coupling takes place, the results are worth a closer look.

3.7.2 Interaction of eye and hand in the dual-task – spatial and temporal coupling in a more general context

In all experiments the amplitude of eye and hand movements was smaller in the dual-task than in the single-task condition. This resulted in a generally increased accuracy of eye and hand movements when they were executed simultaneously. Moreover, simultaneous execution with a far distracter as in experiments 2 and 4 reduced the global effect for eye and hand. A change from single- to dual-task conditions in itself does not speak for separate target representations as long as this change is similar for eye and hand. However, this cannot be determined because single- and dual-task conditions were compared separately for eye and hand.

What speaks against the assumption of a shared target representation is the finding that simultaneous execution caused the amplitudes of eye and hand to change in different directions during simultaneous execution. This resulted in an approximation of the amplitudes in experiments 1 and 2 and suggests that the separate target representations are not completely independent of each other, but interact by exchanging spatial information (Bekkering, 1995; Tipper, Howard, & Paul, 2001).

The single-task analyses showed that the influence of concurrent eye on hand movements tended to be larger than vice versa. This may be explained by an asymmetry of the reciprocal interaction. However, it could also be argued that the target representation of the hand during execution is continuously modified by the eye position signal (Adam, Ketelaars, Kingma, & Hoek, 1993; Hansen & Skavenski, 1985).

Whereas the global effect provides an insight into the spatial coupling of eye and hand, it does not address temporal coupling. Temporal coupling can be investigated by comparing eye and hand latencies in single- and dual-task conditions. Similarly to amplitudes, the latencies of eye and hand approached each other during concurrent execution in all experiments (although this was not significant for hand movements in experiment 2), i.e., saccadic latencies increased in the dual-task condition, whereas manual latencies decreased. Such an effect has been reported previously, e.g., for the interaction of pointing movements and saccades (Mather & Fisk, 1985) and for onset latency after target direction change in concurrent eye and hand tracking (Engel & Soechting , 2000). The rapid preparation of the hand movement is at the expense of the time available to prepare the eye movement, suggesting that both motor systems draw on shared processing capacities. This interpretation is supported by the fact that saccadic onset to a second target was found to be considerably delayed until an arm movement to the first target was completed (Neggers & Bekkering 2000).

The approximation of saccadic and manual latencies can only be explained by information being exchanged from eye to hand. The approximation of saccadic and manual latencies can only be explained by information being exchanged from eye to hand. The idea is that separate go signals exist for eye and hand, but the preparation process of one movement type is informed about and influenced by the preparation of the other. Planning a hand movement influences the latency of eye movements, and vice versa. Neither common go signals nor independent processing without information exchange can explain the latency changes from single- to dual-task. With a common-go signal, the dual-task could not have opposite effects on the latency of eye and hand. Neither would independent processing without information exchange lead to shorter latencies in one effector. If the independent processes worked in parallel, the dual task would not have any effect on latency. If the independent processes worked sequentially using shared resources, the latency should always increase in the dual task.

Both the approximation of amplitudes and of latencies represent an effective mechanism for coordinating eye and hand. Similar amplitudes and therefore, landing positions, ensure optimal conditions for the pickup of further visual information to correct the ongoing movement. Similar latencies, and therefore, movement end times, support this mechanism by ensuring that the time at which eye and hand land on the object is not too different, which is important, for example, when objects move.

3.8 Conclusion

Our results suggest that eye and hand are coupled by two separate but interacting target representations, because the global effect of eye and hand was similar in some experiments, but different in others. This coupling happens at an early stage of movement preparation, i.e. at the stage of target selection. Further evidence for an exchange of information between the eye and hand motor systems is that their amplitudes and latencies approached each other when both movements were executed concurrently.

This convergence seems to be necessary to synchronise the time and position at which eye and hand land on a target object. As hand movements are typically accompanied by simultaneous eye movements in everyday life, this synergy enables the organism to optimally interact with its environment.

3.9 Acknowledgements

The authors thank Marc Hassenzahl for a thorough preliminary review of the manuscript, Iain Gilchrist, Anne Häberle, and Martin Fischer for inspiring comments, and Judy Benson for copyediting the manuscript.

3.10 References

Abrams, R. A., Meyer, D. E., & Kornblum, S. (1990). Eye-hand coordination: oculomotor control in rapid aimed limb movements. *Journal of Experimental Psychology: Human Perception and Performance, 16,* 248-267.

Adam, J. J., Ketelaars, M., Kingma, H., & Hoek, T. (1993). On the time course and accuracy of spatial localization: basic data and a two-process model. *Acta Psychologica Amsterdam, 84,* 135-159.

Aitsebaomo, A. P. & Bedell, H. E. (2000). Saccadic and psychophysical discrimination of double targets. *Optometry and Vision Science, 77,* 321-330.

Bekkering, H. (1995). *Eye-hand coordination: cooperative and competitive systems?* Unpublished doctoral dissertation, Rijksuniversiteit Limburg, Maastricht, Netherlands.

Bekkering, H., Abrams, R. A., & Pratt, J. (1995). Transfer of saccadic adaptation to the manual motor system. *Human Movement Science, 14,* 155-164.

Biguer, B., Prablanc, C., & Jeannerod, M. (1984). The contribution of coordinated eye and head movements in hand pointing accuracy. *Experimental Brain Research, 55,* 462-469.

Coeffé, C. & O'Regan, J. K. (1987). Reducing the influence of non-target stimuli on saccade accuracy: predictability and latency effects. *Vision Research, 27,* 227-240.

Coren, S. & Hoenig, P. (1972). Effect of non-target stimuli upon length of voluntary saccades. *Perceptual and Motor Skills, 34,* 499-508.

de Graaf, J. B., Pélisson, D., Prablanc, C., & Goffart, L. (1995). Modifications in end positions of arm movements following short-term saccadic adaptation. *Neuroreport., 6,* 1733-1736.

Delreux, V., Vanden-Abeele, S., Crommelinck, M., & Roucoux, A. (1991). Interactions between goal-directed eye and arm movements: Arguments for an interdependent motor control. *Journal of Motor Behavior, 23,* 147-151.

Doyle, D. & Walker, R. (2001). Voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research, 139,* 333-344.

Eggert, T., Sailer, U., Ditterich, J., & Straube, A (2002). *Differential effect of a distractor on primary saccades and perceptual localization.* Manuscript submitted for publication.

Engel, K. C. & Soechting, J. F. (2000). Hand-eye coordination in two dimensional tracking. *Society for Neuroscience Abstracts*, 1721-1721.

Findlay, J. M. (1981). Local and global influences on saccadic eye movements. In D.F. Fisher, R. A. Monty, & J. W. Senders (Eds.), *Eye Movements: Cognition and Visual Perception* (pp. 171-179). Hillsdale, NJ: Lawrence Erlbaum Associates.

Findlay, J. M. (1982). Global visual processing for saccadic eye movements. *Vision Research, 22,* 1033-1045.

Findlay, J. M. (1983). Visual information processing for saccadic eye movements. In A. Hein & M. Jeannerod (Eds.), *Spatially oriented behavior* (pp. 281-303). New York: Springer.

Fischer, M. H. & Adam, J. J. (2001). Distractor effects on pointing: the role of spatial layout. *Experimental Brain Research, 136,* 507-513.

Frens, M. A. & Erkelens, C. J. (1991). Coordination of hand movements and saccades: evidence for a common and a separate pathway. *Experimental Brain Research, 85,* 682-690.

Gielen, C., van den Heuvel P.J., & van Gisbergen J.A. (1984). Coordination of fast eye and arm movements in a tracking task. *Experimental Brain Research, 56,* 154-161.

Hansen, R.M. & Skavenski, A.A. (1985). Accuracy of spatial localizations near the time of saccadic eye movements. *Vision Research, 25,* 1077-1082.

Jacobs, A. M. (1987). On localization and saccade programming. *Vision Research, 27,* 1953-1966.

Lee, D. (1999). Effects of exogenous and endogenous attention on visually guided hand movements. *Cognitive Brain Research, 8,* 143-156.

Mather, J. A. (1985). Some aspects of the motor organization of the oculomotor system. *Journal of Motor Behavior, 17,* 373-383.

Mather, J. A. & Fisk, J. D. (1985). Orienting to targets by looking and pointing: Parallels and interactions in ocular and manual performance. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 37A,* 315-338.

Neggers, S. F. & Bekkering, H. (1999). Integration of visual and somatosensory target information in goal-directed eye and arm movements. *Experimental Brain Research, 125,* 97-107.

Neggers, S. F. & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology, 83,* 639-651.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9,* 97-113.

Ottes, F. P., Van Gisbergen, J. A., & Eggermont, J. J. (1985). Latency dependence of colour-based target vs nontarget discrimination by the saccadic system. *Vision Research, 25,* 849-862.

Pélisson, D., Prablanc, C., Goodale, M. A., & Jeannerod, M. (1986). Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Experimental Brain Research, 62,* 303-311.

Prablanc, C., Echallier, J. F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. *Biological Cybernetics, 35,* 113-124.

Pratt, J. & Abrams, R. A. (1994). Action-centered inhibition: effects of distracters on movement planning and execution. *Human Movement.Science, 13,* 245-254.

Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2000). Spatial and temporal aspects of eye-hand coordination across different tasks. *Experimental Brain Research, 134,* 163-173.

Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain Research, 105,* 261-275.

Soechting, J. F., Engel, K. C., & Flanders, M. (2001). The duncker illusion and eye-hand coordination. *Journal of Neurophysiology, 85,* 843-854.

Tipper, S. P., Howard, L. A., & Paul, M. A. (2001). Reaching affects saccade trajectories. *Experimental Brain Research, 136,* 241-249.

Tipper, S. P., Howard, L. A., & Houghton, G. (2000). Behavioral Consequences of Selection from Neural Population Codes. In S. Monsell & J. Driver (Eds.), *Attention and Performance XVIII* (pp. 223-245). Cambridge, MA: The MIT Press.

Tipper, S. P., Howard, L. A., & Jackson, S. R. (1997). Selective reaching to grasp: Evidence for distractor interference effects. *Visual Cognition, 4,* 1-38.

Van Donkelaar, P. (1997). Eye-hand interactions during goal-directed pointing movements. *Neuroreport., 8,* 2139-2142.

Van Donkelaar, P. (1998). Saccade amplitude influences pointing movement kinematics. *Neuroreport., 9,* 2015-2018.

Vercher, J. L., Magenes, G., Prablanc, C., & Gauthier, G. M. (1994). Eye-head-hand coordination in pointing at visual targets: spatial and temporal analysis. *Experimental Brain Research, 99,* 507-523.

Watt, R. J. (1987). Scanning from coarse to fine spatial scales in the human visual system after the onset of a stimulus. *Journal of the Optical Society of America A, 4,* 2006-2021.

Welsh, T. N., Elliot, D., & Weeks, D. J. (1999). Hand deviations toward distractors. Evidence for response competition. *Experimental Brain Research, 127,* 207-212.

4 Static hand position affects the landing position of eye movements

4.1 Abstract

The aim of the present study was to determine whether static hand position influences eye position, and if so, whether this influence occurs during target presentation and encoding or shortly before movement execution.

Results showed that the landing position of eye movements was drawn towards the position of the static hand. Thus, hand position influenced eye position.

We hypothesised that if this influence occurred during presentation and encoding of target position, then the ocular error should be independent of a hand movement occurring in the target memorisation period. Indeed, the influence of hand position on eye position was similar both when hand movements stayed at the same position during the entire trial and when they moved away from that position in the target memorisation period. Thus, information about static hand position is integrated into the oculomotor command already during target encoding.

4.2 Introduction

A number of studies have shown that the execution of an eye movement influences the spatial parameters of a coordinated hand movement. For example, hand amplitude could be modified by variations in saccadic amplitude only (e.g. van Donkelaar 1997, 1998). Similarly, under certain conditions saccadic adaptation transfers to the hand motor system (Bekkering et al. 1995; de Graaf et al. 1995). But this influence of one motor system on the other is not unidirectional. The reverse effect has also been discovered: the execution of a hand movement can also influence the spatial parameters of coordinated eye movements. The most striking example for the latter finding is improved eye tracking when accompanied by the hand (Steinbach 1969, Gauthier et al. 1988). In pointing tasks, the trajectory of the eye has been shown to be influenced by a concomitant reach to the target (Tipper et al. 2001).

Not only the execution of an eye movement, but also static eye position influences hand movements. Orientation of the eye *at the time of pointing* systematically influences pointing responses towards the remembered location of both eccentric (Enright 1995) and central targets (Henriques et al. 1998). In the latter study the retinal eccentricity of the target was exaggerated, i.e., pointing direction was biased towards more eccentric positions both when subjects constantly fixated peripheral locations and when they briefly foveated the target before saccading to a peripheral position. Such an overestimation of the eccentricity of visual targets on the peripheral retina was also reported by Bock (1986).

Since the influence of *executed eye and hand movements* on each other is mutual, the question arises if the influence of *static effector position* is also mutual. In other words: the effect of eye position on hand movements has been shown, but can hand position also influence eye movements? Such an effect has been suggested by Tipper et al. (2001) who proposed that even if the hand is not performing a response towards the target, its position may influence the trajectories of a saccade. Similarly, studies on temporal coordination suggest that hand position may serve as target for the eye. For example, Neggers and Bekkering (2000) have shown that gaze is locked to the target of an ongoing hand movement. In their study, subjects were not able to initiate a saccade towards a new target as long as the execution of a hand movement towards a different target was not completed. According to the authors, this result speaks for visual attention being tied to the target of the hand movement. Such an anchoring of gaze to the hand target in the temporal domain could also occur in the spatial domain.

We tried to find out whether such an influence of static hand position on the landing position of eye movements exists by altering the experimental paradigm of Henriques et al. (1998). More specifically, we were interested in distinguishing three possibilities: A) static hand position does not influence eye position, B) static hand position influences eye position at the time the target is presented and encoded, C) static hand position influences eye position at the time the response is executed, i.e. read out from memory.

In condition 1 (TOHAND), eye movements were directed to the position of the hand, in condition 2 (FROMHAND), away from the position of the hand, and in condition 3 (TOHANDSTART), to the position at which the hand was before moving elsewhere in the target memorisation phase (see also Figure 1). We hypothesised that A) if static hand position does not influence eye position the horizontal eye error would not differ between these three conditions. B) if static hand position influences eye position at the time the target is encoded, then the horizontal error should be different in conditions 3 (TOHANDSTART) and 2 (FROMHAND), but not in 3 (TOHANDSTART) and 1 (TOHAND), and C) if static hand position influences eye position a the time the eye movement is executed, then the horizontal error should be different in conditions 3 (TOHANDSTART) and 1 (TOHAND), but not in 3

(TOHANDSTART) and 2 (FROMHAND). For a better overview, these hypotheses and the respective predicted results are displayed in Table 1.

Table 1 Overview of hypotheses and associated expected results

		Hypothesised influence of hand position on eye position	Expected results in paradigm 1 to 3 (1 = TOHAND, 2 = FROMHAND, 3 = TOHANDSTART)
Hypothesis	1	none	1=2=3
	2	at the time of target encoding	$1 \neq 2$ $3 \neq 2$ $3 = 1$
	3	at the time of eye movement execution	$1 \neq 2$ $3 = 2$ $3 \neq 1$

4.3 Method

4.3.1 Subjects

Eight subjects were recruited from employees of the department. They were three women and five men between 30 and 42 years of age with normal or corrected-to-normal visual acuity. All of them were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield 1971), except for subject AS who was ambidextrous.

4.3.2 Apparatus

Subjects sat in a darkened room in front of a table. Their right elbow rested on a padded support and their head was stabilised by a chin rest. A 15-inch flat screen color monitor (NEC MultiSync LCD 1525S) was firmly screwed to the table at an angle of 50° and at a distance of approximately 35 cm from the subject's eyes. The monitor provided a frame frequency of 72 Hz at a spatial resolution of 1280*1024 pixels. The screen was reinforced by an additional pane of perspex about which the subjects were informed.

Hand movements were measured with the ultrasonic system Zebris (Isny, Germany). It measured the location of a speaker 1 cm in diameter that was attached to the tip of the subject's right index finger at a sampling rate of 200 Hz. A calibration was performed at the beginning of each session based on a set of four markers with known 3-D coordinates.

Eye movements were monitored with the infrared corneal reflection device IRIS (Skalar, Delft, Netherlands), the output of which was digitised at a rate of 1 kHz.

A personal computer was used for experimental control, visual presentation, and data collection. The video signals were controlled by a PC via a TIGA (Texas Instruments Graphics Adapter) graphics board. The stimuli consisted of green (fixation for hand), red (fixation for eye) and white (memory target) spots 0.5 deg in diameter. The stimuli appeared on a dark grey background.

4.3.3 Procedure

At the beginning of each session several calibration trials were performed by having the subject fixate and point towards targets at known eccentricities. For each condition, the subjects performed 10-20 practice trials before recording began.

At the beginning of a trial the green spot appeared on the screen and remained there for 4 sec. 2 sec after onset of the green spot, a red spot appeared for 2 sec. The subjects were requested to align their hand with the green spot and their eye with the red spot. 0.5 sec after disappearance of the red spot, a white spot appeared for 0.3 sec at the centre of the screen. The subjects were asked to remember the position of the white spot, but not to make an eye movement towards it. Immediately after offset of the stimulus, the background illumination of the screen was turned off leaving the subject in complete darkness. After an interval of 2 sec in the dark, a beep tone was given as signal for the subject to execute a saccade towards the memorised position of the white spot. The next trial started 3 sec after the beep.

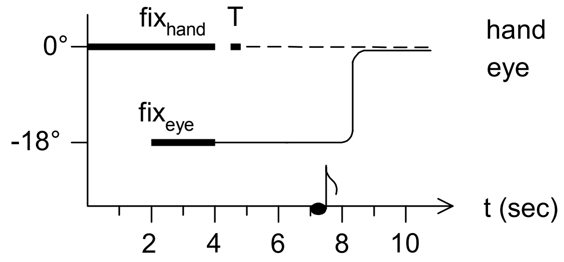
The positions of the white (target) and the red (eye fixation) spot were vertically shifted towards +2 deg, whereas the position of the green (hand fixation) spot was vertically shifted towards –2 deg. The white target was always presented centrally. Horizontal target position varied slightly, i.e, between one of the positions –2 deg, -1 deg, 0 deg, 1 deg, 2 deg, equally distributed across one session. The red spot was always presented peripherally. Horizontal position of the red spot varied randomly but equally distributed between –22 deg, -20 deg, -18 deg on the left side, or 18 deg, 20 deg, 22 deg on the right side.

Three paradigms were employed in which the position of the hand was varied (see figure 1). In paradigm 1, saccade to hand (hereafter: TOHAND), the horizontal position of the green spot corresponded to the central position of the target. Consequently, the ensuing saccade is directed towards the hand. In paradigm 2, saccade away from hand (hereafter:

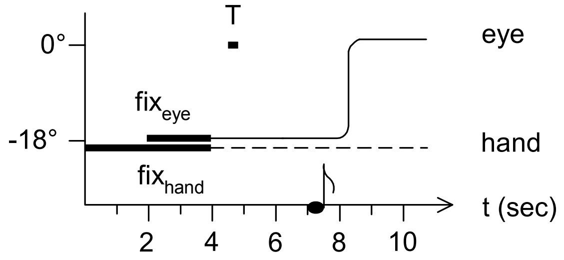
FROMHAND), the green spot was presented at the same horizontal position as the red spot, i.e., the fixation spots of eye and hand were at the same peripheral position. The ensuing saccade is directed away from the hand. In paradigm 3, saccade to hand start (hereafter: TOHANDSTART), the horizontal position of the green and the target spot was again identical, but subjects were instructed to execute a hand movement towards the position they were fixating right after blanking of the screen. The ensuing saccade is directed towards the position of the hand before it started moving.

Each condition consisted of 60 trials. The three conditions were counterbalanced within and across subjects.

1.) TOHAND



2.) FROMHAND



3.) TOHANDSTART

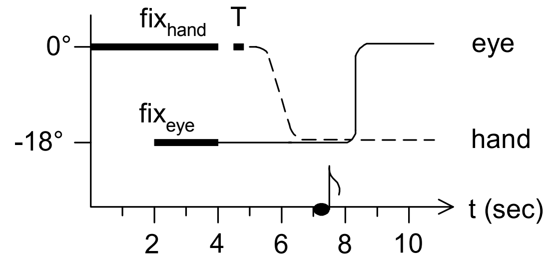


Figure 1 Schematic diagram of three experimental conditions with varying start and end positions of hand. $\mathrm{Fix}_{\mathrm{eye}}$ indicates position and duration of red eye fixation spot, $\mathrm{fix}_{\mathrm{hand}}$ of the green hand fixation spot, T of target. The note indicates the time of the beep tone (go signal for saccade).

4.3.4 Data processing

Pointing position was defined as the horizontal coordinate of the index finger marker.

All data were stored and analysed off-line. Calibration of eye and hand movements was performed by means of a third-order polynomial calibration based on fixation data or pointing data, respectively. The beginning of a hand or eye movement was defined as the moment at which the velocity of the hand or eye exceeded 10% of peak velocity. Movements below 10 deg/sec hand velocity or 50 deg/sec eye velocity were discarded from further analysis. The end of the hand or eye movement was defined as the moment at which the velocity of the hand or eye fell below 10% of peak velocity. Maximal latency for a hand or eye movement was set at 1000 ms, minimal latency at 80 ms.

To be included in futher analysis, trials had to conform to the following criteria: no occurrence of reactive eye or hand movements towards the memory target, fixation of eye and hand when memory target disappears, "fixation" of hand when eye movement occurs. In condition 3, hand movements had to be completed before the memory saccade was executed.

The dependent variable of interest was the ocular horizontal error (distance of movement endpoint from target). Negative horizontal error values indicate an undershoot, positive values an overshoot. For each subject and condition, those values of the horizontal error deviating more than two standard deviations from the respective cell mean were omitted from further analyses.

The horizontal error of the eye was analysed by means of a repeated measures analysis of variance with the three-level factor experimental condition (TOHAND, FROMHAND, TOHANDSTART). The Mauchley test was used to determine sphericity of the data and, when found to be significant, the Huynh-Feldt correction was applied to determine significance.

4.4 Results

The horizontal eye error depended on the position of the hand *at the time the target was presented* (see Figure 2 and 3).

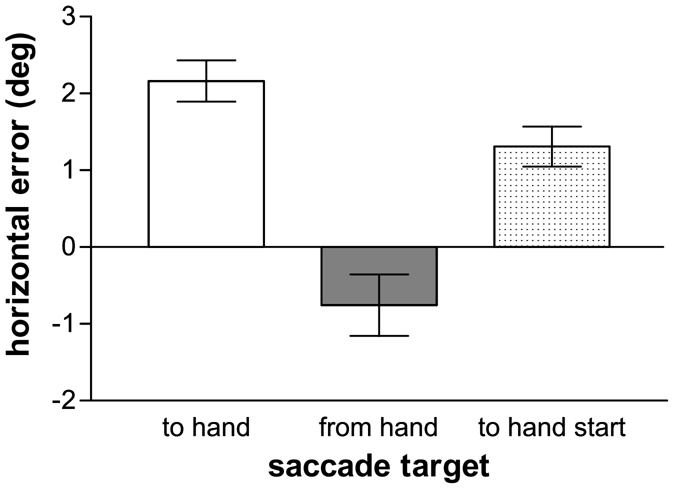


Figure 2 Mean horizontal error and standard error of the mean (N=8) for each condition

It was significantly different across the three conditions (F(1,14;7.98) = 5.47; p<.05). Eye movements overshot in condition TOHAND (mean error = 2.16 deg) and TOHANDSTART (mean error = 1.31 deg). In contrast, eye movements undershot in condition FROMHAND (mean error = -0.76 deg). Post hoc exploration (Scheffé) revealed that condition FROMHAND was significantly different from condition TOHAND (p<.05). This implies that hand position indeed influences eye position. If the eye saccades to the hand, it overshoots. If the eye saccades away from the hand, it undershoots. Thus, in both cases it is drawn towards the hand.

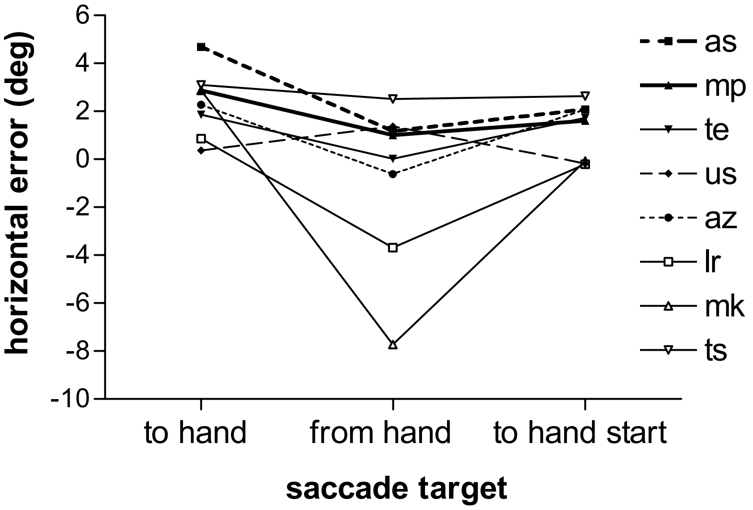


Figure 3 Mean horizontal error for each subject and condition

In order to determine whether the influence of the hand on the eye occurs during target encoding or during execution of the eye movement, a post hoc test was performed. In case of an influence during encoding, condition TOHANDSTART should be different from FROMHAND, but not from condition TOHAND. In case of an influence during execution, condition TOHANDSTART should be different from condition TOHAND, but not from condition FROMHAND (see also Table 1). Post hoc exploration revealed only a tendentially larger difference of condition FROMHAND than of condition TOHAND from condition TOHANDSTART. As shown in Figure 2, both in TOHAND and TOHANDSTART eye movements overshot, whereas they undershot in FROMHAND. This may be interpreted in the direction of hypothesis 2: the influence of static hand position on eye position seems to be larger at the time that target position is encoded than at the time the eye movement is executed.

To further explain the pattern found we performed a separate analysis for each subject. The data of four subjects with equal variances (according to the Levene test) across the three conditions were analysed by means of a one-way ANOVA with the grouping variable condition. Of these four subjects, two (TE and LR) showed significant differences across conditions ($F=5.12$, $p<.01$ and $F=3.51$, $p<.05$). More specifically, these differences concerned the conditions TOHANDSTART and FROMHAND, but not TOHANDSTART and TOHAND (post hoc LSD).

For the subjects with unequal variances the horizontal eye error across conditions was compared by means of a Kruskal-Wallis test. One subject (MK) showed significant differences across conditions ($\chi 2=17.42$, $p<.0001$). Since no post-hoc test for the Kruskal-Wallis test exists, data of the same subject were also submitted to a one-way ANOVA. As the results were very similar ($F=18.06$, $p<.0001$), it seems reasonable to use the results of the post-hoc (LSD) of this analysis for interpretation. As in the other two subjects with significant differences across conditions, this subject had different errors in condition TOHANDSTART and FROMHAND, but not in condition TOHANDSTART and TOHAND. Thus, the data from single subjects also support hypothesis 2: hand position seems to have a larger influence on eye position at the time that target position is encoded than when the eye movement is executed.

However, the difference between condition FROMHAND and TOHANDSTART was too small to conclusively reject hypothesis 3, an influence during target position execution. The differences observed may be obstructed both by large interindividual differences (see Figure 3) and by a generally high variability of responses.

4.5 Discussion

The present data showed that static hand position influences eye position. They also provided some evidence that this influence occurs rather at the time that target position is presented and encoded than at the time when the eye movement is executed. The landing position of eye movements is drawn towards the static position of the hand, irrespective of whether the hand has been at the target location all the time (TOHAND) or whether it moved away from it during the memorisation period of the target (TOHANDSTART). This resulted in an overshoot of hand movements. When the eye moved away from the hand and towards the target (FROMHAND), it was also drawn towards the hand, as shown by an ocular undershoot. Hence, it appears that information about hand position is integrated into the oculomotor command already at an early stage, when the representation of the target is built up. Interestingly, in models of saccade generation (e.g. Robinson 1975, Gancarz & Grossberg 1999), signals arising from the hand do simply not show up.

Such a mechanism suggests that the organism tries to align not only the hand with the eye, as already known, but also the eye with the hand. Consequently, the temporal linking of the eye to the hand motor system shown, for instance, by Neggers and Bekkering (2000) extends to the spatial domain. Functionally, it may ensure an optimal control of a hand movement or grasp by visual feedback, even if the hand is not actively performing any action.

These results are somewhat contrary to the notion of Henriques et al. (1998) of a dynamic map of visual space which is continuously updated until the decision to execute a movement is made. In contrast, our data suggest that a representation of the target is constructed at the time of its presentation. Information about hand position is integrated into this representation. However, Henriques et al. (1998) probed the representation of the hand target, whereas we dealt with an eye target. Whereas the target for the hand requires a transformation from retinal into body-centred coordinates, no such transformation is required for the eye target. Thus, it seems plausible that the eye target representation is already constructed during target presentation.

However, due to the large variability in the data, our interpretation can only remain tentative. To reduce the variability, a replication of the present experiment with fully fixed head (e.g., by using a biteboard) could be helpful. Otherwise, the idea that hand position may influence eye movements is supported by an older observation that pursuit movements of the eye improve with simultaneous hand movements (see Introduction). That such an influence also exists for static hand position is an interesting finding that is worthwhile of further investigation.

4.6 References

Bekkering H, Adam JJ, van-den-Aarssen A, Kingma H, Whiting HT (1995) Interference between saccadic eye and goal-directed hand movements. Exp Brain Res 106: 475-484

Bock O (1986) Contribution of retinal versus extraretinal signals towards visual localization in goal-directed movements. Exp Brain Res 64: 476-482

de Graaf JB, Pelisson D, Prablanc C, Goffart L (1995) Modifications in end positions of arm movements following short-term saccadic adaptation. Neuroreport 6: 1733-1736

Enright JT (1995) The nonvisual impact of eye orientation on eye-hand coordination. Vision Res 35: 1611-1618

Gancarz G, Grossberg S (1999) A neural model of saccadic eye movement control explains task-specific adaptation. Vision Res 39: 3123-3143

Gauthier GM, Vercher JL, Mussa IF, Marchetti E (1988) Oculo-manual tracking of visual targets: control learning, coordination control and coordination model. Exp Brain Res 73: 127-137

Henriques DY, Klier EM, Smith MA, Lowy D, Crawford JD (1998) Gaze-centered remapping of remembered visual space in an open-loop pointing task. J Neurosci 18: 1583-1594

Neggers SF, Bekkering H (2000) Ocular gaze is anchored to the target of an ongoing pointing movement. J Neurophysiol. 83: 639-651

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9: 97-113

Robinson DA (1975) Oculomotor control signals. In: Lennerstrand F., Bach-y-Rita P. (eds.). Basic Mechanisms of Ocular Motility and Their Clinical Implications. Oxford: Pergamon, p. 337-374

Steinbach MJ (1969) Eye tracking of self-moved targets: the role of efference. J Exp Psychol 82: 366-376

Tipper SP, Howard LA, Paul MA (2001) Reaching affects saccade trajectories. Exp Brain Res 136: 241-249

van Donkelaar P (1997) Eye-hand interactions during goal-directed pointing movements. Neuroreport 8: 2139-2142

van Donkelaar P (1998) Saccade amplitude influences pointing movement kinematics. Neuroreport 9: 2015-2018

5 Predictive pointing movements and saccades towards a moving target

5.1 Abstract

The aim of the present study was to investigate whether and if so, how velocity information is used to control predictive manual pointing movements and saccades. Subjects were asked to intercept an occluded moving target as if it were still visible. The velocity of the target changed during its course from 6°/sec to either 2°/sec or 10°/sec. The target was visible at its final velocity for either approx. 50 ms, 100 ms, or 150 ms before it disappeared. The distance over which the target traveled was fixed. Subjects kept their eyes fixated while the target moved. The behavior of eye and hand was similar. Movements overshot the slow target and undershot the fast target. Thus, responses were biased in the direction of the target's initial velocity. This effect was even more pronounced when the duration of the final velocity was short. At short and intermediate final velocity durations, subjects aimed at the same position irrespective of the target's velocity. We suggest that this is due to insufficient time to detect a velocity change rather than to insufficient processing time, because latency and movement time did not decrease with final velocity duration.

Movement amplitude did not vary with latency, showing that the subjects did not take their latency into account when aiming at the target, but instead, adopted a strategy of aiming further ahead when the target was fast. Amplitude was also more related to the position of velocity change than to final velocity duration. Both findings suggest that target velocity is not extrapolated. The subjects' reaction seems to be based on a certain increment added to the position of velocity change.

5.2 Introduction

Moving targets are as common in everyday life as stationary ones. To execute a hand or eye movement towards a moving as opposed to a stationary target, information about target velocity as well as target position is needed. An accurate use of these two sources of information might be even more important if the target disappears before the movement is executed, because in such a case the ongoing eye or hand movement cannot be modified by using visual information about the target. When online comparison with the target is not possible, the eye or hand movement must be based on information obtained from the target at some point before it disappears. However, the kind of information used must still be determined.

Several studies dealing with manual pointing movements and saccadic eye movements towards moving targets have investigated whether and if so, how target velocity is used for movement control. Figure 1 categorizes tasks typically applied in this context.

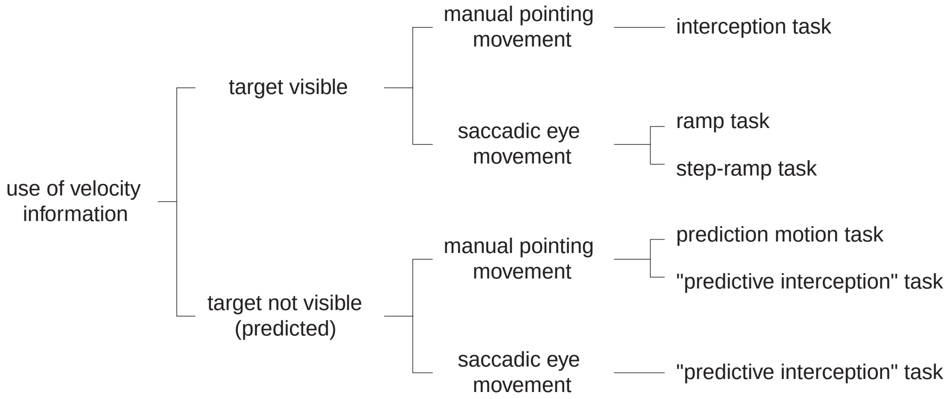


Figure 1 Categorization of tasks investigating the use of velocity information for the control of saccades and pointing movements

Most of these studies involved visible, moving targets. A typical task for hand movements is the interception task. The subject has to intercept or "catch" a moving target with the hand.

Typical tasks for eye movements that involve visible targets are the ramp task (the target starts moving away from the fixation spot) and the step-ramp task (Rashbass, 1961). The step-ramp task generally requires that subjects fixate a stationary target. At some point in time, the target changes position to another location on the screen (the step), from where it proceeds to move at a constant velocity. The ramp and step-ramp tasks first evoke a catch-up saccade before the pursuit movement starts. It is assumed that the programming of the catch-up saccade takes into account the target motion occurring during the ramp. To do this, the system must estimate (i.e., predict) target position at the time that the saccade occurs. However, Heywood and Churcher (1981) have argued that the saccadic amplitudes in these tasks can be explained by strategies that do not necessarily involve motion extrapolation. They concluded that subjects use a strategy in which they sample a target position about 100 ms before the saccade and add a constant to it (Heywood & Churcher, 1981; Ron, Vieville, &

Droulez, 1989). They based this conclusion on the finding that saccadic amplitude towards targets with different velocities correlated better with target position 100 ms before the saccade than with target position at the time of the saccade. In contrast, a more recent study showed that information about target motion is used to plan saccadic amplitude to a moving target (Gellman & Carl, 1991). Since information about target position alone cannot explain the saccadic amplitudes observed in this double-step experiment, the authors concluded that the saccadic system extrapolates target motion.

It is interesting to ask whether and if so, how such extrapolation takes place, if the target has already disappeared when the movement is executed. Such a task shows some major differences from the classic (step-) ramp paradigm. In a step-ramp task, the predictive mechanisms of pursuit and saccades overlap, whereas we were interested in the predictive mechanisms of saccades only. Moreover, the mechanisms for planning and execution may differ because different go-signals are involved with catch-up saccades in a (step-) ramp task than are used with predictive saccades (i.e., to the location of an occluded target). In a step-ramp task the step triggers a reflexive saccade. A catch-up saccade is performed in a ramp task when the target exceeds a certain retinal eccentricity. In contrast, in a task requiring movement to the location of an occluded target, the resulting predictive saccades are triggered willfully, i.e., they are intentional saccades. Thus, it seems inappropriate to compare saccades to (step-) ramp targets with predictive saccades towards moving targets.

Studies of predictive pointing movements or saccades towards moving targets that are absent during the latency period are rare.

One classic task for hand movements is the prediction motion task. In this task, a target begins moving towards an end point but disappears before arriving. Subjects are asked to react at the time they assume the target would have arrived at the end point. Instead of a direct estimation of target location, this task requires the estimation of temporal coincidence. The subject’s response in a prediction motion task may be determined either by cognitive motion extrapolation, i.e., an internal representation of the target’s visible motion (as concluded by DeLucia & Liddell, 1998) or by a timing mechanism, i.e., an estimation of time to contact made before the target disappears and the use of a clocking process that counts the time until the target reaches this estimated time to contact (Tresilian, 1995).

The main aim of our study was to investigate the spatial aspect of prediction, i.e., prediction of a target’s location. More specifically, we sought to determine whether saccadic and pointing amplitudes are determined by the use of information about target position at a certain point, or if target velocity is extrapolated. Therefore, a task was developed that cannot be solved by a simple timing mechanism (the so-called “predictive interception” task). This task involved a horizontally moving target that changed its velocity during its course. While the distance traveled by the target was kept constant, the presentation time of the velocities was varied. Thus, the target always disappeared at the same place. After it disappeared, the subjects made a movement towards the predicted location of the target where it would have been had it continued to move.

If the subjects based their responses solely on information about target position at the moment of its disappearance, we would expect movement amplitude to not vary with target presentation time. In contrast, a variation of movement amplitude with presentation time would speak for the use of target velocity information.

In addition, we used a dual-task methodology to determine whether the mechanisms for motion prediction are similar for eye and hand movements. The dual-task methodology in its original form requires subjects to perform a primary task while at the same time performing a second task. In the study of eye-hand coordination, single-task refers to a task of either eye or hand movements, whereas dual-task refers to combined eye and hand movements (see Bekkering, Adam, Kingma, Huson, & Whiting, 1994). The underlying assumption is that if responses in the dual-task condition do not differ from those in the single-task conditions, both movements are controlled by independent processes. If there is a difference, common processes are likely to be involved.

5.3 Method

5.3.1 Subjects

Six subjects (two women and four men, between 26 and 42 years of age) participated in the experiment. All subjects had normal vision or contact-lens corrected vision and were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971).

5.3.2 Apparatus

The subjects were seated in a darkened room in front of a table with their right elbow resting on a padded support and their head stabilized by a chin rest. A 15-inch flatscreen color monitor (NEC MultiSync LCD 1525S) was firmly screwed to the table at an angle of 50° and approximately 35 cm distant from the subject's eyes. The monitor provided a frame frequency of 72 Hz at a spatial resolution of 1280*1024 pixels. Position update of the moving stimulus occurred at every frame. An additional pane of plexiglass reinforced the screen. A small spot

5 mm in diameter and serving as the starting position for the finger was glued 1 cm below the center of the screen at 0° horizontal visual angle.

A personal computer was used for monitoring the experiment, visual presentation, and data collection. The video signals were controlled by a PC via a TIGA (Texas Instruments Graphics Adapter) graphics board. The stimulus appeared on a dark gray background.

5.3.3 Behavioral task ("predictive interception")

At the beginning of a trial, the subject aligned the eye and right index finger with the glued fixation spot in the centre of the screen. The target was a small white spot 0.5 deg in diameter, which appeared at –8° visual angle (8° to the left from the fixation spot) and started to move towards the right. Its vertical coordinate was always 0°. The spot initially moved at a fixed velocity of 6°/sec before changing either to 2°/sec or 10°/sec (slow or fast *final velocity*). This final velocity was visible for either short (approx. 50 ms), intermediate (approx. 100 ms), or long duration (approx. 150 ms) (*final velocity duration*) before the spot disappeared. More specifically, the frame rate of 72 Hz (i.e., the duration of one frame was 13.88 ms) allowed presentation times of only 42 or 56 ms (3 or 4 frames) for the short final velocity duration, 97 or 111 ms (7 or 8 frames) for the intermediate final velocity duration, and 139 or 153 ms (10 or 11 frames) for the long final velocity duration. The target always started and disappeared at the same position.

Trial types resulting from the different combinations are schematically illustrated in Figure 2.

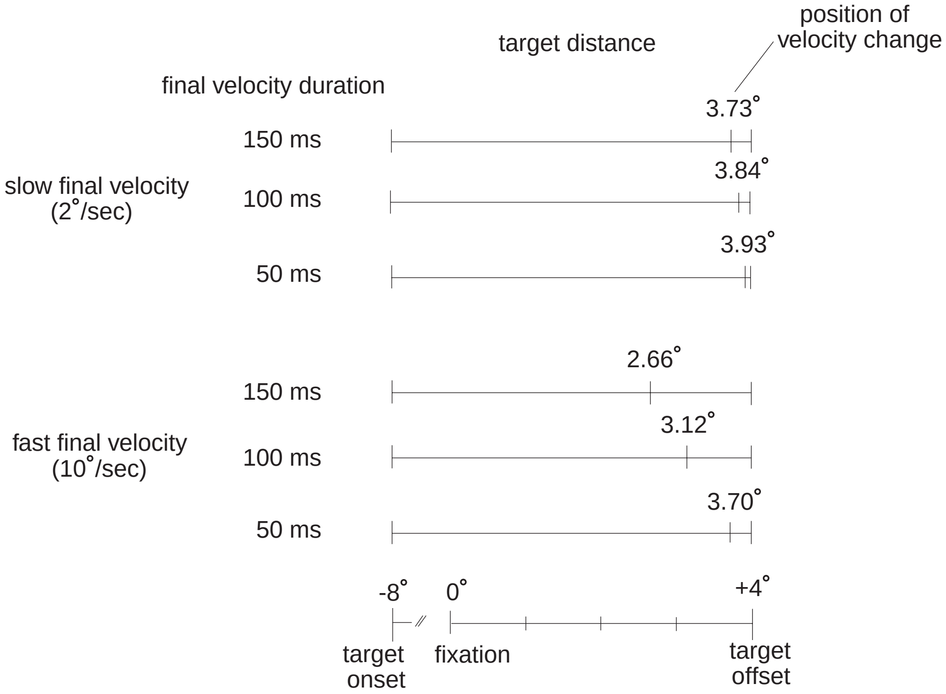


Figure 2 Schematic representation of target position in the six different trial types. The change in target velocity occurred at the same moment, but at different positions depending on the final velocity and the final velocity duration of the target.

At the moment the target arrived at +4°, the target and the background illumination of the monitor were simultaneously turned off and the subject was in complete darkness. A blank screen was the cue for the subject to begin moving.

The subjects had been told previously that the spot continued to move in the darkness. They were asked to "intercept" this occluded target with their eyes only, hand only (single-task conditions), or eyes and hand concurrently (dual-task condition). Figure 3 shows a sample trial of the dual-task condition. The subjects were also told that target motion would change to a higher or lower velocity in each trial. They were, however, unaware that the target always disappeared at the same position.

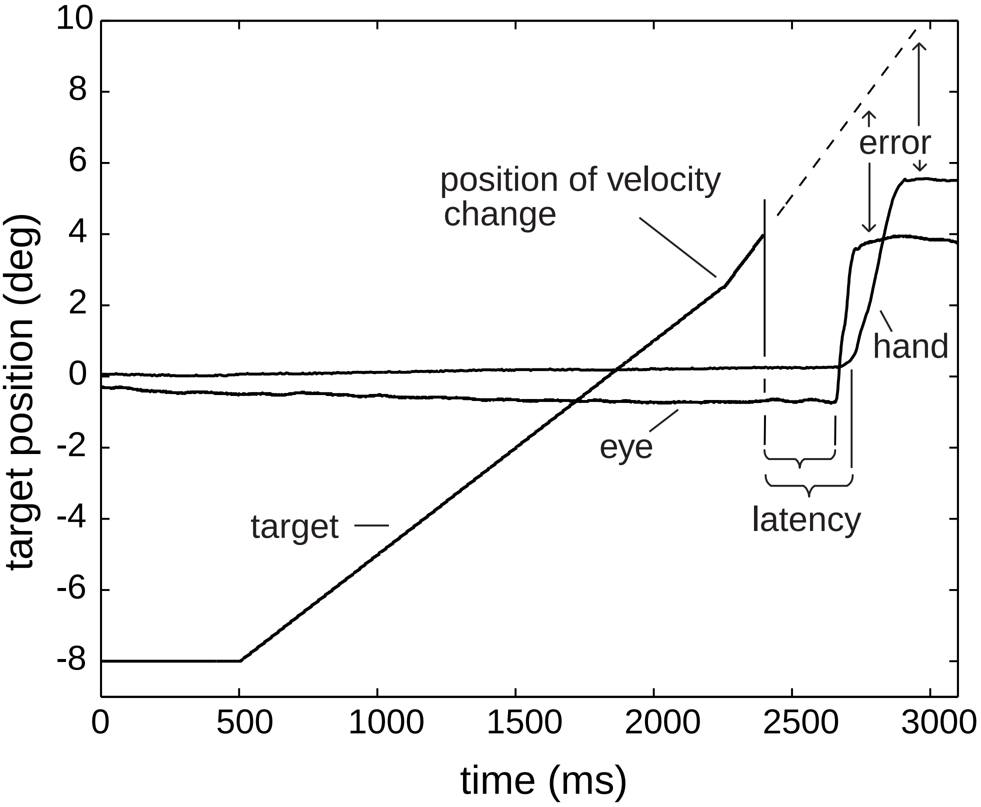


Figure 3 Sample trial of eye and hand movements to a fast target with long final velocity duration. The dotted line represents the actual position of the target if it had continued to move visibly. The difference between this position and the hand or eye end position shows the end position error (identical with the amplitude error when the movement starts from the center). Latency is the difference between target offset and movement onset.

In tasks involving the hand, the subjects were informed about the plexiglass reinforcement of the screen and asked to place their fingertip directly on the screen. No feedback on performance was given. Because all the subjects had gained experience with this task in several preceding pilot studies, no practice trials were performed. As the subjects had received no feedback on performance in these pilot studies, participation probably did not lead to a training of the response, but only to an increased familiarity with the rather complex task.

Each condition consisted of 120 trials with the two final velocities and the three final velocity durations in a pseudorandomised order. Each subject participated in all three experimental conditions, the order of which was counter-balanced.

5.3.4 Measurement of hand and eye movements

An ultrasonic speaker 1 cm in diameter was attached to the tip of the subject's right index finger. The spatial 3-D location of this speaker was measured at a sampling rate of 200 Hz by means of an ultrasonic device (Zebris, Isny, Germany). A calibration was performed at the beginning of each session based on a set of four markers with known 3-D coordinates. There was a mean accuracy of 3.4 mm over all sessions. Another calibration procedure involved having the subject point to targets at known eccentricities at the beginning, the middle, and the end of each session. Pointing position was defined as the horizontal coordinate of the index finger marker.

Eye movements were monitored with an infrared corneal reflection device (IRIS, Skalar, Delft, Netherlands), the output of which was digitized at a rate of 1 kHz. Several calibration trials were performed at the beginning, in the middle, and at the end of each session by having the subject fixate targets at known eccentricities.

All data were stored and analyzed off-line. Calibration of eye and hand movements was performed by means of a third-order polynomial calibration based on fixation data or pointing data, respectively. The beginning of a hand or eye movement was defined as the moment at which the velocity of the hand or eye exceeded 10% of peak velocity. Movements that did not reach 20 deg/sec hand velocity or 50 deg/sec eye velocity were eliminated from further analysis. The end of the hand or eye movement was defined as the moment at which the velocity of the hand or eye fell below 10% of peak velocity. Maximal latency for a hand or eye movement was set at 1000 ms, minimal latency at 80 ms. Thus, trials with movement onset before target offset were also excluded from the analysis. Only data for the left eye are presented.

During the hand-alone condition, trials in which a saccade occurred were discarded.

Eye and hand amplitudes were calculated for each factor level (see data analysis). Those values deviating more than two standard deviations from the respective cell mean were considered outliers and were omitted from further analyses.

Overall, each subject performed an average of 347 trials, 40% of which were discarded mainly because of the large number of staircase saccades occuring in the dark and because of blink artefacts.

5.3.5 Data analysis

Four dependent variables were analyzed for eye and hand movements: amplitude, amplitude error, latencies, and movement time. The amplitude of eye and hand movements was defined as the distance between the respective start and end position. The amplitude error was calculated as the primary amplitude of eye or hand minus target amplitude. Target amplitude was defined as the movement amplitude required to hit the virtual target that had continued to move in the dark at one of the two final velocities. It was computed as the time difference between the moment the eye or hand landed on the screen and the moment the target disappeared multiplied by the final velocity of the target + 4°. Negative error values indicate an undershoot, positive values an overshoot. A smaller error therefore indicates smaller movement amplitude. Latency was defined as the time interval between target offset and response initiation. Movement time was defined as the time interval between response initiation and the end of the movement.

Amplitude error, latency, and movement time were analyzed by means of a 2x2x2x3 repeated measures analysis of variance with the factors *movement type* (eye, hand), *task condition* (single, dual), *final velocity* (slow, fast), and *final velocity duration* (short, intermediate, long). Post hoc analyses were performed using the Scheffé test.

Generally, movements with a longer latency require larger movement amplitude. An incorrect amplitude, i.e., an amplitude error, can arise either because the velocity of the target or the individual latency is not taken into account. In other words, either the amplitude does not vary with the latency or it does not vary with the final target velocity. For this reason, a further analysis of the amplitude was performed to determine whether movement amplitudes differed across latencies and/or final velocities (as described in the Results).

5.4 Results

5.4.1 Amplitude error

The mean amplitude errors for eye and hand are shown in table 1 for each factor and in figure 4 for each factor level combination.

Table 1 Marginal means of manual and ocular amplitude error and standard deviations (in parentheses) between subjects separately for each factor, i.e., task condition, final velocity, and final velocity duration (each cell represents the mean of subject means, N=6)

	task condition		*final velocity*		*final velocity duration*		
	single	*dual*	*slow*	*fast*	*short*	*inter-mediate*	*long*
amplitude error hand (deg)	-0.95 (1.01)	-1.24 (1.03)	1.27 (1.13)	-3.60 (1.39)	-1.21 (0.92)	-1.07 (0.91)	-1.06 (1.18)
amplitude error eye (deg)	-0.05 (1.75)	-0.06 (3.57)	1.22 (2.55)	-1.80 (2.98)	-0.19 (3.01)	-0.42 (2.38)	-0.24 (3.07)

There was a significant main effect for final velocity ($F_{1,4}$ = 58.04; p<.01). Movements overshot for targets with slow final velocity (2°/sec), whereas they undershot for those with fast final velocity (10°/sec). In absolute values, the amplitude error was smaller for the slow target.

Two interaction effects were observed. First, there was an interaction of movement type and final velocity ($F_{1,4}$ = 9.06; p<.05). The amplitude errors of eye and hand differed only for the fast target (p<.05), not for the slow target.

Second, there was an interaction of final velocity and final velocity duration ($F_{1,8}$= 11.80; p<.01). The absolute amplitude error was smallest for targets with long final velocity duration (i.e., around 150 ms), particularly for the fast target. This interaction was primarily due to the behavior of hand movements, because it was not significant when the same analysis was performed on eye movements alone. With decreasing final velocity duration, there was larger undershoot in the case of the fast target, whereas there was larger overshoot in the case of the slow target. Thus, the change of the initial velocity was not fully taken into account at intermediate and short final velocity duration. Post-hoc exploration showed that the amplitude error for the slow and the fast target differed for all durations (all p's <.0001). Moreover, the amplitude error for the fast target at short duration was significantly larger than for the fast target at long duration (p<.05).

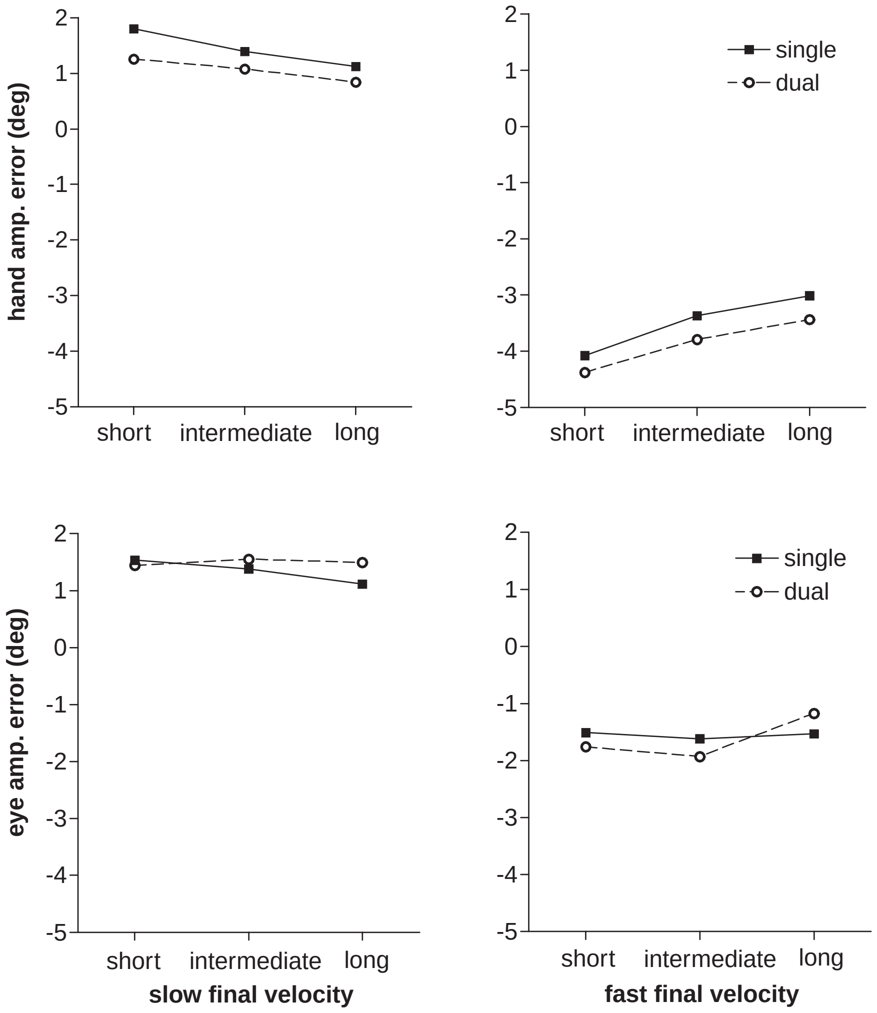


Figure 4 Mean pointing and saccade amplitude errors across different task conditions, final velocities, and final velocity durations

The amplitude error decreased with increased final velocity duration. This might be due to better detection or encoding of the velocity change or increased processing time. Such processing might take place during the latency period or during the movement itself. To check whether processing time increased with final velocity duration, latency and movement times were analyzed separately.

5.4.2 Latency

Mean latencies of eye and hand for each factor level combination are shown in table 2.

Table 2 Mean eye and hand latencies (standard deviations in parentheses) between subjects for all factor and level combinations, i.e. task condition, final velocity, and final velocity duration (each cell represents the mean of subject means, N=6)

		slow			*fast*		
		short	*intermediate*	*long*	*short*	*intermediate*	*long*
latency hand	single task	374 (144)	373 (142)	342 (128)	406 (160)	384 (120)	398 (154)
	dual task	368 (140)	353 (127)	365 (135)	377 (128)	381 (138)	377 (142)
latency eye	single task	289 (81)	276 (94)	286 (83)	297 (84)	307 (102)	291 (91)
	dual task	334 (111)	340 (116)	363 (131)	365 (135)	355 (125)	365 (130)

There was a significant main effect for final velocity ($F_{1,4}$ =9.07; $p<.05$). Latency was higher for targets with fast final velocity (10°/sec) than for those with slow final velocity (2°/sec). There was also an interaction of movement type and final velocity duration ($F_{1,4}$ = 7.57; $p<.05$). At all final velocity durations, the latency of eye movements was lower than that of hand movements ($p<.0001$). Moreover, hand movement latency was higher for targets with short (approx. 50 ms) final velocity duration than for targets with long (approx.150 ms) final velocity duration ($p<.05$).

5.4.3 Movement time

Mean movement times of eye and hand for each factor level combination are shown in table 3.

Table 3 Mean eye and movement times (standard deviations in parentheses) between subjects for each factor, i.e. task condition, final velocity, and final velocity duration (each cell represents the mean of subject means, N=6)

		slow			*fast*		
		short	*intermediate*	*long*	*short*	*intermediate*	*long*
movement time hand	single-task	247 (73)	261 (88)	259 (72)	263 (82)	264 (81)	264 (93)
	dual-task	270 (104)	272 (107)	273 (103)	277 (115)	277 (100)	271 (101)
movement time eye	single-task	66 (31)	64 (25)	60 (20)	62 (31)	69 (36)	66 (27)
	dual-task	55 (21)	58 (22)	55 (23)	60 (38)	59 (33)	64 (37)

There was a significant main effect for movement type ($F_{1,4}=23.34$; $p<.01$). Movement time was larger for hand movements than for eye movements. There was also an interaction of task condition and final velocity ($F_{1,4}=8.96$; $p<.05$). Movement time tended to be higher for the fast than for the slow target ($p<.05$), particularly in the dual-task condition ($p<.01$).

5.4.4 Origin of amplitude error: neglected target velocity or neglected latency

Generally, subjects did not correctly intercept the moving target, because an amplitude error could be observed under all conditions. Such an error might arise because the subjects do not adjust movement amplitude to their latencies (longer latencies require a larger amplitude), or because they do not take into account the velocity of the target. In the former case, no difference in amplitudes for movements of short or long latencies would be expected. In the latter case, no difference in amplitudes towards the slow and the fast target would be expected.

For this analysis, the additional factor *latency group* was introduced. Data were collapsed across single- and dual-task conditions, because task condition had no effect on or did not interact with the amplitude error. Within each of the six combinations of final velocity and final velocity duration, latencies of hand movements were sorted according to their size and split along their median into two equally large categories (short/long latencies). The same was done for latencies of eye movements. The resulting variables received the names "latency group hand" and "latency group eye", each had the levels short and long. The mean hand amplitude was then calculated for each combination of latency group hand, final velocity, and final velocity duration. The same procedure was performed for eye amplitudes. The resulting amplitude values were submitted to a 2x2x2x3 repeated measures ANOVA, the within-subject factors being movement type (eye/hand), latency group (short/long), final velocity (slow/fast), and final velocity duration (short/intermediate/long).

There was no main effect or interaction involving latency group. Thus, the amplitude was not larger for movements with longer latencies. There was also no main effect for final velocity. Thus, the amplitude was not generally larger for movements towards the fast target. There was, however, an interaction of final velocity and final velocity duration ($F_{1,10} = 8.92$; $p<.01$). Post-hoc exploration revealed that the amplitude differed for the fast and slow targets only when the final velocity duration was long ($p<.01$). Thus, at short and intermediate durations, subjects always landed at the same position regardless of the target velocity. At long duration, target velocity was taken into account and movements became larger when the target was fast.

5.4.5 Velocity extrapolation versus use of position information

Eye and hand movement amplitudes differed with final velocity duration. However, the position of velocity change varied with final velocity duration. To determine whether subjects based their response on an estimation of target velocity during the second time interval or on an estimation of the position of velocity change plus an added value, eye and hand movement amplitudes were correlated (Spearman rank order correlation) with final velocity duration and the position of velocity change across all conditions and factor levels for each subject. The resulting correlation coefficients (see Table 4) were Fisher's Z-transformed and submitted to a 2x2 repeated-measures analysis of variance, using the within-factors *movement type* (eye/hand) and *prediction basis* (final velocity duration/position of velocity change). There was a significant main effect for movement type ($F_{1,5} = 11.20$; $p<.05$), showing that the correlations were generally higher for hand amplitude than for eye amplitude. There was also a significant main effect for prediction basis ($F_{1,5} = 12.83$; $p<.05$), showing that the absolute correlation was higher for position of velocity change than for final velocity duration. There was no interaction of movement type and prediction basis. Although the correlation coefficients were overall low, the subjects' eye and hand responses seemed to be based more on the position at which the velocity change took place than on an integration of velocity over a given time interval.

Table 4 Spearman rank order correlations of eye and hand amplitudes with final velocity duration and position of velocity change per subject

	hand amplitude		*eye amplitude*	
subject	*final velocity duration*	*position of velocity change*	*final velocity duration*	*position of velocity change*
AS	-0.07	-0.17*	0.01	-0.06
JD	0.04	-0.35**	0.08	-0.02
MP	0.04	-0.12	0.05	-0.09
OK	-0.01	0.02	0.05	0.05
TE	0.02	-0.13*	0.21**	-0.16*
US	0.16*	-0.34**	-0.01	-0.08
Σ	0.03	-0.18	0.08	-0.06

(* $p<.05$, ** $p<.01$)

5.5 Discussion

The goal of the present study was to examine the role of target motion prediction for saccades and hand pointing movements. On the basis of our findings we conclude that target velocity is taken into account, but that eye and hand movements are guided by adopting a particular response strategy rather than by extrapolating target motion.

5.5.1 Sampling of position or velocity information?

As a rule, eye and hand movements overshot the slow target and undershot the fast target. A similar effect has been reported for eye movements to horizontal ramp targets: low ramp speed results in overshooting, and fast ramp speed in undershooting catch-up saccades (Heywood & Churcher, 1981). Likewise, in a task involving continued manual tracking of an object after its disappearance, subjects underestimated accelerated and overestimated decelerated targets (Gottsdanker, 1952). Subjects do not seem to fully utilize information about target acceleration or deceleration (e.g., Bairstow, 1987; Brenner, Smeets, & de Lussanet, 1998; Port, Lee, Dassonville, & Georgopoulos, 1997).

There are two possible alternative explanations for how subjects guide their interceptive response. First, a certain increment could be added which is based on an estimation of target position at a certain moment. Second, target velocity could be extrapolated.

If the subjects had used an estimation of the target's position at the last possible moment, i.e., just before it disappeared, they would have always aimed at the same position for targets with the same final velocity. This is because the subjects were not aware that the target always disappeared at the same position with always the same fast or slow velocity at that point. The amplitude (or the relative amplitude error) should be independent of the final velocity duration. This was clearly not the case. Undershoot of the fast target and overshoot of the slow target decreased with increasing final velocity duration. Thus, subjects did not seem to sample target position right before the target disappeared.

Target position might also be sampled at the time the target changed its velocity. This is indeed suggested by the finding that hand amplitude correlated to a larger extent with the position of velocity change than with the final velocity duration. These results argue against a process of velocity extrapolation that guides hand movements. Instead, subjects seemed to take the position of velocity change into account and added an increment to this position. As the hand amplitude differed towards the fast and the slow targets, at least at long final velocity duration, this increment was smaller in the case of a slow target and larger in the case of a fast target. Therefore, target velocity was not ignored, but was probably used only in terms of a rough "faster" or "slower" judgment, not as representation of an actual velocity. Similarly, although subjects hit faster moving targets further ahead of the point of disappearance in a study of Brouwer, Brenner, and Smeets (2002), the authors argued that the subjects took the target's velocity only indirectly into account and actually responded to the changing target position.

5.5.2 Is increased processing time responsible for the decreasing error with long final velocity duration?

The finding that hand amplitude was the same for targets at final velocity durations of approximately 50 and 100 ms shows that presentation times in this range were not sufficient to fully evaluate target velocity. A possible interpretation is that short presentation times do not provide enough information for velocity change. Gottsdanker (1956) suggested that for the perception of velocity changes previous velocities are averaged within some interval of time in a weighted function. If this time interval is too short, subjects may not be able to perceive or encode a change in velocity.

Alternatively, subjects may perceive the velocity change but lack sufficient time to process this information aptly. It has been previously proposed for eye movements that higher processing time allows for better extrapolation of target motion (Gellman & Carl, 1991). Another alternative, based also on the idea of restricted processing time, is that subjects are able to perceive and process information about velocity change, but that there is not enough time to produce the full specification of a complex pattern of movement. This interpretation implies that the processed information could not be used to program and execute a correct response. Van Donkelaar, Lee, and Gellman (1992) found that a time interval of 200 to 400 ms is necessary to determine the velocity of the target and to use it for an appropriate manual interception response of visible targets.

Processing may occur either during the latency period or during movement execution. If increased processing time accounted for a change of reaction with long final velocity duration, latency or movement time would be expected to increase with final velocity duration as well. However, this was not the case. In contrast, hand movement latency even decreased with increasing final velocity duration. Therefore, lack of processing time cannot be the reason for similar amplitude regardless of target velocity. Instead, the results indicate that the absence of an amplitude difference for slow and fast targets at short and intermediate duration is due to restricted time to perceive and/or encode the velocity change.

The increasing latency with decreasing final velocity duration may be explained as follows. It is assumed that subjects correct their baseline response (i.e., towards the target moving at initial velocity) if they detect a velocity change. If, however, the velocity change appears late in the target's trajectory, the corrective response might not be completely programmed at the time of the go-signal, thereby delaying response initiation. Moreover, latencies increased when moving towards the fast rather than towards the slow target. Subjects may prepare themselves to carry out the required movement at a certain point in time. Expectation of this point in time may stem from the mean time difference between target onset and the go-signal. As the target always traveled the same distance in the present experiment, the time varied during which the target traveled at the initial, constant velocity. Fast targets were visible for an overall shorter time than slow targets, thereby reducing the time for response preparation. Hence, for fast targets, subjects might simply not yet be in the necessary "state of readiness to respond to the stimulus" (Henry & Rogers, 1960, p. 450).

Movement time also tended to increase for the fast compared to the slow target, but this was significant only for the fast target in the dual-task condition compared to the slow target in the single-task condition. We can only speculate on the meaning of this finding, which does not contribute to the question of restricted processing time being responsible for the increased error with short and intermediate final velocity duration.

5.5.3 Nature of prediction strategy

The higher correlation of hand amplitude with the position of velocity change suggests that subjects did not extrapolate velocity but rather used a certain response strategy. However, this strategy was not fully successful, since there was still a considerable amplitude error. To determine more precisely the nature of the strategy adopted, we analyzed how the observed amplitude error emerged. On the one hand, subjects may estimate the target's velocity, but fail to consider that a longer latency also requires larger movement amplitude. On the other hand, subjects may take their latency into account when planning the response, but may disregard the target's velocity. The data speak for the first alternative. Subjects did not take their latency into account. Since they did not generate a larger movement when their response was delayed, they ignored that the target had traveled a larger distance during this delay. If this is assumed, the larger amplitude error found for the fast target can also be explained. The latencies were not shorter for the fast target (see also table 2). In contrast, they were higher. Consequently, the larger error cannot be explained as due to reduced time for processing target velocity information. Instead, the fast target traveled further than the slow target during the latency period. If movement amplitude does not increase with latency, the resulting amplitude error will be larger for the fast target. This effect is even increased by the observed higher latency towards fast targets.

The data show that subjects adjusted their movement amplitude towards the target's velocity (i.e., made a larger movement towards the fast and a smaller movement towards the slow target) at long final velocity duration. The finding that movement latency was generally not taken into account but movement amplitude still varied for the fast and slow targets again indicates that subjects did not predict the target's position by extrapolating target motion. Instead, the response seems to result from a strategy of simply aiming further ahead when the final target was fast than when it was slow. Such a strategy would correspond to the one suggested by Heywood and Churcher (1981), except that they assumed that the constant would be added to the position of the target at the last possible moment. In our experiment, the constant seemed to be added to the position of velocity change.

5.5.4 Interaction of eye and hand

The reactions of eye and hand when intercepting an occluded moving target can be considered basically similar. Nevertheless, the amplitude errors of eye and hand differed more for the fast than for the slow target. The hand undershot the fast target to a larger extent than the eye did. This is probably due to the generally higher latency of hand movements, which increases the error for the hand, particularly for the fast target that has traveled a larger distance during this latency period.

Although eye and hand movements showed a tendency to approach each other when executed concurrently, the effect was not significant. This finding may be due to the high standard deviation observed. Basically, the results suggest that the prediction mechanism or response strategy was similar for eye and hand. However, care must be taken when generalizing the results. The strategy observed, which allows only for a coarse prediction of target position, may have resulted from the complexity of the predictive interception task. Further experiments are needed to clarify if subjects make more use of target velocity information under conditions of reduced task complexity, e.g., by providing feedback about the success of interceptive movements or by extending the final velocity duration.

5.6 Acknowledgements

We wish to thank Marc Hassenzahl who made important suggestions and criticism. We also thank Anne-Marie Brouwer for helpful comments on a previous version of the manuscript, and Judy Benson for the stylistic revision.

5.7 References

Bairstow, P. J. (1987). Analysis of hand movements to moving targets. *Human Movement Science, 6,* 205-231.

Bekkering, H., Adam, J. J., Kingma, H., Huson, A., & Whiting, H. T. (1994). Reaction time latencies of eye and hand movements in single- and dual-task conditions. *Experimental Brain Research, 97,* 471-476.

Brenner, E., Smeets, J. B., & de Lussanet, M. H. (1998). Hitting moving targets. Continuous control of the acceleration of the hand on the basis of the target's velocity. *Experimental Brain Research, 122,* 467-474.

Brouwer, A., Brenner, E., & Smeets, J. B. (2002). Hitting moving objects: is target speed used in guiding the hand? *Experimental Brain Research, 143,* 198-211.

DeLucia, P. R. & Liddell, G. W. (1998). Cognitive motion extrapolation and cognitive clocking in prediction motion tasks. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 901-914.

Gellman, R. S. & Carl, J. R. (1991). Motion processing for saccadic eye movements in humans. *Experimental Brain Research, 84,* 660-667.

Gottsdanker, R. M. (1952). The accuracy of prediction motion. *Journal of Experimental Psychology, 43,* 26-36.

Gottsdanker, R.M. (1956). The ability of human operators to detect acceleration of target motion. *Psychological Bulletin, 53,* 477-487.

Henry, F. M. & Rogers, D. E. (1960). Increased response latency for complicated movements and a "memory drum" theory of neuromotor reaction. *Research Quarterly, 31,* 448-458.

Heywood, S. & Churcher, J. (1981). Saccades to step-ramp stimuli. *Vision Research, 21,* 479-490.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9,* 97-113.

Port, N. L., Lee, D., Dassonville, P., & Georgopoulos, A. P. (1997). Manual interception of moving targets. I. Performance and movement initiation. *Experimental Brain Research, 116,* 406-420.

Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. *Journal of Physiology, 159,* 326-338.

Ron, S., Vieville, T., & Droulez, J. (1989). Target velocity based prediction in saccadic vector programming. *Vision Research, 29,* 1103-1114.

Tresilian, J. R. (1995). Perceptual and cognitive processes in time-to-contact estimation: analysis of prediction-motion and relative judgment tasks. *Perception and Psychophysics, 57,* 231-245.

Van Donkelaar, P., Lee, R. G., & Gellman, R. S. (1992). Control strategies in directing the hand to moving targets. *Experimental Brain Research, 91,* 151-161.

6 Haptic target texture influences the kinematics of pointing movements, but not of eye movements

6.1 Abstract

A number of studies suggest that the motor systems of eye and hand are coupled because they use identical representations of the target. We tested this assumption by comparing eye and hand movements towards targets of different haptic texture, a target attribute which is behaviourally relevant only to the hand, not the eye. Pointing to a slippery target (fur) resulted in longer hand movement time than to a rougher target (sandpaper). This effect was due to an increased ratio of time spent in deceleration. In contrast, eye movement time was invariant across different haptic target textures. As information about target texture was used in a different way by eye and hand, their overall representations of the target are not identical.

6.2 Introduction

A number of studies have demonstrated that eye and hand are closely coupled. Often, a change in the parameters of one motor system is associated with a change in the parameters of the other system. For example, changes in saccadic amplitude have been shown to transfer to the hand motor system (Bekkering et al. 1995, van Donkelaar 1998). These findings have been interpreted as evidence for the spatial coupling of eye and hand, or more specifically, for the use of the same target representation.

However, in daily life hand movements need a much more detailed representation of the target than eye movements (Sailer et al. in press a). For an accurate grasping movement, for example, information about various characteristics of the target object, such as its weight or texture, is indispensable. This information, however, is irrelevant for an eye movement towards the same object. In line with this assumption, we recently suggested and found evidence that eye and hand may use two separate but interacting target representations rather than a common one (see chapter 3, Sailer et al. in press b).

The present study expands further on the question of whether eye and hand are based on overall identical target representations or not. If eye and hand use identical target representations, any change in represented target attributes should become manifest both in eye and hand behaviour. Therefore, changes in target attributes relevant only to the hand should not only change the parameters of hand movements, but also of eye movements. To this aim, we asked subjects to look and point to (i.e., touch) targets of different surface texture, a target attribute relevant only for the execution of hand movements, not of eye movements. For accurate hand movements, the different friction of these surfaces has to be considered in order to avoid slipping, whereas this parameter does not play a role for eye movements. If the eye uses the same target representation as the hand, this target characteristic would be expected to influence eye movements as well.

If, in contrast, eye and hand use information about the target in different ways, they cannot be said to rely on the same target representation. If the target representation for hand movements incorporates more target characteristics than that for eye movements, target attributes relevant for hand movements should induce changes in hand movement parameters only, but not in eye movement parameters. In this case, hand movements could be said to rely on a separate or more elaborate representation of the target than eye movements.

Using another condition we addressed the question of what changes the target representation, i.e., its seen or its touched characteristics. Texture seems to be a highly salient object attribute for the haptic system, but less so for the visual system (Klatzky et al. 1987), leading the authors to conclude that the haptic and visual systems have distinct encoding pathways. We tried to distinguish between the effect of haptic contact with the object and its visual appearance on target representation. Under one condition, the texture seen did not coincide with the texture eventually touched; under the other, the texture seen was identical with the texture touched. We hypothesise that only the physical contact of the hand with the target texture changes the target representation for hand movements because of its direct relevance for action.

6.3 Method

6.3.1 Subjects

Twelve subjects (4 women and 8 men aged 26 to 41 years), participated in the experiment. They had normal vision or vision corrected by contact lenses and were right-handed. All subjects were naïve with respect to the purpose of the study.

6.3.2 Stimuli

The targets were two round patches of similar brown colour but of different materials (2.6 cm in diameter). One patch was coarse-grain sandpaper (grit 30), the other was short-haired soft fur. One patch was attached 6 cm to the left, the other them 6 cm to the right from the centre of the screen of a 15" flat-screen monitor (NEC MultiSync LCD 1525S). The monitor provided a frame frequency of 72 Hz at a spatial resolution of 1280*1024 pixels. The flat screen was firmly screwed onto a table at an angle of 50°. An additional pane of perspex reinforced the screen. The targets were affixed to the surface of this reinforcement. A fixation spot for the eye was displayed at the centre of the screen. A small spot of 5 mm diameter glued 1 cm below the centre of the screen served as the starting position for the finger.

After a pseudorandomised interval of 100-500 ms the fixation spot for the eye disappeared, and a 12-mm-long arrow pointing either to the right or left was presented at the same position for 100 ms. The subjects were requested to look and point at the patch located in the direction of the arrow as fast as possible. The task and setup are diagrammatically shown in Figure 1.

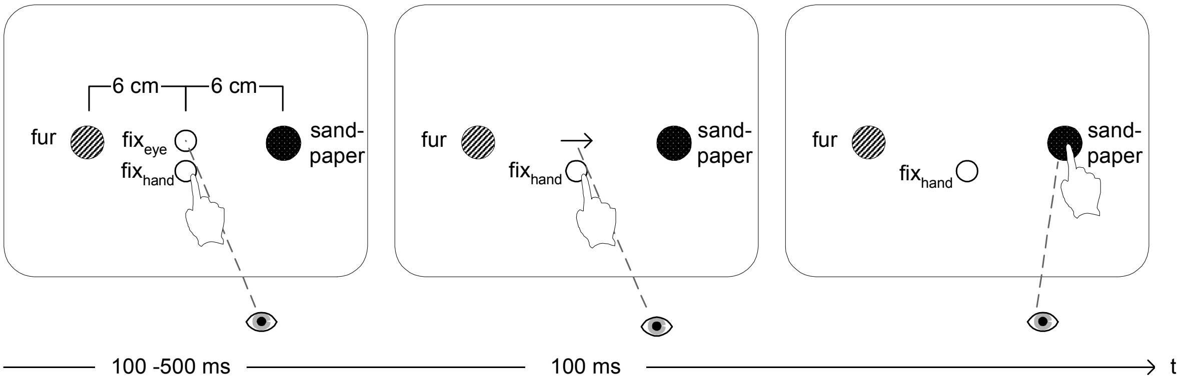


Figure 1 Schematic illustration of setup and task for an example trial

Under one experimental condition, the "haptic and visual identification" condition, the subjects were asked to land directly on the patches with their fingertip. This condition involved a control condition with two neutral brown cardboard patches instead of the fur and sandpaper patches, i.e., there was one cardboard patch to the left and one to the right of the centre of the screen.

Under a different experimental condition, the "only visual identification" condition, another perspex pane was placed over the fur and sandpaper patches so that the subject's finger did not land on the material itself, but on the perspex pane covering it. Thus, the subjects saw the different textures of fur and sandpaper, but always touched the perspex pane.

Each condition consisted of 20 trials to the right and 20 to the left in a pseudorandomised order. Each subject participated in all experimental conditions. The order of conditions, the position of the stimuli, and the subject's gender were counterbalanced. Half of the subjects had the fur on the right side and the sandpaper on the left under both conditions. For the other half of the subjects, it was the opposite.

The video signals were controlled by a PC via a TIGA (Texas Instruments Graphics Adapter) graphics board. The stimuli appeared on a dark grey background. Each subject sat in a darkened room 35 cm from the screen with the right elbow resting on a padded support. One ultrasonic speaker 1 cm in diameter was attached to the tip of the subject's right index finger. The spatial 3-D location of this speaker was measured at a sampling rate of 200 Hz by means of an ultrasonic device (Zebris). At the beginning of each session a calibration was performed based on a set of four markers with known 3-D coordinates. A further calibration procedure involved having the subject point to targets at known eccentricities with full vision of hand and target. Pointing position was defined as the horizontal coordinate of the index finger marker.

Eye movements were monitored with an infrared corneal reflection device (IRIS Skalar), the output of which was digitised at a rate of 1 kHz. The subject's head was stabilised by a chin rest. At the beginning of each session, a calibration was performed by having the subject saccade to targets at known eccentricities.

Data of hand and eye movements were stored and analysed offline. Eye and hand movements were calibrated by means of a third-order polynomial based on fixation data. The beginning of an eye or hand movement was defined as the moment at which the velocity of the eye or hand exceeded 10% of peak velocity, while subsequently exceeding 50 deg/sec for a saccade and 20 deg/sec for a hand movement. The end of the eye or hand movement was defined as the moment at which the velocity of the eye or hand fell below 10% of peak velocity. Maximal latency for a saccade or manual movement was set at 600 ms, minimal latency at 80 ms. Only the parameters of the first saccade or manual movement were analysed.

6.4 Results

The following movement parameters (dependent variables) were investigated: latency, movement time, amplitude, ratio of deceleration time to movement time, peak velocity, end position variability.

Latency was defined as the time between the onset of the arrow and movement initiation. Movement time was defined as the time between the onset and the end of movement. Amplitude was defined as the distance between the movement's start and end position. Deceleration time was defined as the time from peak velocity to the end of the movement. End position variability was defined as the standard deviation of the end position of the eye or hand movement.

First, a separate 2 x 2 x 2 repeated measures analysis of variance was performed for the dependent variables latency and movement time with the factors *movement type* (eye/hand), *texture identification* (haptic and visual/visual only), and *material* (fur/sandpaper). In this as well as in all the ANOVAs performed, the *position of stimuli* (left/right) was introduced as a between subjects factor. Stimulus position had no effect in all the analyses performed.

No significant effects were found for latency, showing that texture identification or material affected the latencies neither of eye nor of hand movements.

Not surprisingly a main effect for movement type was found for movement time (F=378.83; df=1,10; p<.0001), indicating longer movement times for hand movements. There was also an interaction of identification with material (F=13.49; df=1,10; p<.01). Movement time for the fur and the sandpaper differed more when they were identified both haptically and visually than when they were identified only visually. Haptic contact resulted in longer movement time towards the fur, and in shorter movement time towards the sandpaper (see Figure 2). This interaction was, however, primarily due to hand movements, as indicated by a further interaction of movement type with identification and material (F=13.67; df=1,10; p<.01) with subsequent post hoc analysis (Scheffé). Eye movement time in itself did not differ with identification or material.

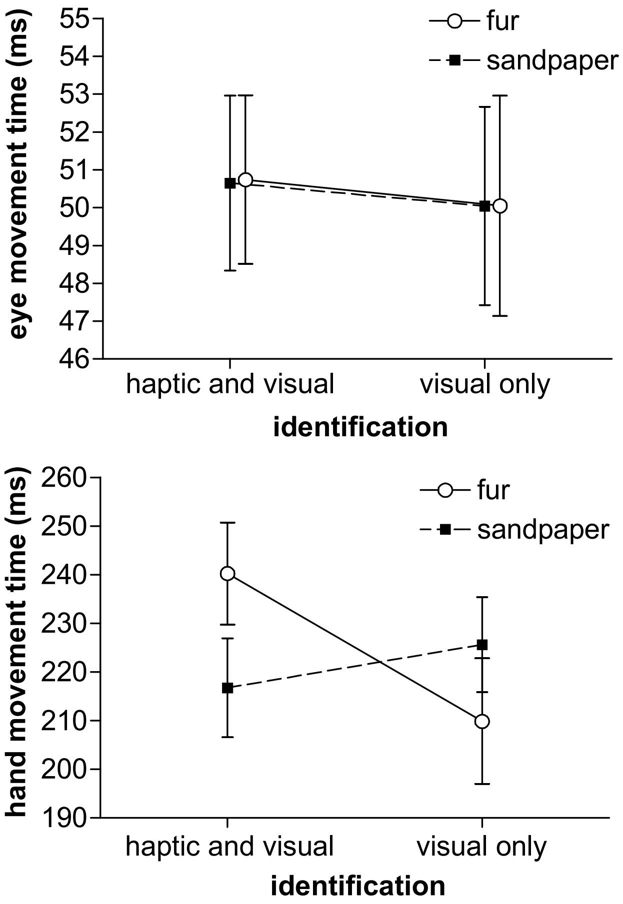


Figure 2 Mean eye and hand movement time and standard error of the mean (N=12), depending on type of identification and material. Top: eye movements; bottom: hand movements (note different scaling!).

To further analyse movement time, a separate analysis was performed comparing the movement time for the two experimental materials fur and sandpaper under the haptic and visual identification condition with only the movement time for the cardboard material under the control condition. To this aim, the dependent variable movement time was submitted to a separate 2 x 3 (movement type x material) repeated measures analysis of variance. A significant main effect for movement type (*F*=362.24; *df*=1,10; *p*<.0001) indicated longer movement times for hand movements. More interestingly, there was also a significant main effect for material (*F*=3.84; *df*=2,20; *p*<.05), showing the longest movement time for the fur, an intermediate value for the control material, and the shortest value for sandpaper. Moreover, an interaction of movement type and material (*F*=5.08; *df*=2,20; *p*<.05) and subsequent Scheffé test of this interaction revealed that the main effect for material was primarily due to hand movements showing the above pattern. Eye movement time was not changed by varying the texture of the target.

This difference in movement time was not due to differences in amplitude, as shown by a one-factorial repeated measures analysis of variance comparing hand amplitude towards the three materials fur, sandpaper (haptic and visual identification condition only) and control (*F*=1.52; *df*=2,22; n.s.). Hand movement amplitude was constant across the three materials touched.

Next, we determined whether the increased movement time for hand movements was due to a proportionally longer deceleration time or lower peak velocity. Movement time and peak velocity were each submitted to separate repeated measures ANOVAs with one single three-leveled factor (material). There was a significant main effect for ratio of deceleration time to movement time (*F*=5.56; *df*=2,20; *p*<.05), showing the highest ratio for the fur, an intermediate ratio for the control material, and the lowest ratio for sandpaper. Thus, pointing to sandpaper resulted in a significantly less relative amount of time spent in deceleration (*m*=0.15, *sd*=0.15, *N*=12) compared to that for fur (*m*=0.27, *sd*=0.19, *N*=12) and the control patch (*m*=0.24, *sd*=0.11, *N*=12) (Scheffé *p*<.05). No effect for peak velocity was found. As subjects did not make a faster or slower movement depending on the texture of the target, the change in movement time was due to different amounts of time spent in deceleration.

As the subjects consistently reported that they experienced the furry patch as slippery, they may have been less precise when hitting the fur than the other targets. Therefore, we investigated whether the variability of landing positions of the fingertip on the furry patch was different from that on the sandpaper and the control patch. To determine this, end position variability was submitted to a repeated measures ANOVA with the single three-leveled factor (material). No effect for end position variability was found. Subjects thus maintained a constant landing position across targets of different textures.

6.5 Discussion

The present experiment showed that target attributes relevant to the hand motor system change the kinematics of only hand movements, not of eye movements. Movement time was longer for hand movements towards the furry patch than towards the sandpaper patch. Eye movement time did not vary with target texture.

Thus, eye and hand movement kinematics are not coupled by an identical target representation. Information about haptic target texture is obviously incorporated into the target representation for hand movements to adjust the movement. Although it cannot be ruled out that it is also incorporated into the target representation for eye movements, it does not become behaviourally manifest. The fact that the available information about the target is used in different ways for eye and hand movements raises doubt about the assumption of identical target representations.

The difference in target representation which influenced hand movements was mainly caused by haptic contact with the target material. When target texture was identified only visually, hand movement time did not change. This replicates the finding of Fikes et al. (1994) for grasping movements. They showed that reaching for a slippery dowel led to slower movement time prior to contact. The authors concluded that "visually cued, but haptically relevant characteristics of objects can have temporal consequences prior to contact as well" (p.329). The results of our study show that visual cueing alone does not affect precontact movement time, as there were no differences when subjects pointed at the perspex pane above the target texture. Under this condition, the visual information did not coincide with the haptically experienced information. Subjects saw the fur and sandpaper, but touched the perspex. In this case, the movement was determined by what was touched and not by what was seen. The behaviourally relevant information used to guide the movement is important, not the visually apparent information. The same can be said for eye movements, because object texture that is irrelevant for accurate eye movements did not affect their kinematics.

The variations in movement time were due to variations in the ratio of deceleration time to overall movement time. This raised the question of the functional role of the dependency of deceleration ratio on target texture. Findings from the pointing literature showed that the deceleration ratio, i.e., the time taken for homing-in of an object, is longer for greater precision requirements (Weir 1994). In the present experiment, subjects had to ensure that the force applied to the target was below a certain threshold to keep the finger from slipping on the target. This threshold was higher for the sandpaper than the fur. Pointing to fur requires higher precision, because the range of force has to be smaller in order to avoid slipping. To ensure that the force applied to the furry target stays within this limited range, lower velocity right before contact may be necessary. This may have lengthened the deceleration phase. In contrast, for the sandpaper target, subjects could simply aim straight ahead and let the material stop them.

Overall, the data suggest that the eye and hand motor systems make selective use of the information that is behaviourally relevant for each. This became manifest as independent variation in eye and hand behaviour dependent on the apparent situation. For eye movements it would in fact be counterproductive to be slowed down by a slippery target texture. For hand movements, in contrast, this slowing down is essential in order to avoid slipping off the target. As the requirements for accurate movements differ for eye and hand, it seems efficient that both represent and use the available target information differently in order to ensure optimal performance.

6.6 References

Bekkering, H., Abrams, R.A., & Pratt, J. (1995), Transfer of saccadic adaptation to the manual motor system. Hum. Mov. Sci, 14, 155-164.

Fikes, T.G., Klatzky, R.L., & Lederman, S.J. (1994), Effects of object texture on precontact movement time in human prehension. J Mot. Behav., 26, 325-332.

Klatzky, R.L., Lederman, S.J., & Reed, C. (1987), There's more to touch than meets the eye: The salience of object attributes for haptics with and without vision. J Exp. Psychol. Gen., 116, 356-367.

Sailer, U., Eggert, T., & Straube, A. (in press), Implications of distractor effects for the organization of eye movements, hand movements, and perception. Prog. Brain Res.

Sailer U., Eggert T., Ditterich J., Straube A. (in press) Global effect of a nearby distracter on targeting eye and hand movements, J Exp. Psychol. Hum. Percept. Perform.

van Donkelaar, P. (1998), Saccade amplitude influences pointing movement kinematics. Neuroreport, 9, 2015-2018.

Weir, P.L. (1994), Object property and task effects on prehension. In K.M. Bennett & U. Castiello (Eds.), Insights into the reach to grasp movement, Advances in psychology, 105, Elsevier, Amsterdam, pp. 129-150.

7 Summary and conclusions

In this thesis, we investigated mechanisms of eye-hand coordination and their dependence on the task context. In the course of this research, we tried to gain new insight into the question of up to which level during movement generation eye and hand use the same information.

Movement generation can be conceptualised as a cascade process involving the stages visual input, target selection, movement programming, movement initiation, movement execution, and movement end (see Figure 1).

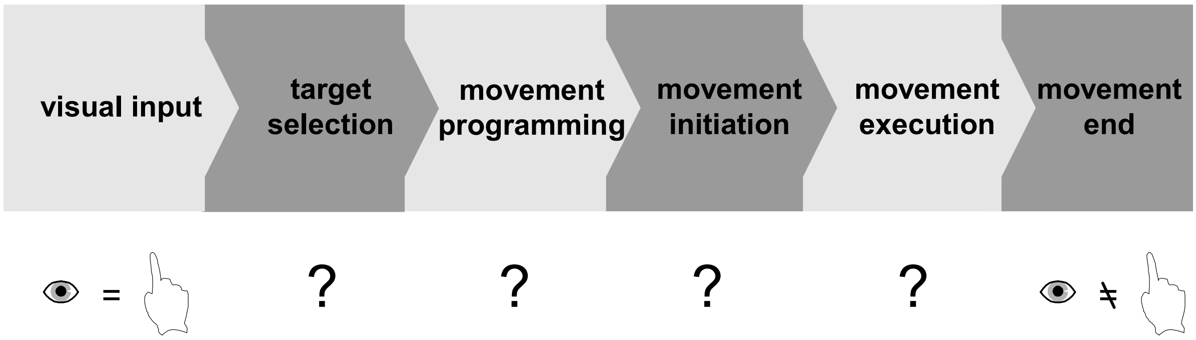


Figure 4 Stages of movement generation and respective degree of shared information by eye and hand

It is logical that at the earliest stage, during visual input, the hand receives all information about the target through the eye. Therefore, the information used by eye and hand at this stage is identical. It is equally obvious that at the end of a movement, when the target is eventually contacted, different muscles and joints are involved. What is not known so far, however, is what happens at the other stages, or at which of these stages the separation of the information used by eye and hand takes place.

We tried to analyse this question by the experiments presented in this thesis. Temporal and specifically spatial coupling at the stage of target selection are investigated in chapter 3, spatial coupling at the stage of movement programming in chapter 4, temporal coupling during movement initiation in chapter 2. The coupling during target position prediction as investigated in chapter 5 could either be assigned to the stage of target selection or movement programming. The level at which different target attributes investigated in chapter 6 affect the movement generation process may be either target selection, movement programming, or movement execution. Although not all of the experiments performed can unequivocally be assigned to one of these stages, we believe that trying to figure out the level at which coupling of eye and hand is measured is a first step towards clarifying the discrepant results in the field of eye-hand coordination.

In the following, the hypotheses and results of each of these chapters will be reviewed before presenting some general conclusions and future research trends.

7.1 Chapter 2: Spatial and temporal aspects of eye-hand coordination across different tasks

In this epxeriment the temporal and spatial coupling of eye and hand were investigated.

7.1.1 Temporal coupling

With regard to temporal coupling, we tried to find out whether eye and hand use a common signal for movement initiation or if they use two separate signals. We investigated the conditions under which the reaction patterns of eye and hand are similar by means of tasks whose influence on parameters of eye movements is already known. The response of hand movements to these tasks has so far been only partially investigated. The following tasks were used: steps (requiring fixation of a stepping target), steps flashing (stepping target with very short presentation time), gap (fixation spot is turned off before presentation of the target), memory (movement towards a remembered target), scanning (targets are always visible), and antigap (movement towards a location oppposite the target).

In particular, two questions were of interest: 1) do the latencies of eye and hand change in a similar way across conditions?, and 2) does coupling of eye and hand change across conditions?

The mean latencies showed an almost parallel change of eye and hand latencies across conditions. Moreover, latencies could be divided into one cluster of lower latencies containing the conditions steps and gap, and one cluster of higher latencies containing the conditions memory, scanning, and antigap. These clusters reflect the distinction into reflexive and intentional saccades as proposed, for instance, by Pierrot-Deseilligny (1991). Reflexive, externally triggered saccades are reactive, non-volitional and triggered by the sudden appearance of an external target. Intentional, internally genereated saccades, are volitional and triggered internally by a target that may be remembered or imagined. Antisaccades and scanning saccads are therefore intentional saccades. It is assumend that reflexive and intentional saccades are generated by different cortical circuits.

Interestingly, hand movements were organised in the same clusters as eye movements. This suggests that the distinction into reflexive and intentional movements also applies to hand movements. The main difference between this clusters does not seem to lie in the availability of visual target information, because in condition scanning the targets were continuously visible. The difference rather seems to be the amount of cognitive information required to execute the task. The scanning task involves cognitive processes because - similar to the antissaccade task - it requires the suppression of a reflexive eye movement and the release of an intentionally triggered movement upon a defined external start signal.

Such a parallel change of ocular and manual latencies with changes in conditions suggests that both types of movement access the same information. If , however, eye and hand used the same signal to trigger movements, their latencies should show a high trial by trial correlation independent of the task. This was not the case. Thus, eye and hand cannot use the same trigger signals. For the intentional tasks (memory, scanning and antigap) the correlation was significantly higher. Thus, temporal coupling of eye and hand was higher with intentional tasks. We suggest that with intentional cases, eye and hand still use separate trigger signals, but that these signals are synchronised by cognitive processes common or superordinated to eye and hand. Thus, eye and hand share more information when their movements are intentional. Alternatively, the same brain structures may be involved for eye and hand when movements are intentional, but not when they are reflexive.

7.1.2 Spatial coupling

In contrast to temporal coupling, the results for spatial coupling were more ambiguous. First, the errors of eye and hand changed differently across positions, and second, their end positions were not correlated. However, end position correlations are rarely high in studies on eye-hand coordination. As end positions are the result of both movement planning and execution, missing correlations do not necessarily imply an absent coupling of eye and hand. Possible interferences during movement execution of each effector could mask such a coupling. We suggest that end position correlations are not an optimal measure of spatial eye-hand coordination, because they can only be reliably interpreted when they are present. Consequently, a different methodology was chosen to investigate spatial coupling in the following experiments, namely the dual-task methodology. Also, pointing in far space may induce an even higher noise ratio. Consequently, our setup was changed in the following experiments from pointing in far space to pointing in near space.

7.2 Chapter 3: Global effect of a nearby distracter on targeting eye and hand movements

The aim of the experiments in this chapter was to find out if eye and hand use the same spatial representation of the target at the stage of target selection. To this aim, the responses of eye or/and hand to the so-called “global-effect”- paradigm were investigated. The global effect describes the tendency of saccades to land in-between a target and a simultaneously presented nearby distracter.The effect occurs only when the saccade is executed before the location and identity of the target have been completely determined. Thus, the global effect occurs at the level of target selection only. It has not been investigated yet whether such a global effect also occurs with hand movements.

We hypothesised that if eye and hand share one target representation on the level of target selection, the global effect should be the same for eye and hand. If eye and hand use separate target representations at this level, differential effects of the distracter on eye and hand movements would be expected.

In experiment 1, the distracter was always less eccentric than the target (near distracter). In experiment 2, the distracter was always more eccentric (far distracter). In experiment 3, the distracter was always less eccentric and its presentation time was varied. In experiment 4, the distracter was either less or more eccentric. Both single- and dual-task conditions were administered: eye and hand movements were measured both when executed alone and concomitantly.

7.2.1 Hand movements

There was also a global effect for hand movements. Hand movements were also drawn towards the distracter. In the case of the near distracter (experiment 1), hand amplitude became smaller, and in the case of the far distracter, hand amplitude became larger (experiment 2). Interestingly, this global effect was independent of whether hand movements were accompanied by eye movements (dual-task) or not (single-task). Thus, subjects did not simply point to where they were looking. This suggests that the global effect is not an effect specific to the eye that just transferred to the hand motor system. Instead, the hand seems to have its own global effect.

7.2.2 Comparison of global effect for eye and hand

In experiment 1 and 2 this global effect was the same in direction and magnitude for eye and hand movements. This suggests that the distracter affects both eye and hand movements at the stage of target selection. The similarity of the global effect for eye and hand movements implies also that eye and hand are coupled at this stage, at least by an exchange of information between two separate target representations, or even by a shared target representation.

However, in experiment 4 with randomised presentation of the near and far distracter, only eye movements showed a global effect in the presence of the near distracter, whereas hand movements did not. Such a differential effect of the distracter on eye and hand movements would not be possible with a common target representation for eye and hand. Thus, eye and hand seem to rely on two separate representations of the target that interact by an exchange of information.

7.2.3 The global effect is independent of presentation time

Experiment 3 showed that the global effect is independent of the presentation time of target and distracter. Although movements became more accurate with increasing presentation time, particularly hand movements, the global effect was not abolished. This suggests that, independent of the availability of visual target information, both eye and hand movements are executed on the basis of an early target representation which is not updated at a later point in time. The reason might be a strategy of trying to maximise the speed of movement initiation. Fine adjustment of the hand to the target might typically be performed during later phases in the movement. However, the opportunities for such an online-correction of hand movements were reduced under the conditions of the present experiment, because simultaneous eye movements and sight of the moving hand were prevented.

7.2.4 Latency interactions

When eye and hand movements were executed concomitantly, the latencies of eye and hand consistently approached each other compared to when they were executed alone. Eye movement latency increased and hand movement latency decreased in the dual-task condition. Such a behaviour speaks for two separate signals for movement initiation that are coordinated by an exchange of information. In this way, the temporal distance in which eye and hand start and land are approximated. This is important, for example, when targets move. In such a case, hand movements need to be based on information taken in by the eye not to far apart in time.

7.3 Chapter 4: Static hand position affects the landing position of eye movements

The goal of this experiment was to determine whether static hand position influences the landing position of eye movements, and whether this influence – if present- occurs during target presentation and encoding or shortly before movement execution. An influence of hand position during movement execution on eye movements has long been known, for example for pursuit movements.

To this aim, we used three different paradigm. In paradigm TOHAND, subjects made a saccade towards the position of the static hand. In paradim FROMHAND, subjects made a saccade away from the position of the static hand. In paradigm TOHANDSTART, subjects made a saccade towards the start potion of the static hand.

We hypothesised that if static hand position influenced eye position, the ocular error should be different for the three paradigms. If this influence occurred during target encoding, the ocular error should be the same when eye movemens are directed towards the permanent position of the hand (TOHAND) and when they are directed towards the start position of the hand (TOHANDSTART). If this influence occurred shortly before movement execution, i.e. when information about target position is being read out from memory, then the ocular error should be the same when eye movements are directed away from the permanent position of the hand (FROMHAND) or away from the end position of the hand (TOHANDSTART).

Indeed, the ocular error was different for the three conditions. Thus, hand position influences eye position. We also found evidence that this influence occurs during presentation and encoding of the target, and not when target information is accessed from memory. This was because the ocular error showed a tendency to be different in conditions FROMHAND and TOHANDSTART, but not between TOHAND and TOHANDSTART. Thus, contrary to hand movements, the interaction of hand position with the eye target seems to occur already during presentation of the target. This seems logical given that there is no need for eye movements to remap the intial retinal target representation depending on the movement of the hand. In contrast, for hand movements, the transformation of retinal target location into a hand-centred target representation requires the retinal location to be remapped depending on the movement of the eye.

To our knowledge, this is the first study showing such an influence of static hand position on the landing position of eye movements.

7.4 Chapter 5: Predictive pointing movements and saccades towards a moving target

As shown in chapter 3 and 4, eye and hand are spatially coupled. Signals related to hand movements influence the target representation for eye movements. However, the way in which such a target representation is built up depends on the target. The processes to determine where a target is are more complex if the target is no longer physically there when the response is executed. This gets even more complicated when the target is moving.

The aim of the experiment in chapter 5 was to determine the influence of higher order strategies on the coupling of eye and hand movements. In other words, are the strategies to determine the predicted position of a moving target similar for eye and hand, and do they influence each other?

The task was to predict the position of a moving target which disappeared at a certain position. The subjects were told to try to „intercept“ the moving target with their eyes and/or hand as if it continued to move. The target started moving with a velocity of 6°/sec and changed during its course either to 2°/sec or to 10°/sec. The target in its final velocity was visible either for 50ms, 100ms, or 150ms before it disappeared. It moved over a constant distance. During the entire trial, the subjects kept their eyes fixated on a fixation spot at the centre of the screen. Both single- and dual-task conditions were applied, i.e. parameters of eye and hand movements were measured both with single and combined execution.

The results showed a similar behaviour of eye and hand. Movements towards the slow target (2°/sec) were too large, movements towards the fast target (10°/sec) were too small. That means that the reactions were adjusted approximately to the initial velocity of the target moving at 6°/sec. Moreover, the amplitude error was dependent on the duration of the final velocity. With short and intermediate final velocity duration, subjects looked and pointed to the same position, independent of the final velocity of the target. With the longest final velocity duration, however, the absolute amplitude error was reduced, both when the target was fast and slow. Thus, with fast final velocity the movement became smaller, and with slow final velocity, the movement became larger. Because long final velocity duration led to different end positions for the fast and slow target, the velocity of the target seems to be used to predict the position of the moving target.

Insufficient consideration of target velocity with short final velocity duration could be due to insufficient time to *perceive* a velocity change. Alternatively, the velocity change may be correctly perceived, but the time to further *process* this information may be insufficient. Should insufficient processing time be the reason for the “ignorance” of final velocity with short duration, then latencies and movement times should also decrease with short compared to long final velocity duration. As this was not the case, insufficient time to perceive a change in velocity can be considered to be the reason for the absent effect of final velocity on the amplitude errors with short duration.

Moreover, it was found that movement amplitude did not vary with latency. Subjects did not make a larger movement when their latency was higher – which would be necessary, because the target has moved further during a longer latency period. Like this, latency is not used for planning a movement to the predicted location of a moving target. The subjects' behaviour can therefore not be called extrapolative. Instead, they seemed to use a strategy of roughly assessing whether the target was fast (or slow), and then pointing or looking somewhat further ahead (or making a smaller movement). In addition, amplitude was related more closely to the position at which the target changed its velocity than to the final velocity duration. That means that although subjects can tell the difference between a fast and a slow target, they do not use this information for an extrapolation of velocity. Instead, they aim at a position that has a certain distance to the position at which the change of velocity occurred. This distance is larger in the case of a fast target than in the case of a slow target.

This strategy seemed to have been used both by eye and hand movements. Thus, prediction seems to pass off in a similar way for both these movement types.

However, care has to be taken with regard to generalising this prediction strategy to other tasks. The observed strategy might be induced by the complexity of the task. Further experiments should be performed to find out whether information about target velocity can be better used in tasks with reduced complexity. One possibility would be to investigate just one aspect of prediction, i.e., either temporal or spatial prediction.

7.5 Chapter 6: Haptic target texture influences the kinematics of pointing movements, but not of eye movements

In this experiment we used a somewhat different approach to determine whether eye and hand use the same or separate target representations. We argued that the same target representation can be assumed if information about the target is used in a similar way by eye and hand.

Therefore, we changed a target characteristic which is relevant to the hand motor system only: haptic texture. Varying this attribute should result in changed parameters of hand movements. If eye and hand use the same overall target representation, or are tightly coupled, it is expected that such a change in texture would also influence the parameters of eye movements. If eye movements turned out to be unaffected by texture, that would rather speak for separate overall target representations.

The task was to look and point as fast as possible to targets of different haptic texture: fur, sandpaper and a control material.

Different target texture influenced the kinematics of hand movements, i.e., movement time was larger when the target was slippery (fur). This effect was not found for eye movements. Therefore, the kinematics of eye and hand movements were not coupled. The longer movement time with targets of lower friction was due to a relatively longer deceleration phase. It has long been known that hand movements are executed in two phases: A ballistic acceleration phase, which is mostly preprogrammed, is followed by a relatively longer deceleration phase in which online corrections are performed (Woodworth 1899, for a review see Elliott et al. 2001).

In the present experiment, the deceleration phase of movements towards slippery targets was longer probably because these movements are being braked earlier to avoid slipping off the target upon contact. The longer deceleration phase leads to an overall increased movement time. This effect was not reflected in the behaviour of eye movements.

The change in hand movement time with haptic texture disappeared for hand movements when the texture was only seen, not touched. Thus, only those attributes relevant to actual movement execution have an effect, not the visually apparent information. Similarly, for eye movements haptic texture is not behaviourally relevant. Therefore, this information does not affect eye movements. These findings suggest that the coupling of eye and hand depends on the behavioural relevance of the stimulus.

It would be interesting to investigate if the present results would be different could the haptic stimulus be made behaviourally relevant for the eye. This could be achieved by a task that requires exact eye movements, for example, by having very small samples of textures and requiring a verbal identification of the material. In these cases, it is necessary for eye movements as well to take texture into account. Under such conditions, behavioural changes in hand movements could indeed spread to the eye movement system.

7.6 General conclusion

This thesis could provide only exemplary insights into the research in the field of eye-hand coordination. However, two points may have become evident: first, the main questions in the field of eye-hand coordination are straightforward and can be roughly separated in questions about temporal and spatial coupling, respectively. Temporal coupling refers to whether eye and hand use one common or two separate command signals to initiate their movements, spatial coupling refers to whether eye and hand use the same spatial representation of the target. Second, the answers to these questions are not as simple as they first seem. That is to say, in the course of our research it turned out that this coordination is influenced by a number of factors: the stage during movement generation at which it is measured (chapter 3), the cognitive involvement (chapter 2) or task complexity (chapter 2 and 4), the type of movement (static or not, chapter 5) the stimuli and behavioural relevance (chapter 6). To resolve the current discrepancies in eye-hand coordination research, the influence of each of these factors has to be probed.

In the domain of temporal coupling, we found evidence that eye and hand movements are based on two separate signals to initiate the movement (chapter 2), but that these signals can be synchronised by higher order processes. Further evidence for separate start signals for eye and hand was found in chapter 3, because the latencies of eye and hand approached each other with combined execution. The kinematic parameters during movement execution were not coupled (chapter 6).

In the current literature, much less is known about spatial than about temporal coupling. Therefore, the larger part of this thesis was devoted to the analysis of spatial coupling. We showed that eye and hand seem to be based on separate target representations already at the stage of target selection (chapter 3). In this chapter, the necessity is emphasised to determine the processing level or the stage during movement generation at which coupling of eye and hand occurs. As the spatial eye and hand responses were found to be very similar under some conditions, these separate target representations seem not to be completely independent from each other, but interact by exchanging information.

Such an exchange of information, or integration of spatial information from one motor system into the target representation of the other, was also demonstrated in chapter 4. Even static hand position, without the execution of any movement at all, influenced the landing position of eye movements. Similar strategies of eye and hand in the spatial domain were also found for predicted targets (chapter 5). The behaviour of eye and hand with regard to predicted targets was not different. One might speculate that as in chapter 2 with higher temporal coupling in the case of intentional tasks, spatial coupling may be higher with increased cognitive involvement.

The finding of separate target representations for eye and hand comes as a surprise, because previous literature rather favoured the idea of one common target representation for eye and hand (e.g. Gielen et al. 1984, Nemire & Bridgeman 1987). The idea of a single representation to support all our visually-guided activity (Marr & Nishihara 1978) is intuitively attractive because of its simplicity. Thus, the question arises of what use the systems could have by using separate target representations.

Under natural conditions, accurate hand movements require much more detailed information about the target than eye movements. To grasp an object, information about its size, weight, texture, etc. has to be taken into account. This information, which is irrelevant for making an eye movement towards the same object (as shown in chapter 6), has to be incorporated in the target representation for the hand. Therefore, it seems reasonable to assume that the target or configuration representation for hand movements is separate (and that it lasts longer and can be read out at a later point in time than that for eye movements).

Moreover, two representations of different targets for eye and hand at the same time allow a greater flexibility of the system. The eye could already start to represent a new target while the hand is still acting on the basis of information about the old target. Such a strategy would be helpful when planning sequential movements in advance. For instance, when picking up an object, the eyes went on to a new area before the fingers touched the object (e.g. Pelz et al., 2001). This indicates that the saccade to the new target is planned during the ongoing hand movement. In other words, while the hand is performing a movement on the basis of the representation of one target, the representation of the new eye target is already built. However, such a behavior may only occur under conditions of predictable target locations as is the case in real-life situations. Neggers and Bekkering (2000) found in a laboratory experiment that no second eye movement could be initiated until the hand movement towards the first target was completed. Nevertheless, this effect is also compatible with the idea of separate target representations. Possibly the system makes less use of a flexible handling of target representations under the restricted conditions of a laboratory experiment.

7.6.1 Future research

Clearly, the experiments presented in this thesis posed new questions that should be addressed in future research. The questions directly concerning the single experiments can be extended to the following topics:

7.6.1.1 How does the spatial coupling of eye and hand depend on the method of measurement?

In chapter 2, there was no difference in end position correlations of eye and hand for reflexive and intentional tasks. Overall, the correlations observed were very weak. This might also be due to the method of pointing in far space. It would be interesting to find out if this relationship is improved when pointing in near space and if differences in end position correlations across conditions are present then.

Similarly, the methods for measuring goal-directed hand movements found in the literature are quite different. Some authors require the subjects to use a handle, others a pen, some use pointing in near space and others in far space. Some of the discrepancies in the results of different authors may be due to the use of such different methods. This is suggested by differential results in the same task with key pressing and handle use (Bekkering et al. 1996) and the involvement of different brain areas in far pointing and near pointing (Weiss et al. 2000). We think it would be beneficial to find out how results in eye-hand coordination depend on the method of measurement. To do this, the same task should be performed with different methods and the results of these methods should be compared. For example, the saccadic tasks we used could be repeated with and compared for pointing in near and far space.

7.6.1.2 Is there evidence for intramodal distracter effects?

Chapter 3 showed that the distracter affected both the target representation of eye and hand, and chapter 4 that static hand position influences eye position. Using a similar „global effect“-paradigm, it would be interesting to find out whether the hand also acts as distracter for the eye and vice versa. In such an experiment, the hand could be placed at a position close to where the target of the eye appears. It would be expected that the eye again lands in-between hand and target position. A finding like that would increase the evidence for an influence of hand position on the target representation of the eye.

7.6.1.3 How is eye-hand coordination modulated by action intention?

Our data showed that stimuli which are behaviourally relevant to the hand motor system only do not change the parameters of the ocular motor system (chapter 6). Such behavioural relevance is induced by the task and the resulting action intention. Depending on the task, the same stimuli can be either behavioural relevant or not. It would be interesting to find out whether an effect reverse to the one reported in chapter 6 can be obtained for stimuli that are behaviourally relevant to the eye only. Such a task could involve subjects to read and point to letters. For reading, the letters need to be accurately identified and therefore, accurate eye movements are necessary. For hand movements, letter identity is irrelevant in this task and should therefore not influence hand movement parameters.

Closely related to this question is the following one:

7.6.1.4 Is eye-hand coordination different during grasping than during pointing?

Experiments investigating this question would address the task and intention dependence of eye-hand coordination and at the same time provide a more natural task background. In contrast to pointing movements, grasping movements require much more information about the target. Size, expected weight, and surface characteristics have to be considered and are taken in via the eye. Accordingly, more accurate eye movements are required for grasping than for pointing. This could lead to higher correlations between the landing positions of grasping and eye movements (than is observed between pointing and eye movements). Thus, the coupling to the eye in grasping movements could be higher than in pointing movements.

7.6.1.5 How can what we know about eye-hand coordination in the laboratory be generalised to the natural environment?

In order to be able to generalise from laboratory experiments, the behaviour in the laboratory always needs to be linked to that in real-life situations. A trend to include more natural environments in eye-hand coordination studies (e.g., illuminated rooms, 3D objects) is also evident from the current research literature.

In chapter 3, we found a distracter effect for both eye and hand movements. Hand movements landed in-between the target and the nearby distracter. However, in everyday life all our hand movements are executed in the presence of distracters and we always land on the target. To disentangle these differences, we suggest that the conditions in the laboratory should be gradually made more similar to those in the natural context. On the one hand, the apparently absent distracter effect in the natural context is certainly due to permanent information about the target and the hand position relative to it. On the other hand, the predictability of target location could also play a role. It has been shown that during initial exposure, subjects scan a scene and make a series of fixations on the objects before the first reaching movement is initiated (Hayhoe et al. in press). Thus, subjects have seen target and distracter at least once before they reach towards it. It would be expected that such an increased predictability of target and distracter might lead to the disappearance of the global effect of the hand. Under such conditions, less informations may be exchanged by eye and hand. A laboratory experiment which includes these characteristics of the natural environment as separate conditions could provide important insights into what circumstances cause the global effect.

Another finding coming from our results with interesting implications for the natural context was that the temporal coupling of eye and hand was found to be higher in tasks with increased cognitive involvement (intentional tasks, chapter 2). One might assume that in natural tasks, the cognitive involvement is even higher, because a number of characteristics of both the target and of surrounding objects have to be analysed and taken into account. Thus, if cognitive involvement is a crucial factor determining the temporal coupling of eye and hand, coupling should be even higher in natural tasks. Findings from natural tasks indeed suggest that the hand seems to be regulated by availability of the eye (Pelz et al. 2001). In this study, the hand consistently waited for the eye. The authors conclude that this strategy "removes the need for a separate decision to initiate the hand movement independently of the eye", which would indeed suggest a high correlation between the respective latencies. Unfortunately, latency correlations were not calculated.

This illustrates that currently there is still a large difference between the methods and analyses applied in classic laboratory studies and those applied in more natural contexts. The aim of future research should be to converge these two approaches, finding a compromise between the more descriptive studies in natural contexts and the controlled studies under restricted laboratory conditions. Such combined studies could do justice to both the complexity of eye-hand coordination and the requirements of sound research. Although this very complexity makes things difficult to investigate, we should not forget that it also enables the enormous flexibility of the system that allows us to effectively interact with our environment.

7.7 References

Bekkering H, Pratt J, Abrams RA (1996) The gap effect for eye and hand movements. Perception and Psychophysics 58: 628-635

Elliott D, Helsen WF, Chua R (2001) Woodworth's (1899) two-component model of goal-directed aiming. Psychological Bulletin 127: 342-357

Gielen C, van den Heuvel PJ, van Gisbergen JA. (1984) Coordination of fast eye and arm movements in a tracking task. Experimental Brain Research 56: 154-161

Hayhoe M., Aivar P., Shrivastavah A., Mruczek R. (in press) Visual short-term memory and motor planning, Progress in Brain Research

Marr D, Nishihara HK (1978) Representation and recognition of the spatial organization of three-dimensional shapes. Proceedings of the Royal Society of London B 200: 269-94

Neggers SF, Bekkering H (2000) Ocular gaze is anchored to the target of an ongoing pointing movement. Journal of Neurophysiology 83: 639-651

Nemire K, Bridgeman B (1987) Oculomotor and skeletal motor systems share one map of visual space. Vision Research Vol 27: 393-400

Pelz J, Hayhoe M, Loeber R (2001) The coordination of eye, head, and hand movements in a natural task. Experimental Brain Research 139: 266-277

Pierrot-Deseilligny C, Rivaud S, Gaymard B, and Agid Y (1991) Cortical control of memory-guided saccades in man. Experimental Brain Research 83: 607-617

Weiss PH, Marshall JC, Wunderlich G, Tellmann L, Halligan PW, Freund HJ, Zilles K, Fink GR (2000) Neural consequences of acting in near versus far space: a physiological basis for clinical dissociations. Brain 123 (Pt 12): 2531-2541

Woodworth RS (1899) The accuracy of voluntary movement. Psychological Review 3 (3, Suppl. 13): 1-119.

8 Acknowledgements

I wish to thank in particular

- my supervisor Andreas Straube for his thematic and psychological support,
- Thomas Eggert for lots of explanations, help and programming the experiments,
- Jochen Ditterich for important hardware adjustments and valuable comments on the interpretation of the data,
- Marc Hassenzahl for his encouragement, extensive comments and discussions on each of the experiments and for making me look at the data with a non-expert view,
- my parents for the financial support during all the years of my studies,
- and everybody else who commented and encouraged this research.

9 Appendix A: Deutsche Zusammenfassung

In dieser Arbeit wurden die Mechanismen der Auge-Hand-Koordination und ihre Abhängigkeit vom Aufgabenkontext untersucht. Es wurden neue Kenntnisse darüber gewonnen, bis zu welcher Stufe in der Bewegungsgenerierung Auge und Hand dieselbe Information verwenden. Die Bewegungsgenerierung kann als kaskadenartiger Prozeß verstanden werden, der folgende Stufen umfasst (siehe Abbildung 1):

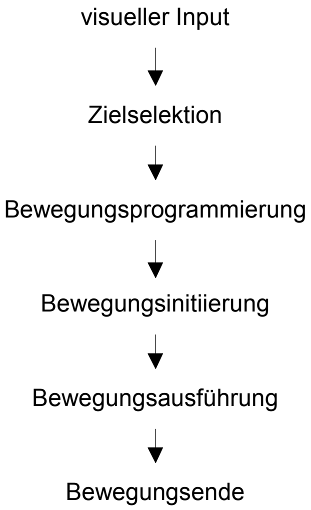


Abbildung 1 Stufen der Bewegungsgenerierung

Auf der ersten Stufe, während des visuellen Inputs, stammt sämtliche Information, die die Hand erhält, aus dem Auge. Daher ist die Information, die auf dieser Stufe von Auge und Hand verwendet wird, identisch. Genauso offensichtlich ist, daß am Ende einer Bewegung, wenn das Ziel tatsächlich berührt wird, bei Hand und Auge unterschiedliche Muskeln und Gelenke beteiligt sind. Um diese Muskeln anzusprechen, sind jeweils unterschiedliche Kommandos und damit unterschiedliche Information erforderlich. Unklar ist jedoch, auf welcher Stufe diese Trennung stattfindet bzw. umgekehrt, bis zu welcher Stufe der Bewegungsgenerierung Hand und Auge gemeinsame Information verwenden.

Die vorliegende Arbeit ist ein Versuch, zur Klärung dieser Frage beizutragen. Zeitliche und besonders räumliche Kopplung auf der Stufe der Zielselektion wurden im Kapitel 3 untersucht, räumliche Kopplung auf der Stufe der Bewegungsprogrammierung in Kapitel 4, zeitliche Kopplung während der Bewegungsinitiierung in Kapitel 2. Die Kopplung während der Vorhersage eines Ziels (Kapitel 5) kann entweder der Stufe der Zielselektion oder der der Bewegungsprogrammierung zugeordnet werden. Unterschiedliche Zieleigenschaften wie in Kapitel 6 untersucht, könnten den Prozeß der Bewegungsgenerierung auf der Stufe der Zielselektion, Bewegungsprogrammierung, oder Bewegungsausführung beeinflussen. Leider können somit nicht alle der durchgeführten Experimente eindeutig einer der Stufen in Abbildung 1 zugeordnet werden. Dennoch ist unserer Meinung nach allein der Versuch, die Stufe, auf der die Kopplung gemessen wird, genauer zu definieren, ein erster Schritt, diskrepante Ergebnisse in der Auge-Hand-Koordination aufzulösen.

Im Folgenden werden die Hypothesen und Ergebnisse jedes Kapitels zusammengefaßt, bevor einige generelle Schlüsse gezogen und zukünftige Forschungstrends diskutiert werden.

9.1 Kapitel 2: Räumliche und zeitliche Kopplung von Hand und Auge in verschiedenen Aufgaben

Wenn von der Kopplung oder Koordination von Augen- und Handbewegungen die Rede ist, kann zwischen zeitlicher und räumlicher Kopplung unterschieden werden. Der Begriff Kopplung (Koordination) bezieht sich auf die Frage, ob Hand und Auge gleiche oder unterschiedliche Information verwenden. Zeitliche Kopplung bezieht sich auf gemeinsame oder getrennte Information zur Bewegungsinitiierung, d.h. Triggersignale, räumliche Kopplung auf Information über den Zielort, d.h. Zielrepräsentationen.

9.1.1 Zeitliche Kopplung

Bei einem gemeinsamen Startsignal von Hand und Auge müssten sich beide in unterschiedlichen Bedingungen auf die gleiche Weise verändern. Im folgenden Experiment wurde der Frage nachgegangen, ob es Hinweise für ein derartiges gemeinsames Signal für die Bewegungsinitiierung gibt. Dazu sollten die Bedingungen untersucht werden, unter denen die Reaktionsmuster von Augen- und Handbewegungen ähnlich sind. Dafür wurden Aufgaben verwendet, deren Einfluß auf die Parameter von Augenbewegungen bereits bekannt ist. So finden sich, je nachdem, ob die Aufgabe eine extern oder intern ausgelöste Augenbewegung erfordert, deutliche Unterschiede in ihrer Ausführung (z.B. bei Parkinson-Patienten). Bislang gibt es jedoch nur vereinzelt Studien über den Einfluß dieser Aufgaben auf Handbewegungen.

Folgende Aufgaben wurden eingesetzt: Steps (der jeweils neue Zielort eines springenden Ziels soll fixiert werden), Steps flashing (springendes Ziel mit sehr kurzer

Präsentationsdauer), Gap (Fixationspunkt wird ausgeschaltet, bevor das Ziel erscheint), Memory (Bewegung auf erinnerten Zielort), Scanning (Zielpunkte sind immer sichtbar), Antisakkade (Bewegung auf den der Fixation entgegengesetzten Zielort).

Im Speziellen sollten zwei Fragestellungen untersucht werden: 1.) verändern sich die Latenzen der Hand ähnlich in den verschiedenen Bedingungen?, und 2.) gibt es Variationen in der Kopplung von Hand und Auge (gemessen anhand von Latenzkorrelationen) über diese Bedingungen hinweg?

Bei den mittleren Latenzen zeigte sich eine fast parallele Veränderung der Augen- und Handlatenzen über Bedingungen. Außerdem ergab eine Analyse der Latenzen eine Einteilung in zwei Gruppen oder Cluster, nämlich eine Gruppe niedrigerer Latenzen für die Bedingungen Steps und Gap, sowie eine Gruppe höherer Latenzen für die Bedingungen Memory, Scanning und Antisakkaden. Diese Cluster spiegeln die Unterteilung von reflexiven und intentionalen Sakkaden wieder, wie sie z.B. Pierrot-Deseilligny et al. (1991) vornehmen. Reflexive (extern ausgelöste) Sakkaden sind nicht willentlich und werden von einem plötzlichen externen Reiz ausgelöst. Intentionale (intern ausgelöste) Sakkaden sind willentlich und intern ausgelöst; das dazugehörige Ziel ist dabei erinnert oder vorgestellt. Antisakkaden und Scanning-Sakkaden sind nach dieser Definition intentionale Sakkaden. Es wird angenommen, daß reflexive und intentionale Sakkaden von unterschiedlichen kortikalen Schaltkreisen generiert werden.

Interessanterweise waren Handbewegungen in denselben Clustern organisiert wie Augenbewegungen. Das lässt darauf schließen, daß die Unterscheidung in reflexive und intentionale Bewegungen auch Handbewegungen charakterisiert. Was die beiden Cluster unterscheidet, ist nicht die Verfügbarkeit visueller Zielinformation, da unter der Bedingung Scanning die Ziele permanent sichtbar sind. Stattdessen liegt der entscheidende Unterschied dieser Cluster vermutlich in der Menge kognitiver Information, die für die Ausführung der Bewegung erforderlich ist. Die Scanning-Aufgabe erfordert kognitive Prozesse, weil bei ihr, ähnlich wie bei der Antisakkadenaufgabe, eine reflexive Sakkade unterdrückt und eine intentionale Bewegung auf ein bestimmtes Startsignal hin ausgelöst werden muß.

Daß sich die Latenzen für Hand und Auge in den verschiedenen Bedingungen parallel verändern, weist darauf hin, daß beide Bewegungstypen auf dieselbe Information zugreifen. Wenn Hand und Auge auch ein gemeinsames Kommando zur Bewegungsinitiierung zugrunde liegt, müssten ihre Latenzen unabhängig von der Aufgabe in jedem Durchgang (Trial) hoch miteinander korrelieren. Dies war jedoch nicht der Fall. Folglich kann man nicht davon ausgehen, daß Auge und Hand dasselbe Startsignal verwenden. Bei den intentionalen Aufgaben, d.h. Memory, Scanning und Antisakkaden, waren die mittleren Korrelationen der Einzeltrials signifikant höher. Die zeitliche Kopplung war bei den intentionalen Aufgaben also höher als bei den reflexiven. Vermutlich gibt es auch bei intentionalen Aufgaben getrennte Startsignale für Auge und Hand. Diese werden jedoch durch kognitive Prozesse synchronisiert, die Auge und Hand übergeordnet sind. Somit teilen Auge und Hand im Falle intentionaler Bewegungen mehr Information. Eine Alternativerklärung wäre, daß bei intentionalen Augen- und Handbewegungen die gleichen Gehirnstrukturen beteiligt sind, nicht jedoch bei reflexiven Bewegungen. Beide Interpretationen sind mit dem Schluß vereinbar, den Frens und Erkelens (1991) aus ihren Daten ziehen. Sie erklären, daß Sakkaden über zwei unterschiedliche Mechanismen generiert werden. Der eine beruht auf visueller Information und wird ausschließlich für die Produktion von Augenbewegungen benutzt, der andere beruht auf visueller und kognitiver Information und wird sowohl für die Generierung von Augen- als auch von Handbewegungen verwendet.

9.1.2 Räumliche Kopplung

Bei der räumlichen Kopplung waren die Ergebnisse weit weniger eindeutig. Einerseits veränderten sich die Fehler von Hand und Auge mit den verschiedenen Bedingungen unterschiedlich, zum anderen waren auch ihre Endpositionen nicht korreliert. Allerdings wird eine solche Korrelation von Endpositionen in Studien zur Auge-Hand-Koordination generell nur sehr selten beobachtet. Da die Endposition das Resultat aus Bewegungsplanung und -ausführung darstellt, können fehlende Korrelationen sowohl auf fehlende räumliche Kopplung zurückzuführen sein als auch auf Prozesse, die mit der jeweiligen Bewegungsausführung interferieren. Es erscheint wahrscheinlich, daß eine potentielle räumliche Kopplung durch Störeinflüsse während der Bewegungsausführung maskiert wird, die unabhängig in beiden motorischen Systemen auftreten. Zu diesem „motorischen Rauschen“ könnten auch die verwendeten Versuchsbedingungen beigetragen haben, die das Zeigen im Fernraum verlangten. Zeigen im Fernraum ist üblicherweise variabler als Zeigen im Nahraum. Aus diesen Gründen wurde in den folgenden Experimenten die räumliche Kopplung von Hand und Auge anstatt mit Endpositionskorrelationen mit Hilfe der im nächsten Abschnitt erläuterten Dual-Task-Methode analysiert. Außerdem wurde für die folgenden Experimente vom Zeigen im Fernraum zum Zeigen im Nahraum übergegangen.

9.2 Kapitel 3: Wirkung eines zielnahen Ablenkers auf Hand- und Augenbewegungen

In dieser Experimentreihe sollten räumliche und zeitliche Kopplung zwischen Hand und Auge mit Hilfe der Dual-Task-Methode (Doppeltätigkeitsaufgaben) untersucht werden, d.h. Hand-und Augenbewegungen wurden sowohl bei einzelner als auch bei kombinierter Ausführung gemessen. Dadurch können sowohl externe Einflüsse bestimmt werden, die getrennt auf die beiden motorischen Systeme wirken, als auch Aussagen über die gegenseitige Beeinflussung der beiden Systeme gemacht werden. Dies ist sowohl für zeitliche als auch für räumliche Parameter möglich.

Um den in der Auge-Hand-Koordination weniger erforschten Teil der räumlichen Kopplung näher zu untersuchen, wurde ein Ablenker-Paradigma verwendet. Für Sakkaden ist bekannt, daß sie, wenn in der Nähe des Ziels gleichzeitig ein Ablenker dargeboten wird, in der Regel dazwischen landen. Dieser Effekt der globalen Ziel-Ablenker-Konfiguration auf die Landeposition von Augenbewegungen wird in der Literatur als „Global effect“ oder „centre of gravity“-Effekt bezeichnet. Es ist bekannt, daß der Global effect nur dann auftritt, wenn die Zielselektion noch nicht abgeschlossen ist. Für Handbewegungen ist dieser Effekt bislang nicht untersucht. Dieses Paradigma eignet sich gut für die Untersuchung der Auge-Hand-Koordination, da die Ergebnisse Rückschlüsse darauf zulassen, bis zu welcher Verarbeitungsstufe die Zielinformation für Hand und Auge gemeinsam verarbeitet wird. Wenn Hand und Auge auf der Stufe der Zielselektion eine gemeinsame Repräsentation des Ziels verwenden, d.h. wenn die Zielinformation, die die Bewegung bestimmt, identisch ist, müßten beide denselben Global effect zeigen. Wenn Hand und Auge unterschiedliche Zielrepräsentationen verwenden, sind unterschiedliche Effekte des Ablenkers auf Hand und Auge wahrscheinlich.

In Experiment 1 war der Ablenker immer näher am Mittelpunkt als das Ziel (naher Ablenker). In Experiment 2, war der Ablenker immer weiter vom Mittelpunkt entfernt als das Ziel (ferner Ablenker). In Experiment 3 war der Ablenker immer näher am Mittelpunkt und seine Präsentationsdauer wurde variiert. In Experiment 4 war der Ablenker abwechselnd näher am oder weiter weg vom Mittelpunkt.

9.2.1 Handbewegungen

Die Ergebnisse zeigten einen Global effect für Handbewegungen. Die Landepositionen der Hand wurden in Richtung auf den Ablenker gezogen. Wenn der Ablenker näher am Mittelpunkt war (Experiment 1), wurde die Handbewegung kleiner, wenn der Ablenker weiter vom Mittelpunkt weg war (Experiment 2), wurde die Handbewegung größer. Interessanterweise war dieser Global effect unabhängig davon, ob Handbewegungen allein (single-task) oder gleichzeitig mit Augenbewegungen (dual-task) ausgeführt wurden. Somit zeigten die Versuchsteilnehmer nicht einfach dorthin, wo ihre Augen waren. Das bedeutet, daß der Global effect nicht spezifisch für das Auge ist und sich schlicht vom Auge auf die Hand überträgt, sondern daß das handmotorische System seinen eigenen Global effect hat.

9.2.2 Vergleich des Global effects für Auge und Hand

Der Global effect war in den Experimenten 1 und 2 in Größe und Richtung derselbe für Hand und Augenbewegungen. Dies läßt darauf schließen, daß der Ablenker sowohl Auge und Hand auf der Ebene der Zielselektion beeinflußt. Die Ähnlichkeit des Global effects für Augen- und Handbewegungen weist auch darauf hin, daß Auge und Hand auf dieser Stufe gekoppelt sind. Für diese Kopplung ist zumindest ein Austausch von Information zweier getrennter Zielrepräsentationen erforderlich, wenn nicht gar eine gemeinsame Zielrepräsentation existiert.

Daß es sich um keine gemeinsame Zielrepräsentation handeln kann, wird allerdings aus den Ergebnissen von Experiment 4 deutlich. Hier wurde abwechselnd der Ablenker näher am Mittelpunkt und weiter vom Mittelpunkt weg dargeboten. War der Ablenker näher am Mittelpunkt, zeigten nur Augenbewegungen einen Global effect, Handbewegungen nicht. So ein unterschiedlicher Effekt des Ablenkers auf Augen- und Handbewegungen wäre mit einer gemeinsamen Zielrepräsentation nicht möglich. Folglich scheinen Auge und Hand zwei getrennte Repräsentationen des Ziels zu verwenden, die durch den Austausch von Information interagieren.

9.2.3 Unabhängigkeit des Global effects von der Präsentationsdauer

Experiment 3 ergab, daß der Global effect nicht von der Präsentationsdauer von Ziel und Ablenker abhing. Obwohl die Bewegungen (v.a. der Hand) mit zunehmender Präsentationsdauer genauer wurden, verschwand der Global effect nicht komplett. Somit werden Augen- und Handbewegung offensichtlich auf der Grundlage einer frühen Zielrepräsentationen ausgelöst, nämlich zu einem Zeitpunkt, wo das Ziel noch nicht richtig vom Ablenker unterschieden wurde. Dies ist unabhängig davon, wieviel visuelle Information über das Ziel insgesamt erhältlich ist. Offensichtlich wird diese Zielrepräsentation auch später nicht aktualisiert. Möglicherweise wird so die Schnelligkeit des Bewegungsstarts optimiert. Genauigkeit könnte auch nach dem Start noch nachgeregelt werden, zumindest für die Hand. Die Möglichkeiten für eine derartige Online-Korrektur waren allerdings in der vorliegenden Experimentreihe beschränkt, da weder Augenbewegungen noch die Sicht auf die Hand möglich waren.

9.2.4 Interaktion von Latenzen

Wenn Augen- und Handbewegungen gemeinsam ausgeführt wurden, näherten sich die Latenzen von Auge und Hand konsistent aneinander an. Die Augenlatenz nahm im Vergleich zur einzelnen Ausführung zu, die Handlatenz ab. Dies spricht für getrennte Kommandos zur Initiierung von Bewegungen, da bei einem gemeinsamen Kommando die kombinierte Aufgabe keine gegenteilige Wirkung auf Hand- und Augenbewegungen ausüben könnte. Stattdessen werden Hand- und Augenbewegungen offensichtlich getrennt initiiert, tauschen aber Information aus über ihre Signale zur Bewegungsinitiierung. Auf diese Art und Weise können die Zeitabstände, in denen Auge und Hand auf dem Ziel landen, aneinander angeglichen werden. Dies ist zum Beispiel wichtig, wenn das Ziel sich bewegt, damit die Handbewegung auf visueller Information beruht, die möglichst aktuell ist.

9.3 Kapitel 4: Einfluß statischer Handposition auf die Landeposition von Augenbewegungen

Das Ziel dieses Experiments war, herauszufinden, ob die statische Position der Hand die Landeposition von Augenbewegungen beeinflußt, und ob dieser Einfluß – wenn vorhanden – während der Darbietung und Einspeicherung des Ziels erfolgt, oder kurz vor der Bewegungsausführung, d.h. beim Auslesen der Information aus dem Gedächtnis. Es ist seit langem bekannt, daß dynamische, also ausgeführte, laufende Handbewegungen die Ausführung von Augenbewegungen beeinflussen, z.B. bei Folgebewegungen.

Drei unterschiedliche Versuchsprotokolle wurden eingesetzt, um diese Frage zu untersuchen. Das Protokoll TOHAND erforderte eine Sakkade in Richtung auf die statische Position der Hand. Das Protokoll FROMHAND erforderte eine Sakkade weg von der statischen Position der Hand. Das Protokoll TOHANDSTART erforderte eine Sakkade in Richtung auf die Startposition der statischen Hand.

Drei Hypothesen wurden gestestet. Erstens, wenn die statische Handposition die Augenposition beeinflußt, müßte der Augenfehler für die drei Protokolle unterschiedlich sein. Zweitens, wenn dieser Einfluß während der Enkodierung des Ziels erfolgt, müßte der Augenfehler der gleiche sein, wenn die Augen auf die permanente Position der Hand (TOHAND), und auf die Anfangsposition der Hand (TOHANDSTART) gerichtet sind. Drittens, wenn dieser Einfluß während des Auslesens der Zielinformation erfolgt, müßte der Augenfehler der gleiche sein, wenn die Augen von der permanenten Handposition weg (FROMHAND), und von der Endposition der Hand (TOHANDSTART) weg gerichtet sind.

Der Augenfehler war tatsächlich unterschiedlich für die drei Bedingungen. Folglich beeinflußt die Position der statischen Hand die Landeposition des Auges. Information über die Position der statischen Hand wird somit in das Kommando für die Augenbewegung integriert. Es wurden ebenfalls Hinweise darauf gefunden, daß dieser Einfluß bereits während der Präsentation und Enkodierung des Ziels erfolgt, und nicht erst, wenn die Zielinformation aus dem Gedächtnis abgerufen wird. Der Augenfehler neigte nämlich dazu, in den Bedingungen FROMHAND und TOHANDSTART unterschiedlich zu sein, aber in den Bedingungen TOHAND und TOHANDSTART war er gleich. Folglich wird – im Gegensatz zu Handbewegungen – die Repräsentation des Ziels für das Auge bereits während der Zieldarbietung aufgebaut. Dies ist allerdings nicht verwunderlich, da für das Auge die anfängliche Zielinformation in retinalen Koordinaten nicht mehr weiter umkodiert werden muß, so wie das für die Hand der Fall ist.

Unseres Wissens ist dies die erste Studie, die einen derartigen Einfluß der statischen Handposition auf die Landeposition von Augenbewegungen zeigt.

9.4 Kapitel 5: Prädiktion eines bewegten Ziels

Kapitel 3 und 4 haben gezeigt, daß Auge und Hand räumlich gekoppelt sind. Signale, die mit der Handbewegung zusammenhängen, beeinflussen die Zielrepräsentation für Augenbewegungen. Allerdings hängt die Art und Weise, in der eine derartige Zielrepräsentation aufgebaut wird, von der Art des Ziels ab. Die Prozesse für die Bestimmung des Bewegungsziels können jedoch unterschiedlich komplex sein, da das Bewegungsziel sowohl unmittelbar gegeben als auch intern generiert (z.B. wie in der Antisakkadenaufgabe in Kapitel 2) sein kann. Um den Einfluß höherer Strategien auf die Kopplung von Hand und Auge zu untersuchen, wurde eine Aufgabe mit einem noch komplexeren intern zu generierenden Ziel verwendet. Die Untersuchungsfrage war, ob die Strategien zur Prädiktion der Position eines bewegten Ziels ähnlich für Hand und Auge sind, und ob sie sich gegenseitig beeinflussen.

Dazu sollten die Versuchsteilnehmer die Position eines bewegten Ziels vorhersagen. Ein bewegter Zielpunkt, der an einem bestimmten Punkt wie hinter einer Wand verschwand, sollte „abgefangen“ werden, so als ob er sich noch weiterbewegen würde. Der Zielpunkt startete mit einer Geschwindigkeit von 6°/sec. Diese veränderte sich dann unterwegs, so daß der Zielpunkt eine Endgeschwindigkeit von entweder 2°/sec oder 10°/sec hatte. Der Zielpunkt war in dieser Endgeschwindigkeit für entweder 50ms, 100ms oder 150ms sichtbar, bevor er verschwand. Er bewegte sich immer über dieselbe Strecke hinweg. Die Versuchsteilnehmer fixierten während der Bewegung des Zielpunkts einen statischen Punkt. Es wurde wieder die schon in Kapitel 3 verwendete Dual-Task-Methode eingesetzt, d.h. die Parameter von Hand und Auge wurden jeweils bei einzelner und bei gemeinsamer Ausführung gemessen.

Die Ergebnisse zeigten ein ähnliches Verhalten von Hand und Auge. Bewegungen auf das langsame Ziel (2°/sec) waren zu groß, Bewegungen auf das schnelle Ziel (10°/sec) waren zu klein. Das bedeutet, daß die Reaktionen in etwa der Anfangsgeschwindigkeit des Ziels (6°/sec) angepasst waren. Darüberhinaus war der Fehler von der Präsentationsdauer der Endgeschwindigkeit abhängig. Bei kurzer und mittlerer Endgeschwindigkeitsdauer zeigten und schauten die Versuchsteilnehmer an dieselbe Position, unabhängig von der Endgeschwindigkeit des Ziels. Bei der längsten Präsentationsdauer verringerte sich der absolute mittlere Fehler jedoch, und zwar sowohl bei der schnellen, als auch bei der langsamen Endgeschwindigkeit. Diese Verringerung des Fehlers entspricht bei der schnellen Endgeschwindigkeit einer verkleinerten, und bei der langsamen einer vergrößerten Bewegung. Weil sich bei der längsten Präsentationsdauer die Endposition für schnelle und langsame Ziele unterscheidet, wird offensichtlich neben der Endposition des Ziels auch die Geschwindigkeitsänderung für die Bewegungsgenerierung verwendet.

Daß bei den kürzeren Präsentationsdauern kein Effekt der Endgeschwindigkeit beobachtet wurde, könnte zwei Gründe haben. Einerseits könnte zu wenig Zeit vorliegen, um die Geschwindigkeitsänderung wahrzunehmen. Andererseits könnte die Geschwindigkeitsänderung zwar richtig wahrgenommen werden, aber zu wenig Zeit vorliegen, um die aufgenommene Information weiterzuverarbeiten. Im zweiten Fall würde man erwarten, daß bei kürzerer Endgeschwindigkeitsdauer auch die Latenzen und die Bewegungsdauern abnehmen. Da dies nicht der Fall war, liegt die fehlende Berücksichtigung der Endgeschwindigkeit bei kurzer Präsentationsdauer wohl eher an der fehlenden Zeit, eine Geschwindigkeitsveränderung wahrzunehmen, und nicht an fehlender Verarbeitungszeit.

Es zeigte sich weiterhin, daß die Bewegungsamplitude nicht mit der Latenz variierte. Somit berücksichtigten die Versuchsteilnehmer ihre Latenz nicht, wenn sie ihre Bewegung auf den Zielpunkt ausführen. Stattdessen schienen sie eher die Strategie zu verfolgen, weiter hinaus zu schauen oder zu zeigen, wenn das Ziel schnell war. Außerdem hing die Amplitude enger mit der Position zusammen, an der das Ziel seine Geschwindigkeit veränderte, als mit der Endgeschwindigkeitsdauer. Diese beiden Ergebnisse lassen darauf schließen, daß die Geschwindigkeit des Ziels im vorliegenden Experiment nicht extrapoliert wurde. Stattdessen zielten die Versuchsteilnehmer auf eine Stelle, die einen konstanten Abstand zu der Position hat, an der die plötzliche Geschwindigkeitsänderung erfolgte. Dieser Abstand war für das schnelle Ziel größer als für das langsame. Dies weist darauf hin, daß die Versuchsteilnehmer zwar den Unterschied zwischen dem schnellen und dem langsamen Ziel erkannten, diesen jedoch nicht für eine Extrapolation der Geschwindigkeit nutzten. Sie machten einfach eine größere Bewegung, wenn das Ziel schnell war, als wenn es langsam war.

Bei der Verwendung dieser Strategie zeigten sich keine prinzipiellen Unterschiede zwischen Hand und Auge. Offensichtlich wurde die Position eines bewegten Ziels für Augenbewegungen nicht anders prädiziert als für Handbewegungen. Die gefundenen Ergebnisse erlauben allerdings keine Verallgemeinerung der Prädiktionsstrategie auf andere Aufgaben, da die beobachtete Strategie auf die Komplexität der Aufgabe zurückzuführen sein könnte. Weitere Experimente sind erforderlich, um zu bestimmen, ob in Bedingungen mit geringerer Aufgabenkomplexität Geschwindigkeitsinformationen über das Ziel für die Reaktion besser verwendet werden. Eine Möglichkeit zur Reduktion der Aufgabenkomplexität wäre die Beschränkung auf nur einen Aspekt der Prädiktion eines Ziels, d.h. zeitliche oder räumliche Prädiktion.

9.5 Kapitel 6: Differentielle Effekte der Oberflächenbeschaffenheit des Ziels auf die Kinematik von Augen- und Handbewegungen

Mit dem Experiment in diesem Kapitel wurde der Frage nachgegangen, ob sich eine Veränderung der Eigenschaften des Ziels und damit auch der Zielrepräsentation, die nur für ein Bewegungssystem relevant ist, durch Kopplung auch auf das andere Bewegungssystem auswirkt. Wir postulierten dafür, daß man von der gleichen Zielrepräsentation sprechen kann, wenn Zielinformation in ähnlicher Weise von Auge und Hand verwendet wird. In diesem Zusammenhang umfaßt die Zielrepräsentation nicht nur wie im bisherigen Verständnis räumliche Information, sondern alle Informationen, die das Ziel charakterisieren.

Zu diesem Zweck wurde die Oberflächenbeschaffenheit des Ziels variiert; eine Manipulation, die nur Bedeutung hat für die Ausführung von Handbewegungen, nicht aber für die Ausführung von Augenbewegungen. Variationen der Oberflächenbeschaffenheit sollten die Parameter von Handbewegungen verändern. Wenn Auge und Hand nun dieselbe Zielrepräsentation verwenden, oder eng gekoppelt sind, könnte eine derartige Veränderung sich auch auf Augenbewegungen durchschlagen. Wenn Augenbewegungen von der Oberflächenbeschaffenheit nicht beeinflußt werden, würde das eher für getrennte Zielrepräsentationen sprechen.

Die Aufgabe war, so schnell wie möglich Zeige- und Augenbewegungen auf Ziele aus den Materialien Fell, Schleifpapier, und Karton (Kontrollmaterial) auszuführen.

Es zeigte sich, daß unterschiedliche Zieloberflächen die Kinematik von Handbewegungen beeinflußten: die Gesamtdauer der Bewegung erhöhte sich bei Oberflächen mit geringer Reibung. Dieser Effekt fand sich jedoch nicht in der Kinematik von Augenbewegungen wieder. Somit ist die Kinematik von Hand und Auge nicht gekoppelt

Es ist seit langem bekannt, daß Handbewegungen in zwei Phasen ausgeführt werden: auf eine ballistische Beschleunigungsphase, die weitgehend vorprogrammiert ist, und während der keine Korrekturen stattfinden, folgt eine Verlangsamungsphase, in der der Arm über Feinkorrektur an das Bewegungsziel herangeführt wird (Woodworth 1899, siehe Überblicksartikel von Elliott et al. 2001). Im Gegensatz zur Beschleunigungsphase wird die Verlangsamungsphase durch plötzliche Veränderungen der Zielposition oder der Augenorientierung beeinflußt. In den vorliegenden Experimenten war bei Handbewegungen mit Oberflächen geringerer Reibung die Verlangsamungsphase verlängert, vermutlich, da diese Bewegungen früher abgebremst werden, um mögliches Rutschen zu vermeiden. Die längere Verlangsamungsphase führt zu der erhöhten Gesamtdauer der Bewegung. Dieser Effekt überträgt sich nicht auf Augenbewegungen.

In einer weiteren Versuchsbedingung wurde beobachtet, daß dieser Effekt auch nur dann für Handbewegungen auftritt, wenn das Ziel wirklich berührt wird (d.h. haptische und visuelle Identifizierung), nicht bei reiner visueller Information über die Zieloberfläche (nur visuelle Identifizierung). Das bedeutet, daß die Eigenschaften des Ziels nur dann eine Auswirkung auf die Bewegung haben, wenn sie direkt bewegungsrelevant sind. Bei fehlender Übereinstimmung von visueller und haptischer Information überwiegt in diesem Fall der Einfluß der haptischen Information.

Diese Ergebnisse bestätigen die Ergebnisse für Greifbewegungen in der Literatur, was ein Hinweis darauf ist, daß die Art und Weise der Objektmanipulation, die auf den unmittelbaren Kontakt mit dem Ziel folgt, nicht entscheidend für die Veränderung der Bewegungsparameter ist.

9.6 Fazit

Diese Arbeit konnte nur exemplarische Einsicht in das weite Feld der Auge-Hand-Koordination geben. Zwei Punkte sollten allerdings klar geworden sein: erstens, die Hauptfragestellungen im Gebiet der Auge-Hand-Koordination können in Fragen zur zeitlichen und räumlichen Kopplung unterteilt werden. Zeitliche Kopplung bezieht sich darauf, ob Auge und Hand ein gemeinsames oder zwei getrennte Signale zur Bewegungsiniitierung verwenden. Räumliche Kopplung bezieht sich darauf, ob Auge und Hand dieselbe räumliche Zielrepräsentation verwenden. Zweitens, die Antworten auf diese Fragen sind nicht so einfach, wie sie zuerst erscheinen. Im Laufe der Experimente dieser

Arbeit zeigte sich, daß diese Koordination von einer Reihe von Faktoren abhängig ist: der Stufe der Bewegungsgenerierung, auf der sie gemessen wird (Kapitel 3), der Beteiligung kognitiver Prozesse (Kapitel 2), der Aufgabenkomplexität (Kapitel 2 und 5), dem Bewegungstyp (statisch oder dynamisch, Kapitel 4), den Stimuli und der Verhaltensrelevanz (Kapitel 6). Um die Diskrepanzen in der aktuellen Forschung zur Auge-Hand-Koordination aufzulösen, muss der Einfluß jedes dieser Faktoren genau untersucht werden.

Im Bereich der zeitlichen Kopplung fanden wir Hinweise darauf, daß Augen- und Handbewegungen auf zwei getrennten Signalen zur Bewegungsinitiierung beruhen (Kapitel 2), aber daß diese Signale durch Prozesse höherer Ordnung synchronisiert werden können. Weitere Belege für getrennte Startsignale wurden auch in Kapitel 3 gefunden, weil die Latenzen von Hand und Auge sich bei gemeinsamer Ausführung annäherten. Die kinematischen Parameter während der Bewegungsausführung waren nicht gekoppelt (Kapitel 6).

In der aktuellen Literatur ist weit weniger über räumliche als über zeitliche Kopplung bekannt. Aus diesem Grund war der größere Teil dieser Arbeit der Analyse räumlicher Kopplung gewidmet. Es stellte sich heraus, daß Auge und Hand schon auf der Stufe der Zielselektion auf getrennten räumlichen Zielrepräsentationen beruhen (Kapitel 3). In diesem Kapitel wird auf die Notwendigkeit hingewiesen, die Verarbeitungsstufe oder die Stufe während der Bewegungsgenerierung zu bestimmen, auf der die Kopplung von Auge und Hand gemessen wird. Da die räumlichen Reaktionen von Auge und Hand unter bestimmten Bedingungen sehr ähnlich waren, scheinen diese getrennten Repräsentationen nicht vollständig unabhängig voneinander zu sein, sondern über den Austausch von Information miteinander zu interagieren.

Ein derartiger Austausch von Information, oder besser gesagt, die Integration von räumlicher Information aus einem motorischen System in die Zielrepräsentaion des anderen, wurde auch im Experiment 4 demonstriert. Sogar die statische Position der Hand, ohne daß überhaupt eine Bewegung ausgeführt wird, beeinflußte die Landeposition des Auges. Ähnliche Strategien von Auge und Hand im Bereich der räumlichen Kopplung wurden auch für prädizierte Ziele gefunden (Kapitel 5). Die Vorhersage der Position eines bewegten Ziels erfolgte für Hand und Auge ähnlich. Hier könnte man spekulieren, daß ähnlich zu Kapitel 2, wo die zeitliche Kopplung bei intentionalen Aufgaben höher war, die räumliche Kopplung mit größerer kognitiver Beteiligung zunimmt.

Das Ergebnis, daß Auge und Hand unterschiedliche Zielrepräsentationen verwenden, mag zunächst überraschend sein. Frühere Literatur favorisierte die Idee einer gemeinsamen Zielrepräsentation für Auge und Hand (e.g. Gielen et al. 1984, Nemire & Bridgeman 1987).

Diese Idee erscheint unmittelbar attraktiv wegen ihrer Einfachheit. Daß dem nun nicht so ist, wirft die Frage auf, welchen Vorteil die motorischen Systeme von Auge und Hand davon haben könnten, getrennte Zielrepräsentationen zu verwenden.

In der natürlichen Umgebung müssen die Zielinformationen für genaue Handbewegungen wesentlich detaillierter sein als für Augenbewegungen. Um ein Objekt greifen zu können, muß z.B. Information über die Größe, das Gewicht und die Oberfläche des Objekts berücksichtigt werden. Diese Information, die irrelevant ist für eine Augenbewegung auf dasselbe Objekt (wie in Kapitel 6 gezeigt), muß in die Zielrepräsentation für die Hand integriert werden. Aus diesem Grund erscheint die Annahme naheliegend, daß die Repräsentation des Ziels für Handbewegungen getrennt ist (und daß sie zudem länger bestehen bleibt und später ausgelesen werden kann als für Augenbewegungen).

Darüberhinaus ermöglicht die gleichzeitige Repräsentation von zwei unterschiedlichen Zielen für Auge und Hand eine größere Flexibilität des Systems. Das Auge könnte bereits anfangen, ein neues Ziel zu repräsentieren, wenn die Hand noch auf der Grundlage von Information über das alte Ziel agiert. So wurde in deskriptiven Studien gezeigt, daß beim Greifen eines Objekts die Augen bereits auf ein neues Ziel gerichtet waren, bevor die Finger das Objekt berührten (z.B. Pelz et al., 2001). Dies weist darauf hin, daß die Sakkade auf das neue Ziel bereits während der laufenden Handbewegung geplant wird.

9.6.1 Zukünftige Forschung

Neben neuen Erkenntnissen über die Auge-Hand-Koordination haben die Experimente in dieser Arbeit auch neue Fragen aufgeworfen, die in zukünftigen Studien geklärt werden sollten. Die Fragen, die sich unmittelbar aus den Einzelexperimenten ableiten lassen, können auf folgende Themen erweitert werden:

9.6.1.1 Wie hängt die räumliche Kopplung von Auge und Hand von der Meßmethode ab?

Wie in Kapitel 2 beschrieben, fanden sich keine Unterschiede der Endpositionskorrelationen von Auge und Hand für reflexive und intentionale Aufgaben. Insgesamt waren die beobachteten Korrelationen sehr niedrig. Dies könnte auch an der eingesetzten Methode des Zeigens im Fernraum liegen. Es stellt sich die Frage, ob der Zusammenhang der Endpositionen von Hand und Auge beim Zeigen im Nahraum besser ist, bzw. ob sich unter der Bedingung des “Nahzeigens” Unterschiede in den Korrelationen über Aufgabentypen hinweg finden lassen.

Generell sind die Methoden zur Untersuchung zielgerichteter Handbewegungen sehr unterschiedlich. In manchen Studien müssen die Versuchsteilnehmer einen Handgriff bewegen, in anderen einen Stift führen, manche messen Zeigen im Nahraum, andere im Fernraum. So könnten einige der Diskrepanzen in den Ergebnissen verschiedener Autoren an der Verwendung solch unterschiedlicher Methoden liegen. Bekkering et al. (1996) fanden beispielsweise unterschiedliche Ergebnisse in der gleichen Aufgabe, je nachdem ob die Versuchsteilnehmer ihre Antwort über das Drücken einer Taste oder das Bewegen eines Handgriffs gaben. Es gibt auch Hinweise darauf, daß unterschiedliche Hirnareale am Zeigen im Nah- und Fernraum beteiligt sind (Weiss et al. 2000). Um mehr über die Methodenabhängigkeit von Ergebnissen der Auge-Hand-Koordination herauszufinden, sollten die Ergebnisse verschiedener Methoden innerhalb einer Aufgabe verglichen werden. Beispielsweise könnten die Aufgaben in Kapitel 2 für Zeigen im Nah- und Fernraum wiederholt und die Ergebnisse gegenübergestellt werden

9.6.1.2 Gibt es Hinweise für intramodale Ablenkereffekte?

Kapitel 3 belegte den Einfluß eines Ablenkers auf die Zielrepräsentation von Auge und Hand; Kapitel 4 den Einfluß der statischen Handposition auf die Augenposition. Es wäre interessant, diese beiden Ansätze zu kombinieren. So könnte mit einem ähnlichen “Global effect”-Protokoll untersucht werden, ob die Hand auch ein Ablenker für das Auge sein kann und umgekehrt. In einem solchen Experiment könnte die Hand in der Nähe der Stelle positioniert werden, an der das Ziel für das Auge erscheint. Es wäre zu erwarten, daß das Auge zwischen Hand und Ziel landet. Ein derartiges Ergebnis würde die Belege für den Einfluß der Handposition auf die Zielrepräsentation des Auges erhärten.

9.6.1.3 Wie wird die Auge-Hand-Koordination durch die Handlungsintention moduliert?

Reize, die für die Ausführung von Handbewegungen relevant sind, nicht aber für Augenbewegungen, ließen die Parameter von Augenbewegungen unverändert (Kapitel 6). Verhaltensrelevanz ergibt sich aus der Aufgabe und der daraus resultierenden Handlungsintention. Je nach der Aufgabe können die gleichen Reize verhaltensrelevant sein oder nicht. In diesem Zusammenhang wäre es interessant herauszufinden, ob ein umgekehrter Effekt wie in Kapitel 6 für Reize gefunden werden kann, die nur für das Auge relevant sind. In einer solchen Aufgabe könnten die Versuchsteilnehmer Buchstaben lesen und auf diese zeigen. Zum Lesen müssen die Buchstaben genau identifiziert werden und deswegen sind genaue Augenbewegungen nötig. Die Identität der Buchstaben ist in dieser Aufgabe für

Handbewegungen irrelevant; deswegen sollte sie die Parameter von Handbewegungen nicht beeinflussen.

Eng mit dieser Fragestellung hängt die folgende zusammen:

9.6.1.4 Ist die Auge-Hand-Koordination beim Greifen anders als beim Zeigen?

Diese Frage berührt einerseits die Abhängigkeit der Koordination von der Handlungsintention, andererseits stellt das Greifen einen natürlicheren Aufgabenhintergrund dar als das reine Zeigen.

Im Gegensatz zu Zeigebewegungen erfordern Greifbewegungen wesentlich mehr Information über das Ziel. Größe, erwartetes Gewicht, und Oberflächeneigenschaften des Ziels müssen berücksichtigt und zunächst über das Auge aufgenommen werden. Dementsprechend sind für das Greifen genauere Augenbewegungen nötig als für das Zeigen. Dies könnte zu höheren Korrelationen zwischen den Landepositionen von Greif- und Augenbewegungen führen (im Vergleich zu Zeige- und Augenbewegungen). Entsprechend könnte die Kopplung mit dem Auge bei Greifbewegungen höher sein als bei Zeigebewegungen.

9.6.1.5 Wie können die im Labor gefundenen Ergebnisse zur Auge-Hand-Koordination auf die natürliche Umgebung verallgemeinert werden?

Um allgemeine Schlußfolgerungen aus Laborexperimenten ziehen zu können, muß das Verhalten im Labor mit dem im natürlichen Kontext in Verbindung gebracht werden. So ist in der Literatur der letzten Jahre der Trend zu beobachten, in die Laborumgebung vermehrt Elemente des natürlichen Kontext einzubeziehen (z.B. beleuchtete Räume, 3D-Objekte).

In Kapitel 3 wurde ein Ablenkereffekt für Augen- und Handbewegungen gefunden. Handbewegungen landeten zwischen dem Ziel und dem benachbarten Ablenker. Im natürlichen Leben werden Handbewegungen jedoch immer in der Anwesenheit von Ablenkern ausgeführt, und landen dennoch immer auf dem Ziel. Um diese Unterschiede aufzulösen, schlagen wir einen Ansatz vor, der die Bedingungen im Labor graduell denen im natürlichen Kontext anpasst. Einerseits liegt der offensichtlich abwesende Ablenkereffekt in natürlichen Umgebungen sicher zumindest teilweise an der dauerhaft erhältlichen Information über das Ziel und die Handposition relativ zum Ziel. Andererseits könnte auch die Vorhersagbarkeit des Zielorts eine Rolle spielen. Wenn man Versuchsteilnehmern eine neue Szene darbietet, tasten sie diese Szene zunächst mit den Augen ab und fixieren dabei die Objekte mehrmals, bevor sie die erste Handbewegung starten (Hayhoe et al. im Druck). Die

Versuchsteilnehmer haben also Ziel und Ablenker schon mindestens einmal vorher gesehen, bevor sie eine Handbewegung auf das Ziel ausführen. Es wäre zu erwarten, daß unter solchen Bedingungen, wo der Ort von Ziel und Ablenker gut bekannt sind, der Global effect für die Hand verschwindet, und daß auch weniger Information zwischen Auge und Hand ausgetauscht wird. Hier könnte ein Laborexperiment Aufschluß geben, in dem diese Eigenschaften der natürlichen Umgebung als getrennte Bedingungen eingeführt werden (visuelles Feedback über die Hand, Prädizierbarkeit der Zielposition, etc.).

Ein anderes Ergebnis mit interessanten Auswirkungen für den natürlichen Kontext, das aus unseren Ergebnissen abgeleitet werden kann, war die höhere zeitliche Kopplung von Auge und Hand in Aufgaben mit erhöhter kognitiver Beteiligung (intentionale Aufgaben, Kapitel 2). In natürlichen Aufgaben ist die kognitive Beteiligung vermutlich noch größer, weil eine Reihe von Eigenschaften sowohl des Ziels als auch der umgebenden Objekte analysiert und berücksichtigt werden muß. Wenn also die kognitive Beteiligung ein wesentlicher Faktor für das Ausmaß zeitlicher Kopplung von Auge und Hand ist, sollte sie bei natürlichen Aufgaben noch höher sein als bei den intentionalen Aufgaben im Labor. Aus den bestehenden Ergebnisse natürlicher Aufgaben könnte man tatsächlich diesen Schluß ziehen. Beispielsweise wartete die Hand in der Studie von Pelz et al. (2001) immer auf das Auge und scheint somit von der Erhältlichkeit des Auges gesteuert zu werden. Die Autoren ziehen den Schluß, daß durch diese Strategie die Notwendigkeit entfällt, eine getrennte Entscheidung zum Initiieren einer Handbewegung zu treffen. Dies sollte sich in Form einer hohen Korrelation der Latenzen von Auge und Hand niederschlagen. Leider berichten die Autoren keine Korrelationen. Dieser Punkt illustriert den gegenwärtig noch großen Unterschied zwischen den Methoden und Analysen in klassischen Laborsstudien und denen im natürlicheren Kontext.

Das Ziel zukünftiger Forschung sollte sein, diese beiden Ansätze aneinander anzunähern und einen Kompromiß zwischen den eher deskriptiven Studien im natürlichen Umfeld und den kontrollierten Studien im eingeschränkten Laborumfeld zu finden. Solche Studien würden sowohl der Komplexität der Auge-Hand-Koordination gerecht werden als auch den Erfordernissen fundierter Forschungsmethoden. Zwar macht ebendiese Komplexität die Erforschung des Themas so schwierig, andererseits ermöglicht sie auch die enorme Flexibilität des Systems und damit eine effektive Interaktion mit unserer Umgebung.

10 Appendix B: Lebenslauf

Name: Uta Sailer

geboren: 19.5.70 in München

seit 1999	Wissenschaftliche Mitarbeiterin in der Neurologischen Klinik der Ludwig-Maximilians-Universität, Klinikum Großhadern, München
1998 - 1999	Wissenschaftliche Mitarbeiterin am Lehrstuhl für Neuropsychologie, LMU München, und Mitarbeiterin am MPI für Psychiatrie, AG Neuropsychologie

1994 - 1998	Studium der Psychologie an der LMU München (Schwerpunkt Organisations- und Wirtschaftspsychologie)
1992 - 1994	Studium der Psychologie an der Universität Konstanz

1987 - 1990	Luitpold-Gymnasium Wasserburg/Inn
1980 - 1987	Gymnasium Trostberg
1976 - 1980	Grundschule Obing

Die in dieser Arbeit zusammengefaßten und diskutierten Ergebnisse stammen zum Großteil aus den folgenden Publikationen:

- Sailer, U., Eggert, T., Ditterich, J. & Straube, A. (2000). Spatial and temporal aspects of eye-hand coordination across different tasks. Experimental Brain Research, 134, 163-173.
- Sailer, U., Eggert, T., Ditterich, J. & Straube, A. (im Druck). Global effect of a nearby distracter on targeting eye and hand movements. Journal of Experimental Psychology: Human Perception and Performance.
- Sailer, U., Eggert, T., Ditterich, J. & Straube, A. (im Druck). Predictive pointing movements and saccades towards a moving target. Journal of Motor Behavior.
- Sailer, U., Eggert, T., Ditterich, J., Hassenzahl, M. & Straube, A. (im Druck). Haptic texture affects the kinematics of pointing movements, but not of eye movements. Neuroreport.