Localization during Pursuit Eye Movement

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Introduction

1.1 Intercepting moving objects

Humans are very good at acquiring complex skills. More than probably any other species they learn a large array of new capabilities after they are born. Special institutions (e.g. schools, sporting clubs, handwork courses, etc.) have been put into operation to optimize the learning of such skills. It can be very pleasurable to acquire or optimize your skills, as is evident from the popularity of sporting clubs. In sports, precise coordination of different body parts is generally important. You must be somewhere at exactly the right time, for example to catch a ball when playing baseball. In other cases you must bring an object like a ball or a dart in such a condition that after you lose contact with it (and thus control over it) the object will move to some intended position. The timing and positioning requirements in sports can be very demanding (e.g. Regan 1992), but ordinary actions in daily life also require precise co-ordination. For example, when grasping an object that has a width of 10 centimeters while you are walking at a moderate speed (i.e. 5 km/hour), your hand will move past the object in less than one tenth of a second. In order to be successful you not only have to position your hand at the right place but it also has to be there at the right time, which is often a very short period. Knowing "the right place" is also far from easy, because at the moment that the brain sends the movement commands to the muscles, the object of interest is not there yet. So, obviously, some kind of prediction must be made. Eye movements are very important to gather the required information for such a prediction. For example, Land and Furneaux (1997) argue that the eyes move in ways that optimize the uptake of information that is useful in such diverse activities as playing table tennis, reading music and driving a car. Moreover, knowing where and knowing when are not independent. Planning to contact a moving object later also means that it must be contacted at another position. For example, when walking past a stationary object you could plan to grasp the object when it is to the right and in front of your body, which would require the arm to move obliquely forwards. Alternatively, you could plan to grasp the object when it is purely to the right of your body, which would require the arm to move rightwards. When you are walking past the object you should start your movement earlier in the first than in the second case.

Several hypotheses have been proposed to come up with an answer to the question how human subjects intercept objects that move relative to their bodies. Often these studies concentrate on the timing aspects of the interception. The reason for focusing on timing is probably the complexity of the task. The moment at which an object is contacted has been considered to be an important piece of information, and several studies have investigated how well people can determine this. In the literature the "optical variable τ (tau)" is often mentioned as a possible information source specifying time to contact (see figure 1a). It is called an "optical variable" because it can be easily acquired from the optical information the subject has. It can be calculated by dividing the object's angle of view by the rate at which this angle increases. This calculation gives the time to contact with the eye. However, it is not exactly correct if the object is not moving towards the eye. This problem can be solved using the same approach of dividing certain variables by their rate of change. If you know where you are going to intercept the target you could use the distance between the hand and that position, and the rate of change of this distance, to estimate the time to contact. Because the distance is not easily available to the subject it is attractive to use an optical variable such as the angle subtended at the eye (see figure 1b). Dividing this angle by its rate of change gives an estimate of the time it takes for the angle to close and thus for the object to reach the position, but only if the object does not change angular velocity. This time is often called the "τ of the gap". Bootsma & Oudejans (1993) suggest that both τ and the "τ of the gap" are used to determine the time to contact between a moving object and some goal position (e.g., the hand). However, whether the time to contact is an important variable in intercepting moving objects remains controversial. For example, Michaels, Zeinstra and Oudejans (2001) suggest that only the optical expansion of the retinal image, rather than τ, is used to guide the moment at which subjects stretch their arm in order to punch a falling ball. There are also theories that τ might be used in different ways (i.e. not as information specifying the "time to be there"). For example, the τ of the gap has been suggested to be used in cases such as golf putting (Craig, Delay, Grealy & Lee 2000). In that case the authors suggest that the golf player has an "intrinsic τ-guide" that is compared with the τ of the gap between the club head and the ball. Good putters are supposed to have acquired a good "intrinsic τ-guide", while less skilled players are not good at controlling this variable. It is not very clear what the authors mean with an "intrinsic τ-guide". They probably mean some kind of model that has developed within the player's brain after many training sessions. Another example can be found in Lee, Georgopoulos, Clark, Craig & Port (2001), in which it is suggested that after an interception point between the object and the interceptor has been determined, the subject tries to keep the τ's of the gaps (i.e. that between object and goal area and that between interceptor and goal area) in a constant ratio. This will ensure that they are closed (i.e. the gap sizes are zero) at the

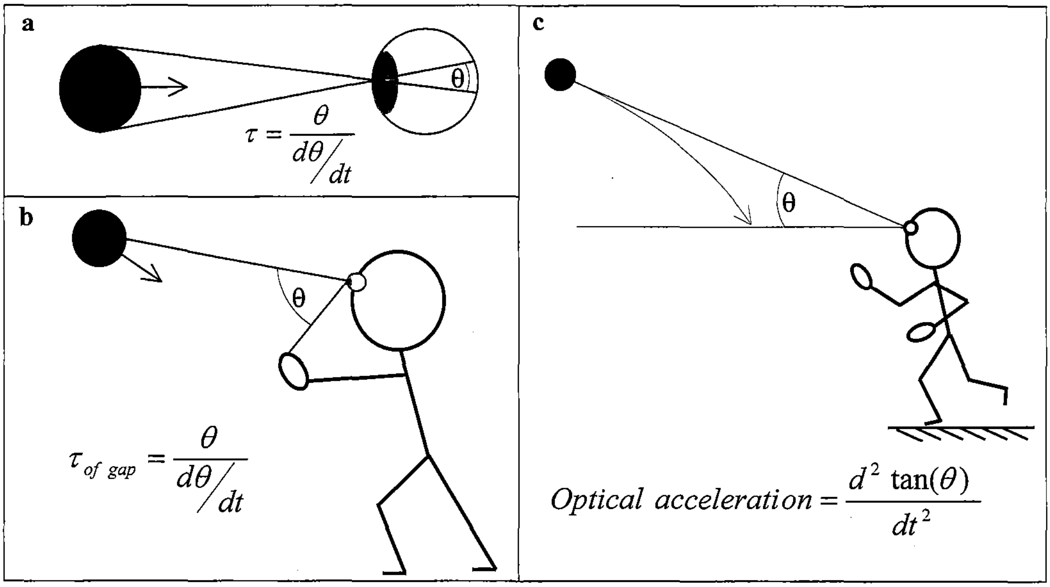

Figure 1: Schematic drawings explaining τ which is the image size divided by the rate of image expansion (a), τ of gap which is the gap between two objects divided by the rate of closure of the gap (b) and optical acceleration which is the second derivative with respect to time of the tangent of the elevation angle of the ball (c).

same time. These studies all assume that the subject knows at which position (s)he is going to contact the object. A complication with such an approach is that the player has to know a position where the object will be before the object gets there. A different solution is that the subject does not know where or when to contact the object but that (s)he follows a strategy that will make him/her end in the right position at the right time. An example of such a strategy is keeping the "optical acceleration" zero (figure 1c) when trying to catch a fly ball in a baseball game (e.g. McLeod & Dienes 1993, 1996). To keep this variable zero the player has to move towards or away from the ball, managing to do so ensures that the ball and the player will be at the same position in the field when the ball reaches eye level.

An important complication that is generally ignored in the strategies mentioned above is that processing visual information takes considerable time. Neuronal delays are certainly not negligible. The time for visual stimuli to reach the visual cortex is between 50 and 100 ms (Schmolesky et al. 1998; Vanni et al. 2004). Moreover, there is some variation in these delays, the delays depend on the contrast in the stimulus (Oram et al. 2002) and they may change with age (Wang et al. 2004). The fact that humans can intercept moving objects shows that the problem of neuronal delays can be overcome. However, these delays have to be taken into account when trying to understand how the task is executed. Mechanisms based on τ or on optical acceleration suggest a variable that could be used, but they do not solve the problem of how this variable is controlled (i.e. how do you keep the optical acceleration zero?). Theories claiming that people acquire complex models, like the "intrinsic τ-guide" in golf putting mentioned above, also do not give much attention to how such models (e.g. "intrinsic τ-guide") deal with neural delays. All these theories do not address the interesting problem of how the internal variable (or model) is synchronized with the external events, which seems difficult if one considers the neuronal delays. In most tasks the delays cannot simply be ignored. Assuming that the time to contact is 100 ms less will often result in a miss. Also, adjusting running speed on the optical acceleration 100 ms earlier will result in being at the correct position 100 ms too late (and most balls would have fallen to the ground by then). Moreover, not only the visual system has delays, but the same holds for the motor system and everything in between, like predictions based on the evaluation of internal models. It takes time for the commands originating within the brain to reach the muscles, for the muscles to contract and for the arm, for example, to move to the goal position. Again these delays are not always the same. The time between the specification of a goal for a hand movement and the hand reaching that goal will depend on the distance to move, whether the hand moves up or down (i.e. against or in the direction of gravity), the use of tools (as is often the case in sports), the intended force with which to contact the object, the intended precision of the movement, etc. This makes it difficult to predict these delays. Considering the close relation between space and time in intercepting moving objects, these delays make the timing or the positioning or both a difficult problem. Whether the positioning or the timing will be considered the major problem depends on how the theory starts. If it starts with the assumption that subjects first choose an interception point, the timing will be the problem. If the assumption is that subjects first choose a time at which to intercept the object the positioning will be a problem. It should be clear from this reasoning that some kind of prediction is essential to succeed in an interception task.

Many studies have shown that human subjects make significant errors when they are asked to localize moving objects. The experiments that are described in this thesis are also concerned with localization errors and we will argue, specifically in chapter five, that the mislocalizations may be the result of mechanisms that have evolved in order to predict a future position of a moving target. In the following section different types of localization errors will be described. After that, in section 1.3, we will come back to the possible relation between localization errors and interception.

1.2 Localization errors

Localization errors have often been attributed to neuronal delays. Fröhlich (1923) found that subjects that were asked to fixate a stationary point perceived a trajectory of a moving target as being shifted in the direction of its movement. Specifically, when the subjects were asked whether the fixation point was exactly in the middle of the trajectory they replied that it was not and when they were asked to indicate the starting or ending point they mislocalized both in the direction of the movement. He wrote that this error was due to the "Empfindungszeit" (perception time). This effect that he found has later been called the Fröhlich effect (e.g. Kirschfeld & Kammer 1999; Kerzel & Müsseler 2002).

Another kind of mislocalization is the mislocalization of the relative positions of a moving and a flashed target. When subjects watch a screen on which a target is moving while suddenly a second target is flashed, the subjects misjudge the relative position of the flashed and the moving target. The relative position is misjudged as if either the moving target was displaced in the direction of its movement or the flash is displaced against the direction of the movement of the moving target (e.g. Nijhawan 1994; Whitney & Murakami 1998; Krekelberg & Lappe 1999; Brenner & Smeets 2000; Eagleman & Sejnowski 2000; Murakami 2001; Baldo, Alexandre, Kihara, Namba & Klein 2002). Because of the paradigm used in these studies, they are often called flash-lag studies.

A third kind of mislocalization is that which is found when subjects are required to indicate the position of a target that is flashed prior to an eye movement. Human subjects often make quick eye movements that bring the eyes at high velocity from one orientation to another. These quick eye movements are called saccades. A target that is flashed just before a saccade is mislocalized in the direction of the saccade. The amplitude of this mislocalization depends on how long before the start of the saccade the target is flashed. In the literature this kind of mislocalization is called pre-saccadic mislocalization. It has often been suggested that this pre-saccadic mislocalization is related to combining eye orientation information with retinal information corresponding to a different time (e.g. Honda 1989; Dassonville, Schlag & Schlag-Rey 1992; Jordan & Hershberger 1994; Morrone, Ross & Burr 1997; Boucher, Groh & Hughes 2001).

A fourth kind of mislocalization is the mislocalization of a target that is flashed while the eyes are moving. That kind of mislocalization is used in the experiments that are the subject of this thesis. When an object in our surroundings moves at a moderate pace or when we move ourselves, and thus all the surroundings move relative to ourselves we can follow the object with our eyes. This type of eye movement is called pursuit eye movement. If the eye movement successfully tracks the object the object's image on the retina will hardly move over the retina. Often during the pursuit, subjects make saccades (which make the eyes move much faster than the pursued object) to catch up with the moving object, but a large part of the pursuit consists of very smooth movements and is therefore called smooth pursuit eye movement. When during a pursuit eye movement a second target is flashed close to the target that the subject is pursuing its position will be mislocalized in the direction of the movement. These localization errors have also been attributed to neuronal delays and to incorrectly combining retinal signals and eye orientation signals (e.g. Hazelhoff & Wiersma 1924; Mita, Hironaka & Koike. 1950; Mateeff, Mitrani & Dimitrov 1981; Mateeff, Hohnsbein 1989; Brenner, Smeets & van den Berg 2001).

More recently some of these mislocalizations have been related to action. Specifically, the errors have been proposed to be useful to overcome the delay between the planning of a manual action towards a moving object and the actual execution of the action. Two kinds of studies contributed to this suggestion. In one kind of study, a flash-lag study, the eyes were not moving (Nijhawan 1994) so that the moving target's image moved over the retina and thus the mislocalization would be based on retinal information. The other kind considers mislocalizations when the eyes are moving in order to track the moving target (Brenner, Smeets & van den Berg 2001; Brouwer, Brenner, Smeets 2002) and thus the mislocalization would be based on information about eye movement.

1.2.1 Mislocalization with stationary eyes

In flash-lag studies the subjects eyes are stationary: the subject is required to fixate on some position. While the subject is doing so a different target is shown that moves past this fixation target. At some time point a second target is flashed close to the moving target. After this sequence of events has been shown to the subject, the subject is required to indicate the relative positions that the flashed and the moving target had at the moment

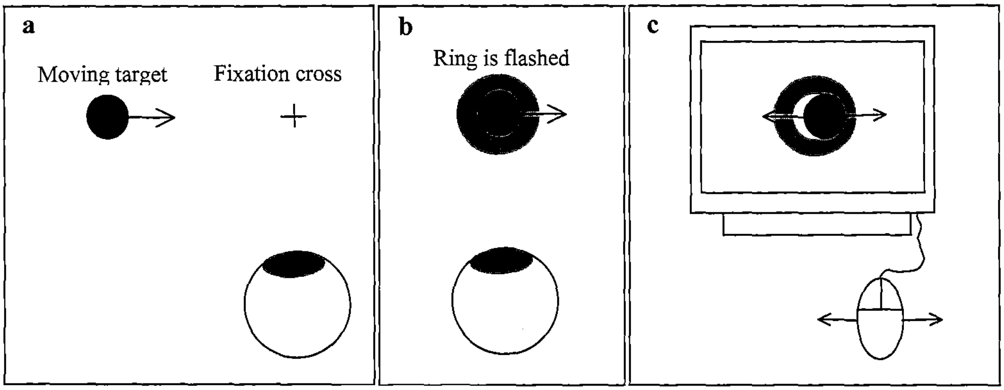

Figure 2: A schematic illustration of the paradigm used in flash-lag studies. In panel (a) the beginning of a trial is shown. The subject is fixating a fixation cross while a target starts to move. When the moving target has reached the fixation cross (b) a ring surrounding the moving target is flashed. After the moving target has reached the end of its trajectory the subject is asked to indicate (for example by using a mouse) where (s)he saw the flashed target relative to the moving target (c). The situation as drawn in panel c illustrates a typical outcome of the experiment.

of the flash. An example of a flash-lag paradigm is shown in figure 2. Because of the way in which the paradigm works it does not answer the question of whether the location of the flash or the position of the moving object is mislocalized. In flash-lag studies the subjects are never asked to indicate the absolute position of either the moving or the flashed target (see the recent reviews by Krekelberg & Lappe 2001 or by Nijhawan 2002). Although some authors seem quite convinced that the moving target is mislocalized and the flashed one is not (e.g. van Beers, Wolpert & Haggard 2001; Schlag & Schlag-Rey 2002), others stress that it is only a relative phenomenon (Krekelberg 2001; Murakami 2001). The flash-lag effect is often related to neuronal delays, the proposed explanation being that it takes longer to process the flash than to process the moving target (i.e. the flash lags). If that interpretation is correct, none of the targets is really mislocalized, the subjects are merely comparing things happening at different moments in time. This is nicely illustrated by an experiment in which subjects were asked to compare the color of a disk that smoothly changed its color with the color of a flashed disk. The subjects always matched the color of the flashed disk with the color that the changing disk had a little later than the flash (Seth, Nijhawan & Shimojo 2000). With attributes like color most people will probably not find it so obvious that the changing disk leads (instead of the flashed disk lagging). Getting an answer to the question whether the flash lags or the moving disk leads would require a different experimental paradigm, namely one that would allow the researcher to measure the perceived absolute position of the flash and the moving disk. For flashed targets the absolute position that is reported depends on the retinal eccentricity of its image (e.g. Bock 1986; van der Heijden, van de Geest, de Leeuw, Krikke & Müsseler 1999). For moving targets this is difficult to measure since the researcher has to specify a moment at which the subject has to judge the position, which will require a cue and so it will be a comparison of two stimuli and thus the same objections as stated above can be raised. One could however ask where a moving target started to move or stopped moving, as Fröhlich (1923) did. In that case it is clear that the moving target is mislocalized.

If the moving target would be mislocalized in the direction of its movement, this mislocalization might be useful to overcome neuronal delays. We do not know whether manual tasks are based on relative or on absolute positional information. If hand movements were based on relative information, the mislocalization of the relative position of a moving target (relative to a stationary background) might be useful to overcome neuronal delays (as Nijhawan suggested 1994). The reasoning would be that misperceiving the object's position in a way that is consistent with the moving object being further than where it physically is, would make a suitable goal for the hand movement because it will take some time for both the hand and the moving target to reach that position. Probably it depends on the conditions whether one uses relative or absolute information (e.g. when the background has no structure, like for instance a blue sky behind a base ball, one cannot use relative information). Since we can intercept luminous objects moving in the dark (Oudejans, Michaels, Davids & Bakker 1999) it is clear that we are able to use absolute information. This might be accompanied by the use of relative information when it is available.

It is not clear what kind of mechanism is responsible for the flash-lag effect. However, neurons that start responding earlier when the image of a moving target moves into their receptive field than when a target is flashed in their receptive field have been found in rabbit and salamander retina's (Berry, Brivanlou, Jordan & Meister 1999). Thus perhaps retinal movement is already extrapolated very early when processing visual information.

1.2.2 Mislocalization with moving eyes

When the eyes are pursuing the moving object the situation is different. The structures within the brain that are responsible for the localization now not only have to deal with the possibly changing retinal input but also with the changing orientation of the eyes. Determining the relative position of the object that is tracked will be difficult because the images of stationary objects now move over the retina. There is no flash-lag effect when the eyes pursue the moving target (Nijhawan 2001). The subjects see the moving (pursued) target and the flashed target at the right *relative* positions. However, if they are asked for the *absolute* position of the flashed target, they do mislocalize it in the direction of the movement. Only the position of targets of which the image moves over the retina seem to be misjudged relative to a flashed target. In agreement with this, during pursuit eye movement the position of a flashed target is mislocalized relative to a stationary target whose image will move over the retina because of the rotation of the eyes (Nijhawan 2001). An example of the paradigm used in the experiments concerning mislocalization during pursuit is given in figure 3. If the position of the target that is pursued would also be mislocalized, this might give the prediction necessary to overcome the neuronal delays. The fact that the relative positions of the flashed and the moving target are not misperceived, contrary to the situation with stationary eyes (i.e. flash-lag), suggests that this is the case. The reasoning would be, similar to what was suggested above for the mislocalization of relative positions, that mislocalising the absolute position of the moving target is the result of a mechanism that predicts a future position of the moving target. The mislocalization of the flashed target appears to depend on many factors. Mitrani and Dimitrov (1982) and van Beers, Wolpert and Haggard (2001) found

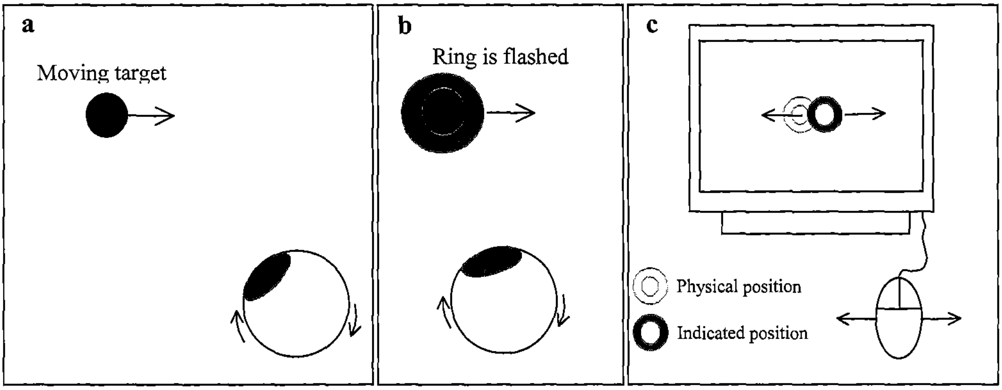

Figure 3: A schematic illustration of the paradigm used in studies investigating localization during smooth pursuit eye movement. In panel a the beginning of a trial is shown. The subject is tracking a moving target. At some random moment during the tracking a target is flashed, in this case a ring surrounding the pursuit target (b). After the pursued target has reached the end of its trajectory the subject is asked to indicate (for example by using a mouse) where (s)he saw the flashed target (c). The situation as drawn in panel c illustrates a typical setting that the subject would make (the physical position is not visible anymore by this time, it had only been visible for about a millisecond).

that flashes in front of the pursuit target are misjudged more than those on or those behind the pursuit target are. The mislocalization can be reduced by the availability of visual references (Mateeff & Hohnsbein, 1989; Brenner, Smeets & van den Berg 2001). Perhaps this is the case because when clearly visible relative information is offered subjects rely (partially) on misjudged relative positional information (i.e. flash-lag), which is mostly not as large as the mislocalization of targets that are flashed during pursuit eye movement. In two studies in which a visible ruler was shown along the path of pursuit, the errors depended systematically on the position along the ruler at which the target was flashed (Mitrani, Dimitrov, Yakimoff & Mateeff 1979; Mateeff, Yakimoff & Dimitrov 1981).

It is not clear what the critical variables resulting in the differences between the responses in all these experiments were, but the mislocalization being in the direction of the eye movement could be the result of the use of efferent eye orientation information. The efference copy of the eye movement command always specifies a position that is a bit further than where the eyes are. Therefore, combining this with the retinal information that corresponds to the current eye orientation will result in mislocalization in the direction of the eye movement. The use of efferent eye orientation information has also been proposed as an explanation for the pre-saccadic mislocalization. In that case the reasoning is that the retinal position of the flash is combined with an efference copy of the eye movement command, which is already shifted in the direction of the saccade in order to drive the eyes in that direction, resulting in a mislocalization in the direction of the upcoming saccade (e.g. Dassonville, Schlag & Schlag-Rey 1992). As will be explained in the next section efferent eye orientation information may be used because it predicts were the target will be in some time. This efferent information is a reliable prediction as is evident from the fact that it is quite successful in guiding the eyes to the future target position.

1.3 Interception and localization errors

It is interesting that there are mislocalizations in the direction of the movement both when the eyes are stationary as well as when they are moving. It seems obvious that different information sources are critical in these two cases. When the eyes are stationary it is the retinal information about moving objects that is constantly changing while during pursuit eye movement the retinal position of the pursued object is not changing, but the eye orientation changes constantly (figure 4). The fact that in both cases moving targets are mislocalised in the direction of the movement may indicate that this is not just some unnecessary perceptual illusion but that it has a function.

Normally when we have to intercept a moving object we try to look at it, and if it moves we follow it with our eyes (e.g. Oudejans, Michaels, Davids & Bakker 1999). We probably do this to keep the image of the object of interest projected at the central part of the retina, which is called the fovea. This region has the highest density of light receptive cells. However ocular tracking may also function as a loop that tries to determine the object's movement by trying to "null" the movement of the target's image. When one has successfully "nulled" the image movement the ocular motor commands are useful information sources concerning the movement of the tracked target. Using these ocular motor commands (i.e. an efference copy of the eye movement commands) may be the way in which the brain tries to predict a future position of a pursued target, which is probably needed to successfully intercept a moving target.

As already suggested in the previous two sections the existence of such a mechanism may also be the reason why people make localization errors when they are asked to localize a moving target at a specific point in time. Perhaps we do not see the target at the position it has at the specified moment but at a position the brain predicts it to be a little later, so that we can aim for the position at which we see the target irrespective of the delays. To visually localize an object one needs information about the retinal position of the object's image and information about the orientation of the eyes. The retinal information is only available after a delay. For the eye orientation the time at which information is available depends on the signal that is used. The important difference between retinal and eye orientation information is that whereas the retinal position may change unpredictably the eye orientation does not, because the subject controls these movements. Consequently, instead of using afferent sensory information, either proprioceptive information from the extra-ocular muscles or the movement of a stationary background on the retina (figure 4) one could use efferent information (the commanded eye orientation). In monkey studies neurons have been found that normally respond to a stimulus at a fixed position relative to the eye, but that just prior to an eye movement respond to a stimulus at a position that is shifted in the direction of the upcoming eye movement (Duhamel, Colby & Goldberg

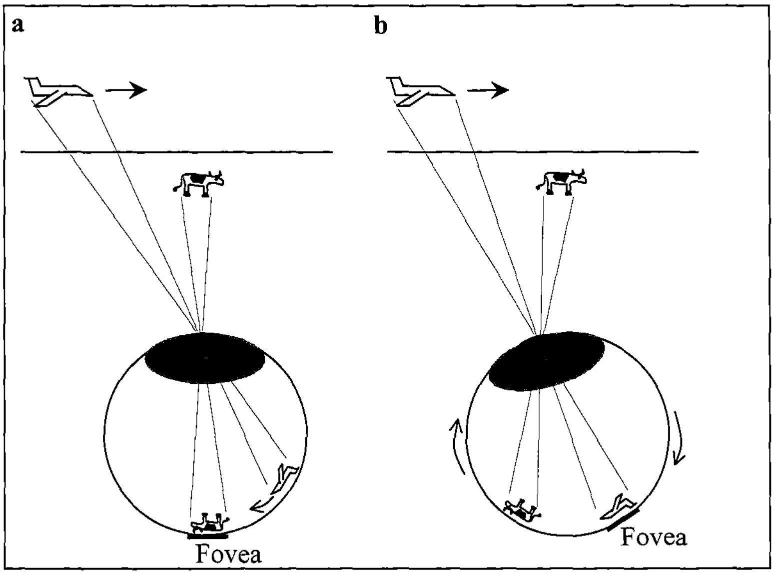

Figure 4: Schematic drawing of what happens on the retina in case the eyes fixate on something stationary (a) and when the eyes pursue something that is moving (b). In panel a the cow is fixated so that its image is projected at the fovea (the highest acuity area of the retina), in that case the image of the moving airplane moves over the retina. In panel b the airplane is fixated so that its image is projected at the fovea, because the airplane moves the eye rotates in order to keep the airplane's image at the fovea, in this case the image of the stationary cow moves over the retina.

1992; Umeno & Goldberg 1997) and also neurons that were tuned to eye movements of certain length and direction that responded before the eye made the movement (Sommer & Wurtz 2002). Sommer and Wurtz argue that these neurons are not relaying signals to the eye muscles. They also inactivated these neurons and observed that when the animals had to make two eye movements in succession the direction of the second eye movement was offset as if the monkey had not totally accounted for the first eye movement. Such findings support the idea that efference copies of the eye movement commands are really used in the primate brain, and Sommer and Wurtz might even have found neurons that relay an efference copy. If the target's image does not move over the retina the retinal position can simply be combined with the eye orientation information. However, when the image moves over the retina a prediction for this movement would also be needed. The brain does not have full control of this movement, and so it has to base the prediction of this movement on afferent information.

The studies described in this thesis focus on the mislocalization during smooth pursuit eye movement. They show that the mislocalization is used in behavior, that it probably depends on efferent eye movement signals and that retinal and eye movement information are combined in a way that could be useful to predict future positions of the target.

Since we only consider some obvious information sources we will not be able to explain the responses of the subjects exactly. We will probably always neglect some important factors that determine the response. This is the case because we do not know what al the factors are that we would need in order to exactly explain each response. Future research may show what information sources are necessary if one wants to explain everything. However, it may not be feasible to control all factors accurately, so that there will always be some unexplained variability in the data (often called noise). Chapter two, which is about the influence of different kinds of cues, can give an example of a factor that has an effect on the response but which is not easy to control. In that chapter we show that it is important where the subject expects the target to appear.

In previous studies that showed that subjects mislocalised a target that was flashed during smooth pursuit the subjects did not have to manually touch the position of the flash but had to indicate it orally or by using a computer mouse. In chapter three we show that the misjudgements found in those studies are also present when a fast hand movement is used to indicate the position. This supports the view that these mislocalizations might be useful for intercepting moving objects that are pursued by the eyes (and that they are not merely perceptual illusions).

In chapter four we present findings supporting the view that the use of the commanded eye orientation (i.e. an efference copy of the ocular motor commands) is responsible for the mislocalization.

Finally, in chapter five we present findings that support the view that moving (pursued) targets are mislocalised in the same way as flashed targets are. We also present a simple model that shows how combining eye orientation information with retinal information shortly after target onset can result in the forward mislocalization of both moving and flashed targets, while it results in non-biased localization of stationary targets. This supports the idea that the mislocalization with stationary eyes and the mislocalization with moving eyes depend on the same adaptive mechanism.

2

Spatial but not temporal cueing influences the mislocalization of a target flashed during smooth pursuit[1]

Gerben Rotman, Eli Brenner & Jeroen B. J. Smeets

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[1] This chapter has been published in Perception (2002) 31: 1195-1203.

Abstract

Human subjects misjudge the position of a target that is flashed during a pursuit eye movement. Their judgements are biased in the direction in which the eyes are moving. We investigated whether this bias can be reduced by making the appearance of the flash more predictable. In the normal condition subjects pursued a moving target that flashed somewhere along its trajectory. After the presentation they indicated where they had seen the flash. The mislocalizations in this condition were compared to mislocalizations in conditions in which the subjects were given information about when or where the flash would come. This information consisted of giving two warning flashes spaced at equal intervals before the target flash, of giving two warning beeps spaced at equal intervals before the target flash, or of showing the same stimulus twice. Showing the same stimulus twice significantly reduced the mislocalization. The other conditions did not. We interpret this as indicating that it is not predictability as such that influences the performance, but the fact that the target appears at a spatially cued position. This was supported by a second experiment, in which we examined whether subjects make smaller misjudgements when they have to determine the distance between a target flashed during pursuit and a reference seen previously, than when they have to determine the distance between the flashed target and a reference seen afterwards. This was indeed the case, presumably because the reference provided a spatial cue for the flash when it was presented first. We conclude that a spatial cue reduces the mislocalization of targets that are flashed during pursuit eye movements. The cue does not have to be exactly at the same position as the flash.

2.1 Introduction

It takes time for retinal stimulation to give rise to a neural response within the brain. This visual latency has consequences for localising moving objects. By the time a position has been determined the object will have moved. To compensate for this the visual system could predict the current position, as suggested by Nijhawan (1994) to explain a phenomenon called the flash-lag effect. However, there is behavioural evidence that such prediction is not responsible for the flash-lag phenomenon (Whitney, Murakami & Cavanagh, 2000; Eagleman & Sejnowski 2000; Brenner & Smeets 2000). If one follows a moving object with ones eyes, its retinal image does not move but the eyes are rotating. In that case the latency of the eye orientation signal has consequences for localization. Duhamel, Colby & Goldberg (1992) found neurons in the lateral intraparietal cortex that start giving a response to a stimulus before an eye movement brings that stimulus into their receptive field. This suggests that efferent information about eye orientation may be involved in localising moving objects (Nijhawan 2001; Brenner, Smeets & van den Berg, 2001). Efferent information is different from afferent information in that it predicts a future eye orientation.

Given the considerations mentioned above it is not surprising that mislocalizations are found in many different experimental settings involving moving targets. We will focus on position judgements during smooth pursuit eye movements. Human subjects misjudge the positions of stimuli that are flashed during a smooth pursuit eye movement. They also misjudge the position at which a pursued target disappears or changes brightness. The mislocalization is in the direction of movement (Hazelhoff & Wiersma 1924; Mita, Hironaka & Koike, 1950; Mitrani & Dimitrov, 1982; Mateeff & Hohnsbein 1989; van Beers, Wolpert & Haggard 2001; Brenner, Smeets & van den Berg, 2001). Hazelhoff & Wiersma (1924) assumed that this phenomenon was exclusively due to visual latencies and they called the mislocalization expressed in time units the perception time (Wahrnehmungszeit). They found that the perception time (on average 104 ms) was independent of the direction and speed of movement. Mita, Hironaka & Koike (1950) showed that the perception time depends on the retinal eccentricity of the flash and on the state of adaptation of the eyes. They too, assumed that these mislocalizations were exclusively due to the visual latency in perceiving the flash, thus implicitly assuming zero latency for the eye orientation signal. Mateeff, Yakimoff & Dimitrov (1981) showed that the position at which a moving target that is pursued by the eyes changes brightness is sometimes mislocalized against the movement direction, which would require a negative perception time. They explained this by introducing latencies for eye orientation signals. A negative perception time arises when such latencies are longer than the visual latency.

Brenner, Smeets & van den Berg (2001) suggested that mislocalizations arise because incoming retinal signals are combined with outgoing oculo-motor commands, without considering neural delays. However other studies show that there are more factors involved than just constant latencies. For instance Mitrani & Dimitrov (1982) and van Beers, Wolpert & Haggard (2001) found that the mislocalization of a target flashed during pursuit was smaller when the flash was presented behind than when it was presented in front of the pursued target, which is not so easy to explain by visual or eye orientation related latencies. Two studies reported results that are particularly hard to explain with constant latencies: Mitrani, Dimitrov, Yakimoff & Mateeff (1979) and Mateeff, Yakimoff & Dimitrov (1981). In both studies subjects were asked to report the position along a ruler at which a pursued target disappeared. In both studies the mislocalizations were smaller near the end of the ruler. This was interpreted as an effect of expectancy: the closer the target comes to the end of the ruler the more certain the subject becomes that it will soon disappear. It has been shown that being able to predict where a flash will occur reduces the error in relative localization in the flash lag effect (Brenner & Smeets 2000; Baldo, Kihara, Namba & Klein 2002). Whether this is also so when the eyes are moving, rather than the retinal image, is not yet known. In the Mitrani et al. (1979) and Mateeff et al. (1981) studies it is not certain that expectancy was the critical factor, because the presence of a reference can also influence the extent of mislocalization (Mateeff & Hohnsbein, 1989; Brenner, Smeets & van den Berg, 2001) and the end of the ruler may have served as such a reference when the target flashed nearby. Moreover the subjects may have been reluctant to specify positions near or beyond the end of the ruler. In the experiments described here we re-investigated the influence of expectancy on the amount of mislocalization during pursuit.

We manipulated expectancy in a number of ways. We distinguish between giving the subjects information that emphasises *when* or *where* the flash would appear. Information about when the stimulus would appear was given by presenting either visual or auditory warning signals before the flash. Information about where the flash would appear was given by showing the whole stimulus twice. Although the when and where of a moving stimulus are obviously related, we reasoned that presenting warning signals at regular intervals primarily indicates when the target will appear, while having seen the target before will primarily cue a certain position as being a likely place for the target to appear.

2.2 Experiment 1

2.2.1 Methods

Subjects were eleven members of our department, including two of the authors. We told them all that the purpose of the warning signals and the repeated presentations was to make the appearance of the flashed target more predictable. They were seated in front of a computer monitor in a dark room. On each trial a pursuit disk appeared moving at a constant velocity from left to right across a light grey background and disappeared. The subjects were instructed to follow this pursuit disk with their eyes. At a random position on its trajectory a target was flashed. The flashed target surrounded the pursuit disk (figure 1). Such a sequence of the pursuit disk travelling across the screen with a target flashed somewhere along its trajectory will be called a motion sequence. After a motion sequence the subjects indicated the position of the flashed target with a computer mouse. They could take as much time as they wanted.

Four different conditions were used (figure 1). In the NORMAL condition the subjects saw the motion sequence once. In the TWICE condition they saw precisely the same motion sequence twice. The mouse pointer was only presented after the pursuit disk had traversed the screen for the second time. The target was flashed at the same position both times. In the THIRD condition two red warning flashes that surrounded the pursuit target preceded the target flash at 500 ms intervals. In the BEEP condition the target flash was preceded by two warning beeps at 500 ms intervals. These preceding warnings could be used to anticipate the moment of the flash.

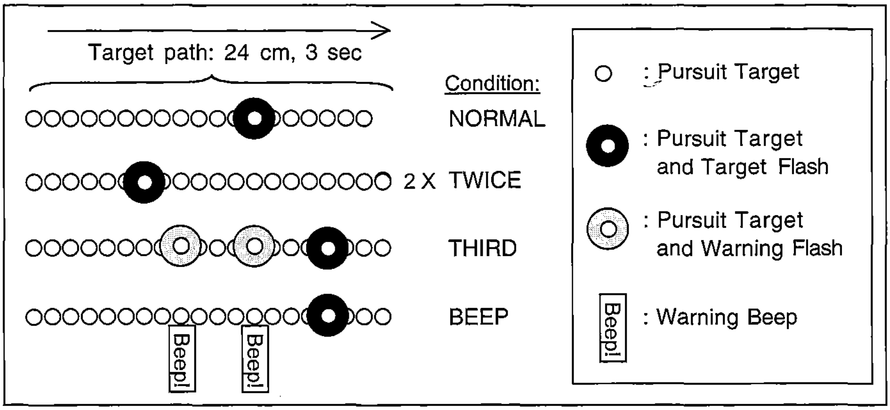

Figure 1: Schematic representation of the stimuli in experiment 1. In the NORMAL condition the pursuit disk moved at a constant velocity across the screen. A flashed target surrounding the pursuit disk was shown at a random position. In the TWICE condition the pursuit target moved across the screen twice with the flashed target both times at the same position. In the THIRD condition two red warning flashes spaced at equal intervals preceded the target flash. The BEEP condition was similar to the THIRD condition but now two warning beeps, instead of flashes, preceded the target flash. In all cases the mouse cursor used by the subject to indicate the position of the target flash was identical to the pursuit disk with the flashed target. Note that not all frames are represented in this figure.

The stimuli were presented on a computer monitor (392x293 mm; 815x611 pixels; 120 Hz). Subjects viewed the monitor from a distance of 60 cm (1cm on screen ≈ 1° visual angle). The trajectory of the pursuit disk was 24 cm long and it was traversed in 3 seconds. The pursuit disk was white and had a diameter of 3 mm (47 cd/m^2). The target flash was a black, 8 mm diameter disk. The warning flashes were red, 8 mm diameter disks (9 cd/m^2). The background was grey (30 cd/m^2). Flashes were presented for one frame. The pursuit disk occluded their centre so that the subjects saw the flash as a ring surrounding the pursuit disk. Target flashes were presented at random positions between 8 and 20 cm along the trajectory. The mouse cursor with which the subject indicated a position was identical to the target flash with the superimposed pursuit disk but remained visible until a judgement was made. The mouse cursor appeared at a random position. A head and chin rest restricted head movements. Horizontal movements of the left eye were monitored with an Ober 2 (Permobil, Meditech) at 1100 Hz. The eye movement recordings were used to ensure that the subjects made no saccades during a 400 ms interval centred on the moment of the target flash. If they made a saccade, the trial was discarded and the subject was notified of this by a beep. If the subject did not know where she/he had seen the target flash she/he could discard the trial herself/himself by pressing the right mouse button. Discarded trials were repeated later during the experiment.

Data were collected in three sessions of approximately 15 minutes. The first session consisted of the conditions: NORMAL, TWICE and THIRD. In the second session the

TWICE condition was replaced by the BEEP condition, so it consisted of conditions: NORMAL, THIRD and BEEP. The third session was a repetition of the first. Per condition there were 30 trials, so each session had 90 trials. These 90 trials were presented in a random order.

Localization bias was defined as the difference in horizontal position between the subjects' response and the target flash (a bias in the direction of pursuit is defined as positive). It was expressed in time units by dividing this difference by the velocity of the pursuit disk.

Our analysis started by checking whether individual settings were approximately on the target 's trajectory, and whether the pursuit during 400 ms around the flash was good. Settings that deviated vertically by more than 3 cm were discarded, as were settings from trials where the gain of the pursuit deviated by more than 50 % from the subject's mean gain in that session.

The next step in our analysis was to exclude subjects whose bias depended on the position on the screen at which the target was presented. We reasoned that such subjects' data were influenced by some other factor than that under study, which might itself be influenced by our manipulations. We checked for an influence of the position on the screen by checking whether the slope of the regression of the error against the target flash' position was significantly different from zero (at $\alpha=0.05$). If it was, that subject's data were discarded.

For the remaining subjects we calculated the mean localization bias for each condition. Subjects' mean localization biases and pursuit gains in the different conditions were compared with those in the NORMAL condition with paired t-tests.

2.2.2 Results

Three percent of all settings were discarded because they deviated vertically by more than 3 cm or the pursuit gain differed by more than 50 % from the mean gain. Five of the eleven subjects had biases that depended on the position on the screen, so we excluded these subjects from further analysis. These excluded subjects all had positive slopes.

The mean localization biases of the six remaining subjects are shown in figure 2. A positive bias is in the direction of pursuit. In all conditions subjects misjudged the target's position in the direction of pursuit. The localization biases in the TWICE condition are significantly smaller than those in the NORMAL condition ($p=0.01$). The other two conditions were not different from the NORMAL condition ($p=0.97$ and $p=0.79$ for conditions THIRD and BEEP respectively).

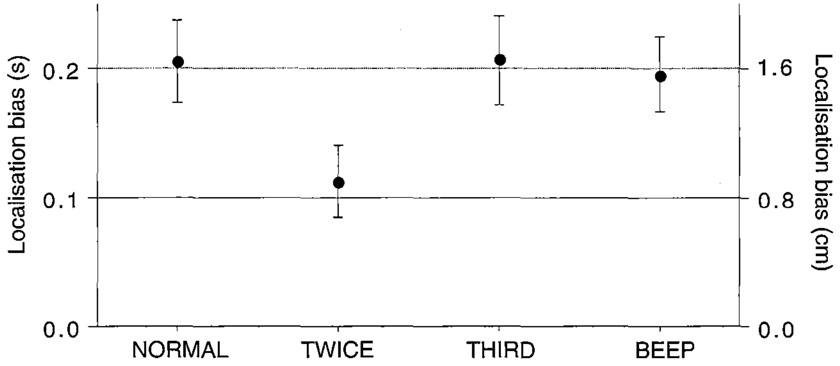

Figure 2: The average (and standard error) of the mean localization biases of six subjects. Only the mean localization bias in the TWICE condition differs significantly from that in the NORMAL condition.

The differences in localization bias are not caused by differences in eye movements because the gain of the pursuit did not differ between condition NORMAL and condition TWICE (p=0.31).

2.2.3 Discussion

The slopes of the localization bias against the flash position were significantly different from zero for five of the eleven subjects. They all had positive slopes, opposite to the findings of Mitrani, Dimitrov, Yakimoff & Mateeff (1979) and Mateeff, Yakimoff & Dimitrov (1981) who found negative slopes. Our experiments were aimed at getting a clearer view on the influence of expectancy. Since we did not use a visible ruler we thought that in our case the position on the screen was not important and therefore randomly selected positions on the screen for each trial. Not having the same positions for the different conditions made us reluctant to compare biases across conditions for subjects whose bias depends on the position. However, including all the subjects does not change our main result that the bias in the TWICE condition was about half the size of that in the three other conditions. The average bias was, however, smaller for the excluded subjects. Presumably they were using an additional source of information that reduced the bias, but which depended on the position on the screen.

The results show that making the appearance of the flash more predictable does not necessarily reduce the mislocalization. The mislocalization only decreased significantly in the TWICE condition. In that condition the exact same stimulus was shown twice. The lack of effect in the other two experimental conditions (THIRD and BEEP) argues against predictability in general being critical. Apparently warning subjects that the flash is about to occur does not make any difference. Only cueing subjects as to where the flash would appear made a difference. Thus apparently it is not the raised expectancy that reduces the bias, but the fact that the second target in condition TWICE appears at a spatially cued position. This is interesting since the cue is presumably misperceived, because it arises from a motion sequence that is identical to that in condition NORMAL. This suggests that the cue does not have to be at the same position as the flash.

To evaluate the suggestion that spatial cueing influences the bias even if the cue is not at the exact same position as where the target was, we conducted a second experiment in which the trial was not shown twice, but a cue was given at a slightly different position than the flashed target. To emphasise the relevance of the cue we asked subjects to report the separation between two sequentially presented positions: that of a static reference and that of a target flashed during pursuit. We compared a condition in which the static reference was shown first followed by the flash during pursuit, with a condition in which the reference was shown after the flash during pursuit. The subjects had to indicate the separation between the two sequentially seen positions. We reason that if the flash during pursuit is shown first it will be mislocalized to the full extent. Therefore a similar bias as in the NORMAL condition in experiment 1 should be apparent in the separation judgements. If the flash during pursuit is shown after the static target, so that subjects are cued about where the flash would occur, the misjudgement should be smaller (as in the TWICE condition).

2.3 Experiment 2

2.3.1 Methods

Subjects were eleven colleagues including one of the authors. All subjects except for this author were naive with respect to the aim of the experiment. The experimental setup was the same as in the first experiment. The subjects had to indicate the distance between two targets. One of the targets was presented very briefly during pursuit, like the flashed target in experiment 1. The other was a static target that was presented for 1 second, giving the subjects enough time to fixate it. There was a 500 ms interval between the two presentations. Two conditions were compared, the PURSUIT-FIRST and the STATIC-FIRST condition (figure 3). In the PURSUIT-FIRST condition the target that was flashed during pursuit was presented first. In the STATIC-FIRST condition the static target was presented first. Otherwise the two conditions were identical.

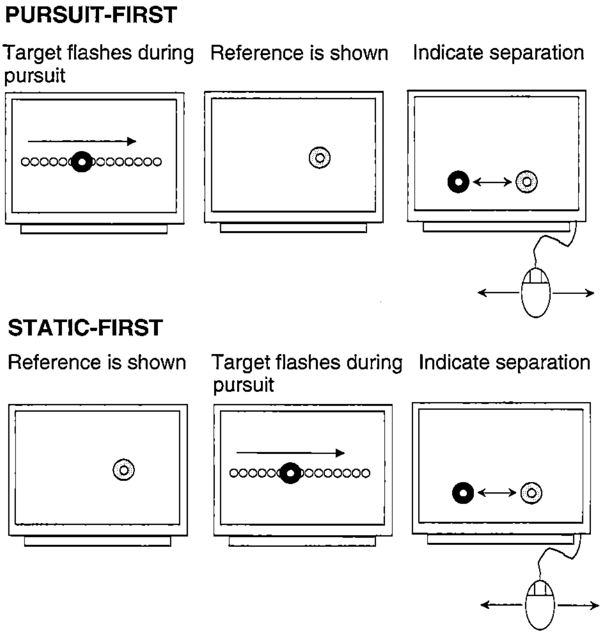

Figure 3: Schematic representation of the stimuli in experiment 2. In the PURSUIT-FIRST condition subjects saw a flashed target during a pursuit eye movement followed by a statically presented target (reference). They then had to indicate the separation. In the STATIC-FIRST condition the statically presented target was shown first and the flashed target second. Otherwise the two conditions were identical.

The static target had the same dimensions as the target that was flashed during pursuit, but it was red instead of black. Presenting a flashed target during pursuit was done in exactly the same way as in the NORMAL condition in the first experiment. The position of the flash was chosen at random from within the same range as in experiment 1. Because subjects mislocalize the flashes in the direction of pursuit the static targets were presented at positions a little further in the direction of pursuit. The position of the static target was chosen at random from the range of positions that the pursuit disk would reach between 100 ms before and 250 ms after the flash. After the subject had seen both targets two disks (a black one and a red one, both with a white centre) were presented at the centre of the screen, below the actual trajectory. Moving the mouse moved them by the same amount in opposite directions. The subject had to indicate the distance between the targets, taking into account which one was shown further to the left. The black disk was identical to the target presented during pursuit and the red disk to the static target. When the subject thought she/he had replicated the separation between the targets she/he pressed the left mouse button. Eye movements during pursuit were checked in the same way as in the first experiment and subjects could discard trials of which they were not sure by pressing the right mouse button. Discarded trials were presented again later in the experiment.

Our measure of performance, distance bias, was the difference between the signed separation set by the subject and the real separation (setting the flash too far to the right is considered a positive bias). It was expressed in time units by dividing this difference by the velocity of the pursuit disk.

Our analysis started by checking whether the gain of the pursuit did not differ too much from the subject's mean gain. Settings from trials in which the gain of the pursuit eye movement deviated more than 50 % from the mean gain were discarded.

We again excluded subjects whose distance bias depended on the position on the screen (for the same reason as in experiment 1). This was done by checking whether the slope of the regression of the distance bias against the position on the screen was significantly different from zero (at $\alpha=0.05$).

For every subject we calculated the mean distance bias for each condition. The biases and pursuit gains in the two conditions were compared with a paired t-test.

2.3.2 Results

Five percent of all settings were discarded because the pursuit gain differed by more than 50 % from the mean gain. Four of the eleven subjects had biases that depended on the position on the screen, so we excluded these subjects from further analysis. They all had positive slopes, indicating that they misperceived the flash in a similar way as the subjects that were excluded in experiment 1.

The mean distance bias, averaged over the remaining 7 subjects, is shown in figure 4. All biases are positive, consistent with a misjudgement of the flash in the direction of the pursuit. The bias is smaller in the STATIC-FIRST condition than in the PURSUIT-FIRST condition ($p=0.01$), indicating that the spatial cue not only works for judging position but also for judging separations. The distance bias did not depend on the real separation for any of our subjects, confirming that the spatial cue need not be at precisely the same position.

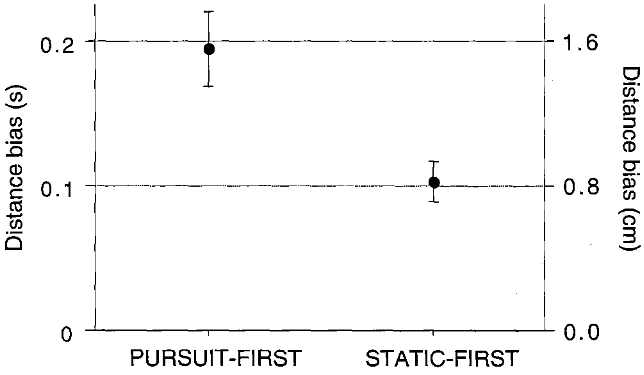

Figure 4: The average (and standard error) of the mean distance biases of seven subjects. The difference between the two conditions is significant.

The difference in distance bias is not caused by differences in eye movements because the subjects' average gains in the STATIC-FIRST condition were not different from those in the PURSUIT-FIRST condition (p=0.10).

2.3.3 Discussion

We have excluded four subjects from our analysis for the same reason as in experiment 1. Again, including these subjects does not make a difference for our main result that the error was smaller in the STATIC_FIRST condition, it only affects the absolute values. The average bias was again smaller for the excluded subjects.

We found that the separation between two sequentially presented targets was misjudged. The misjudgement was consistent with the way in which the positions of the flashes shown during pursuit were misjudged in experiment 1. The misjudgement was smaller in the STATIC-FIRST condition, in which the approximate location of the flash was cued before the flash during pursuit was shown. We conclude that the mislocalization of the position of a target that is flashed during pursuit can be reduced by cueing the approximate position where the flash will appear.

2.4 General discussion

In both experiments we excluded subjects whose settings depended on the position on the screen at which the flash was presented. We did so because we reasoned that they were influenced by other factors than those that we were manipulating. For all these subjects the dependency on screen position was opposite to that found by Mitrani, Dimitrov, Yakimoff & Mateeff (1979) and Mateeff, Yakimoff & Dimitrov (1981). Since we could not explain the dependency on screen position, we felt reluctant to average the errors over the screen, so we excluded these subjects. However including all subjects does not influence the differences between the conditions. It only affects the absolute values.

We found that subjects mislocalize the position of a target that is flashed during a smooth pursuit eye movement in the direction of pursuit. Giving warnings shortly before the moment of the flash did not reduce this bias. Showing the same stimulus twice did. We interpreted this as an indication that it is not the ability to anticipate the flash that influenced the performance, but the fact that the second flash came at a spatially cued position. This was supported by our second experiment. There we asked subjects to judge the position of a flash seen during pursuit relative to a reference seen either before or afterwards. We found that subjects made smaller errors when they had to judge the separation between the flash and a reference seen before, than when they had to judge the separation between the flash and a reference seen after the flash. So again subjects made smaller misjudgements when the approximate position of the flash was cued.

Our second experiment might look a bit like the sequential localization experiment in van Beers et al. (2001). In that experiment van Beers et al. show that when subjects have to null the distance between two flashes seen sequentially during a single pursuit eye movement the duration of the first flash influences the error while that of the second one does not. The first flash was always shown in front of the pursued disk while the second one was always presented behind it. Since they just showed in their second experiment that flashes behind a pursued disk are hardly mislocalized, it is not surprising that they do not find an effect of prolonging the duration of the second flash. That they do find an effect of showing the first flash longer is consistent with flashes in front of the pursuit disk being mislocalized (as shown in their second experiment) and with a reduction of such mislocalization when showing a flash for a longer duration (as shown in their fourth experiment). So, our explanation of their results is that all that is happening is that the first flash is mislocalized less when it is shown for a longer duration, probably due to the additional information from the retinal slip. Such an explanation cannot account for the results from our second experiment since we only presented the target for a long duration when it was static.

Our two experiments differed from each other in two important aspects. Firstly, while in the TWICE condition of the first experiment the reference was exactly at the position of the flash it was only in its vicinity (ranging from -0.8 cm to 2.0 cm) in the STATIC_FIRST condition of the second experiment. Secondly, the first experiment was a localization task while the second was a distance estimation task. The fact that the results were so similar suggests that neither of these differences was important. We conclude that spatial cueing reduces the amount of mislocalization of a flash presented during smooth pursuit.

3

Tapping targets that are flashed during smooth pursuit reveals perceptual mislocalizations[2]

Gerben Rotman, Eli Brenner & Jeroen B.J. Smeets

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[2] This chapter has been published in Experimental Brain Research (2004) 156: 409-414.

Abstract

In various studies subjects have been shown to misperceive the positions of targets that are flashed during pursuit eye movements. They mislocalise them in the direction of pursuit. Nevertheless, Hansen (1979) found that subjects accurately hit targets that are flashed during pursuit with a quick hammer blow. We examined whether this is because there is a fundamental difference between the information that determines our perceptual judgements of a target's position and the information that is used to guide our hand to a similar target. Subjects were asked to quickly tap targets that were flashed during pursuit with their index finger. They systematically tapped ahead of the position of the flash, in accordance with the above-mentioned perceptual mislocalizations. Thus the lack of systematic errors in Hansen's study is not a general property of fast motor responses.

3.1 Introduction

When people are asked to judge the location of a flash that is presented while they are making a smooth pursuit eye movement they make systematic errors: targets are systematically mislocalised in the direction of the eye movement (Hazelhoff & Wiersma, 1924; Mita, Hironaka & Koike, 1950; Mitrani, Dimitrov, Yakimoff & Mateeff ,1979; Mateeff, Yakimoff & Dimitrov, 1981; Mitrani & Dimitrov, 1982; Mateeff & Hohnsbein, 1989; van Beers, Wolpert & Haggard, 2001; Brenner, Smeets & van den Berg, 2001). A possible reason for this is that people combine afferent retinal information with efferent eye orientation information without considering the neural delays that are involved (Brenner, Smeets & van den Berg, 2001). If the mislocalization has such a fundamental origin, it should be found in any task that one examines. However, Hansen (1979) found no systematic mislocalization of targets that were flashed during pursuit when the task was to hit the flash with a hammer. Was there something special about his experiment, or is this a general property of visually guided action?

It may seem obvious that our actions cannot be based on misjudged target positions whenever we are pursuing objects with our eyes, because we can successfully interact with moving objects (and with static objects when we ourselves are moving). However the "wrong" behaviour from the experimenter's point of view is not necessarily wrong from the subject's perspective. "Wrong" behaviour in a rather unusual task, localising flashed targets, might be the consequence of relying on a mechanism that is adapted to suit a more common task: intercepting moving targets. When trying to hit moving targets it could be an advantage to mislocalise the target slightly in its direction of motion because doing so could help to deal with some of the neuronal and muscular delays (Brouwer, Brenner & Smeets 2002).

Why then did subjects have access to accurate information about the location of the target in Hansen's study? And why do subjects not use this information for judgement tasks? The critical difference may be the time interval between the flash and the response. Perhaps accurate information is available initially, but it is quickly lost, because there is no point in remembering old egocentric positions because egocentric positions are always changing (Rossetti, 1998; Rossetti, Pisella & Pélisson, 2000). In judgement tasks people are indeed known to be influenced by events that take place well after the flash (Mitrani, Dimitrov, Yakimoff & Mateeff, 1979). We therefore examined whether the same lack of mislocalization that Hansen found for his hammer blows would also be found in a different fast motor task.

3.2 Experiment 1

We set up our experiment so that the actions would be as natural as possible. Subjects were asked to quickly tap flashes that were presented while their eyes were pursuing a disk. The room was dimly illuminated so that they could always see their hand and the surface on which the targets appeared. They used their index finger to tap the flashes. The pursuit disk moved irregularly within a large area. The flash could appear anywhere within this area, but always near the pursuit disk. The eye could be moving in any direction when the target flashed. These variations ensure that systematic errors that are related to bringing the finger to different positions in space, rather than to the direction of pursuit, cannot bias the results.

3.2.1 Methods

Ten colleagues volunteered to take part in this study after being informed about what they would be required to do. Three were the authors. The others were unaware of the hypothesis that was being tested. The research in this study is part of an ongoing research program that has been approved by the local ethics committee. Stimuli were projected on a large screen (120x158 cm) that was tilted 20 degrees with respect to horizontal. A CRT projector (Sony, VPH 1271QM, 800x600 pixels, 120 Hz) projected the stimuli via a mirror from the rear onto the central part (70x55 cm) of this screen. The projector received its input from an Apple Macintosh G4. The subject was standing in front of the screen (figure 1).

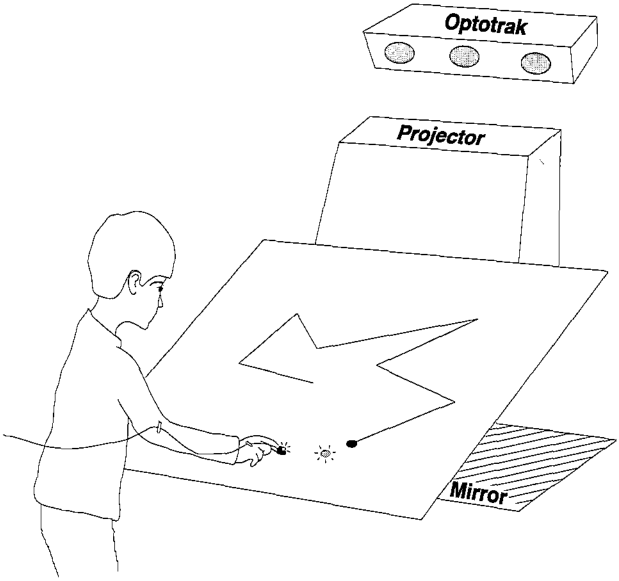

Figure 1: Schematic drawing of the set-up. A flash (grey disk) is just being presented to the subject. The connected line segments indicate a piece of the path that the pursuit disk (black disk) followed; the subject never saw this. In this case the flash is presented ahead of the pursuit target.

A red 15 mm diameter disk (2 cd/m^2) moved along a path of randomly oriented connected line segments (the lines were not visible). The length of each line segment was chosen at random from between 13 and 62 cm. The speed of the pursuit disk was chosen at random from between 16 and 32 cm/s, and changed at every turn. For horizontal target motion this corresponds with angular velocities of about 9-33°/s. For target motion with a vertical component the angular velocity was lower because the screen was not frontoparallel. This range of velocities is similar to that used by Hansen, who used velocities up to 30 °/s. It is below the maximal angular velocity for which subjects can pursue a small dot with a gain that is close to 1. For example, Rottach et al. (1996) found that human subjects pursue a small dot moving at 35.5 °/s with an average smooth pursuit gain of 0.98 for the horizontal component and 0.82 for the vertical component.

Subjects were asked to pursue the red disk with their eyes. Flashes were presented for one frame during one of the segments of the pursuit disk's path. They were presented at a "random" moment, but ensuring that there was a period of at least 500 ms during which the pursuit disk did not change direction both before and after the flash. The subjects were instructed to quickly tap the position of the flash with their index finger. Subjects started their tapping movement from a small wooden bar at the lower right corner of the screen. After they had tapped a flash they had to return their finger to this starting location. The next flash only appeared after they had done so. The mean distance from the starting location to the flash was 73 cm. The pursuit disk always kept moving along its random path, so the experiment was one long pursuit trial with many tapping movements.

The flashes were green 30 mm diameter disks (8 cd/m^2). The flashes were presented at different positions relative to the pursuit disk. We did this because errors in a judgement tasks were found to depend on the distance from the pursuit disk along the pursuit path while the distance in a direction orthogonal to the pursuit path did not matter (Mitrani & Dimitrov, 1982; van Beers, Wolpert & Haggard, 2001). We want to compare our results with those to see whether those perceptual effects are also found here. Flashes were presented at 5 positions on the pursuit disk's path: 45 or 90 mm behind the pursuit disk, at the same position as the pursuit disk, or 45 or 90 mm ahead of the pursuit disk. Beside these 5 categories we also presented flashes 45 and 90 mm from the pursuit disk, in a direction orthogonal to the disk's movement direction. The choice between the two possible orthogonal directions (90° clockwise or counter-clockwise) is rather arbitrary, so we chose a direction at random for each flash. However since we had no reason to expect the direction to matter, and therefore knew that we would pool the two directions, the orthogonal flashes only formed two categories (flashes at 45 and 90 mm distance). Thus altogether there were 7 categories, with 25 flashes presented for each category. The 175 flashes were presented in random order.

The position of the tip of the subject's index finger was monitored at 250 Hz by a movement analysis system (Optotrak 3010; Northern Digital) that tracked an infrared emitting diode (IRED) that was attached to the nail of the subject's index finger. On one of its input channels the Optotrak measured the blue signal of the computer's video output. This signal was used to synchronise the measured IRED positions with the flashes: the flashes were drawn in green as well as in blue, but only the green output was projected to the screen.

Not all flashes could be used in the analysis. In some cases the tap position could not be determined because the subject did not move (presumably because he missed the flash) or because he turned his hand so that the IRED could not be seen by the Optotrak. For the remaining flashes we first determined the tapped position from the projection onto the screen of the final position of the IRED that was attached to the finger. This final position was defined as the first position (after the movement had started) at which the velocity of the IRED was below 6 cm/s and the IRED was less than 2 cm from the screen (note that the finger was closer because the IRED was attached to the nail). We then determined the difference between the positions of the flash and the tap along the direction of the pursuit disk's movement (i.e. the signed distance on the screen). We call this measure the localization bias. A positive value means that it was in the direction in which the pursuit disk was moving. To express the localization bias in time units we divided it by the velocity of the pursuit disk.

We also calculated the signed error in the orthogonal direction (whereby an error in the counter-clockwise direction was considered positive). We did this in order to determine whether there were any general systematic misjudgements of retinal eccentricity (compression or expansion relative to the fovea). Both compression (Müsseler et al. 1999, van der Heijden et al. 1999) and expansion (Bock 1986; Enright 1994; Henriques, et al. 1998) have been reported during fixation. As a measure for the compression or expansion we calculated the slope of the regression of subjects' mean orthogonal errors against the positions of the flash relative to the pursuit disk (along the orthogonal direction). We compared this slope with the slope of the regression of subjects' mean localization bias (in spatial units) against the positions of the flash relative to the pursuit disk along the pursuit disk's path.

Our hypothesis is that the localization bias is caused by combining afferent retinal signals with efferent eye movement signals without considering neural delays (Brenner, Smeets & van den Berg, 2001). If so, the localization bias will not depend on the speed of the movement when it is expressed in temporal units (assuming that the speed of the pursuit disk does not influence neural delays). Two studies found that the localization bias did indeed not depend on the velocity of the pursuit disk when it was expressed as a timing error (Hazelhoff & Wiersma, 1924 and Mita, Hironaka & Koike, 1950) but another one did find a slight decrease of the timing error as velocity increased (Brenner, Smeets & van den Berg, 2001). To see whether there was such a dependency in our experiment we checked the correlation coefficient between the localization bias (expressed in temporal units) and the target velocity. As a measure of the accuracy of the tapping movement we calculated the standard deviation of the localization bias.

3.2.2 Results

The tap position could be determined for 99% of the flashes. The average time from the flash until the subject tapped a position was 734 ms for the quickest subject and 1171 ms for the slowest subject. None of the subjects had a significant correlation (at $\alpha=0.05$) between the localization bias (in temporal units) and the target velocity. The spatial errors in the tapped positions are shown in figure 2. The subjects had a systematic bias to tap too far (30 mm) in the direction of pursuit.

Subjects' mean localization biases at the different relative flash positions are shown in figure 3. The localization bias was smaller when the flash was presented behind the pursuit disk than when it was presented ahead of it. To see whether this dependency on retinal position was due to a general expansion of retinal eccentricity we compared the expansion along the pursuit disk's path with that along the orthogonal direction. The slope of the regression of subjects' mean parallel error (in spatial units) against the flash's position along the pursuit path was 0.17 (i.e. 17% expansion, $t_{88}=5.04$, $p_{\text{two-tailed}} < 0.01$). The slope of the regression of subjects' mean orthogonal error against the flash's position along the orthogonal direction was 0.05 (i.e. 5% expansion, $t_{88}=4.10$, $p_{\text{two-tailed}}<0.01$). These slopes were significantly different from each other ($t_{176}=1.81$, $p_{\text{two-tailed}} < 0.05$). The within-subject standard deviation of the localization bias was 94 ms, which did not differ between the different flash positions (p=0.26; repeated measures ANOVA, with subjects as the repeated measure: $F_{6,54}=1.329$). In spatial units the corresponding standard deviation was 21 mm.

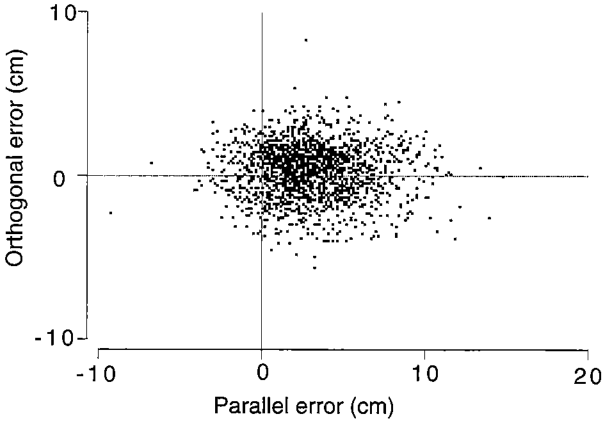

Figure 2: Errors in tapped positions in experiment 1 (1731 points).

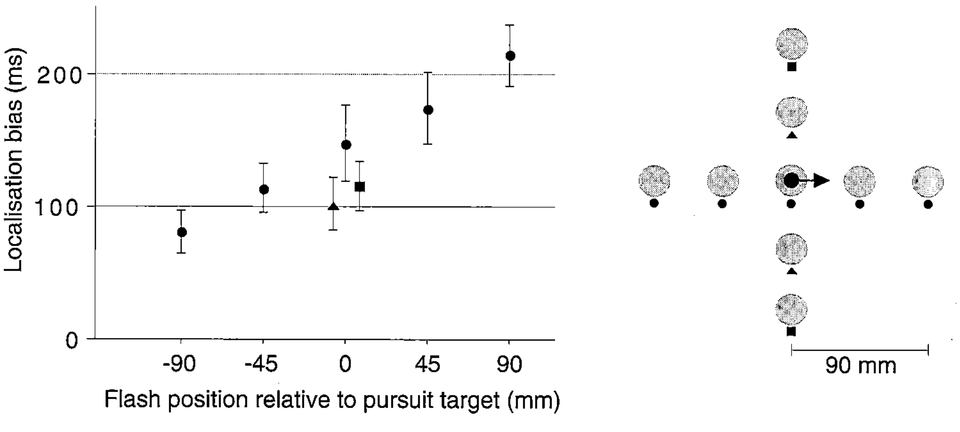

Figure 3: Results of experiment 1. The average and standard error of the ten subjects' mean localization biases (mislocalization along the pursuit disk's path) as a function of the flash position relative to the pursuit target. The relative positions of the flashed targets and the symbols used for the different categories are shown on the right (note that the localization bias is in the direction of the arrow).

3.2.3 Discussion

We found that subjects tap systematically ahead of targets that are flashed during smooth pursuit eye movements. They not only do so for targets that are centred at the same position as the pursuit disk but also for targets at other positions near the pursuit disk. The standard deviation of the localization bias was about the same as in Hansen's (1979) experiment (21 mm is about equal to the 2° Hansen found because the distance of the flash from the subjects' eyes in our set-up was between 50 and 100 cm). However the bias was not consistent with Hansen's (1979) finding that subjects could accurately strike the position of the flash with a hammer. As in judgement experiments (Mitrani & Dimitrov, 1982; van Beers, Wolpert & Haggard, 2001) our subjects mislocalised the targets that were flashed ahead of the pursuit disk more than those that were flashed behind the pursuit disk. Moreover, as reported in van Beers et al. (2001) changing the relative position of the flash in the orthogonal direction makes less difference to the localization bias (a similar but smaller dependency on motion direction has been found during fixation, so this expansion may be a totally independent effect; Watanabe, Sato & Shimojo 2003).

For the eccentrically presented targets we found an overestimation of the distance from the fovea, as has been reported in several experiments in which subjects had to indicate the perceived position of eccentrically flashed targets during steady fixation (Bock 1986; Enright 1994; Henriques, et al. 1998). Interestingly, these were studies in which subjects indicated the perceived position by pointing with the hand. An underestimation of retinal eccentricity was found in other studies that used more complicated methods, like comparing the positions of visible structures in the retinal periphery (van der Heijden et al. 1999; Müsseler et al. 1999).

If the overestimation of the distance from the fovea that we found in the direction orthogonal to the direction of pursuit is also present in the direction of pursuit, we can expect differences in mislocalization between flashes in front of the pursuit disk and ones behind the pursuit disk. The flashes in front of the pursuit disk will be seen further ahead, so that the bias that we calculate will be larger. The flashes behind the pursuit disk will be seen further behind the pursuit disk, so that the bias will become smaller. This is what we find, but the overestimation of distance from the fovea in the orthogonal direction is too small to totally explain the differences along the pursuit direction.

One could argue that since we did not measure eye position we do not know how accurate the pursuit was, and that probably the pursuit disk's image was not always projected exactly at the fovea. A lower gain of pursuit would imply that the timing error is even larger than the values given in figure 3. Lagging behind the pursuit disk would place all flashes further "ahead" on the retina, so that the fovea is not directed at position zero along the abscissa in figure 3, but at a negative value. If so, the timing error at the fovea is smaller than the value suggested by figure 3. One can deduce from figure 3 that the error would be zero at about –200 mm. Thus this effect is too small to challenge the existence of a localization bias at the fovea, because our subject's gaze is unlikely to be more than a few centimetres off target, and it would have to lag about 20 cm behind the pursuit target to account for the error in terms of retinal eccentricity alone.

3.3 Experiment 2

Our first experiment demonstrates that the absence of systematic errors is not a general property of motor responses to flashed targets. However, in experiment 1 the time between the flash and the response was considerable. We proposed in the introduction that the time interval between the flash and the response might be critical. We therefore conducted a second experiment in which we changed the design so as to shorten the interval between the flash and the tap.

3.3.1 Methods

The experimental set-up was the same as in the previous experiment. The same ten subjects participated and we used the same seven categories of relative positions of the flash, but now with twice as many flashes (50) of each category. The main difference was that subjects no longer had to return their finger to a fixed position. After each tapping movement the subjects held their hand at some comfortable position ready to tap the next target. They could even follow the pursuit disk with their finger if they liked. As the hand movements were quicker we could now present a flash for every line segment of the pursuit disk's random path. The flash was presented after the pursuit disk had moved along a line segment for a random period between 500 and 700 ms. After the flash the pursuit disk kept moving along that line segment for another random period between 500 and 700 ms. Thus, the interval between two successive flashes was between 1000 and 1400 ms. Again the pursuit disk kept moving, so the experiment was one long pursuit trail with many tapping targets.

3.3.2 Results

The tap position could be determined for 96% of the flashes. The time between the flash and the tap was much shorter than in experiment 1. On average it was 394 ms for the quickest subject and 559 ms for the slowest subject. The average distance from the hand to the flash at the moment of the flash was about half of the 73 cm that was imposed by the starting bar in experiment 1: it was 22 cm for the closest subject and 48 cm for the furthest. For three of the ten subjects the correlation coefficient between the localization bias (in temporal units) and the target velocity was significantly different from zero when the error was expressed in temporal units (at $\alpha=0.05$). These three correlation coefficients were all negative as in Brenner, Smeets & van den Berg (2001). The slopes were: -2.5, -4.8 and -3.8 ms per cm/s. These correlations could only account for a small proportion of the variance (1.5%, 2.8% and 1.5%). The spatial errors in the tapped positions are shown in figure 4. It is evident that the subjects still had a systematic bias to tap too far in the direction of pursuit.

The overall average of the localization bias was 165 ms (40 mm), which is slightly but not significantly larger than that in experiment 1 ($t_9=2.69$, $p_{\text{two-tailed}}=0.07$, paired t-test, paired on subject). Subjects' mean localization biases at the different relative flash positions are shown in figure 5. The mean localization bias is larger for flash positions ahead of the pursuit disk than for flash positions behind the pursuit disk. To see whether this dependency on retinal position is due to a general expansion of retinal eccentricity we compared the expansion along the pursuit disk's path with that along the orthogonal direction. The slope of the regression of subjects' mean parallel error against the flash's position along the direction of pursuit was 0.29 (i.e. 29% expansion, $t_{88}=6.43$, $p_{two\text{-}tailed}<0.01$). The slope of the regression of subjects' mean orthogonal error against the flash's position in the orthogonal direction was 0.20 (i.e. 20% expansion, $t_{88}=15.71$, $p_{two\text{-}tailed}<0.01$). These slopes were not significantly different from each other ($t_{176}=0.91$, $p_{two\text{-}tailed}=0.18$). The within-subject standard deviation of the localization bias did not differ between the different relative flash positions ($F_{6,\,54}=1.085$, $p=0.38$; repeated measures ANOVA, with subject as the repeated measure,). On average it was 112 ms. In spatial units the corresponding standard deviation was 28 mm.

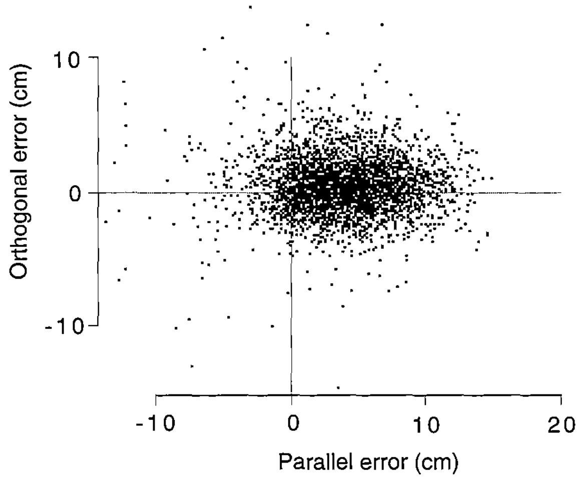

Figure 4: Errors in tapped positions in experiment 2 (3355 points).

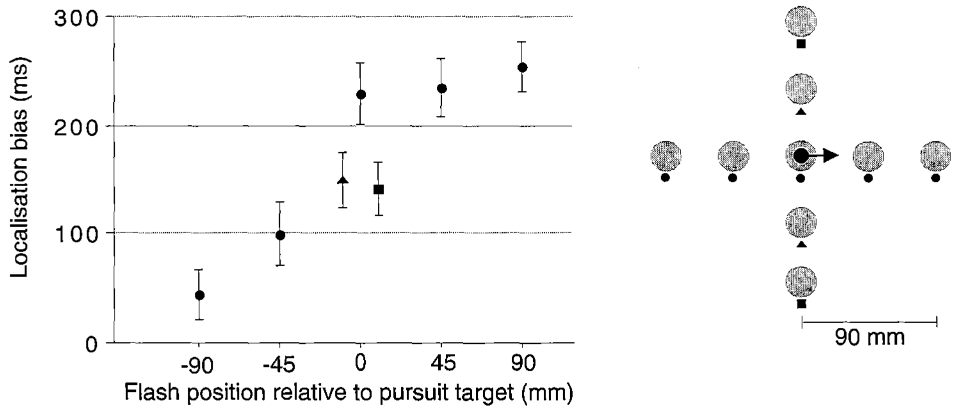

Figure 5: Results of experiment 2. The average and standard error of the ten subjects' mean localization biases (mislocalization along the pursuit disk's path) as a function of the flash position relative to the pursuit target. The relative positions of the flashed targets and the symbols used for the different categories are shown on the right (note that the localization bias is in the direction of the arrow).

3.3.3 Discussion

In this experiment subjects made tapping movements that were a lot quicker than those in experiment 1. Still the localization bias is more comparable with those found in judgement tasks than with those of Hansen (1979), who found no localization bias when subjects struck the flashes with a hammer. In the introduction we argued that the unbiased hammer blows in Hansen's study (1979) may have been based on a rapidly decaying accurate spatial representation (Rossetti, 1998; Rossetti, Pisella & Pélisson, 2000). If so, speeding up the movements in our study should have resulted in more veridical responses. We can reject this hypothesis because the localization bias in experiment 2 is even a bit larger than that in experiment 1, while the subjects reacted faster. The standard deviation of the localization bias is a bit larger than that in experiment 1, but it is still comparable to that found by Hansen (1979).

Again we found expansion of the distance from the fovea for eccentrically presented targets. In this experiment we could not reject the hypothesis that the difference between the localization bias in front of the pursuit disk and that behind the pursuit disk is caused by an overall tendency to overestimate retinal eccentricity.

3.4 General discussion

Hansen (1979) found that flashes presented during pursuit eye movements can be hit accurately with a hammer. In various judgement tasks people misjudge the position of such flashes in the direction of pursuit (Hazelhoff & Wiersma 1924; Mita, Hironaka & Koike, 1950; Mitrani, Dimitrov, Yakimoff & Mateeff 1979; Mateeff, Yakimoff & Dimitrov 1981; Mitrani & Dimitrov, 1982; Mateeff & Hohnsbein 1989; van Beers, Wolpert & Haggard 2001; Brenner, Smeets & van den Berg, 2001). A possible explanation for this difference is that different information is used for the different ways of responding. We therefore set up an experiment in which we asked subjects to make a motor response as soon as they saw the flashed target. In this task subjects did make systematic errors. Thus the lack of systematic errors in Hansen's task is not a general property of motor responses.

What then could be this difference? The variability of the taps in our task was similar to the variability of the hammer blows in Hansen's task, so our subjects were not simply less accurate. Hansen (1979) did not report the timing of the responses, nor the distance to move, but a comparison of our two experiments does not suggest that these factors are critical. One clear difference between Hansen's experiment and ours is that Hansen did the experiment in the dark while ours was done in a dimly lit room. Brenner, Smeets and van den Berg (2001) have shown that a structured background can reduce the localization bias considerably. Thus if the room being dark were the critical difference we would expect the errors to be smaller in our experiment than in Hansen's. There are many other differences between our experiment and Hansen's, but at present we see no reason to expect any particular one of them to be critical. Examples of differences are: the use of hammer blows vs. tapping with the finger, repeated trajectories vs. random trajectories, horizontal pursuit vs. random directions of pursuit, ratio of flashed target diameter to pursuit disk diameter of 12 vs. a ratio of 2, the presence of a vertical line through the flashed target vs. no such line, and flash always exactly on pursuit target vs. flash usually not precisely on pursuit target. Which of these, if any, are critical remains to be examined.

The pattern of mislocalization of targets that were flashed at different positions relative to the pursuit disk was comparable to that found in judgement tasks. Van Beers, Wolpert and Haggard (2001) found large differences between the mislocalization of targets flashed at different positions (relative to the pursuit disk) along the movement direction and little differences for targets flashed at different positions in an orthogonal direction. The flashes that were presented in front of the pursuit target were mislocalized further than those that were presented behind the pursuit target. Mitrani and Dimitrov (1982) also report that the mislocalization is larger for flashes that are presented 5 degrees "ahead" of the fovea than for flashes on the fovea. In our first experiment the dependency on relative position could not be fully explained by a general overestimation of retinal eccentricity, but in the second experiment, in which there was less time between the flash and the tap, it could. Further research is needed to determine the origin of this phenomenon.

We cannot explain why our subjects made systematic errors while Hansen's subjects did not. Neither have we established whether the larger errors for flashes that are ahead of the pursuit disk arise from an overall misjudgement of retinal eccentricity. However it is evident from this study that our actions can be based on systematically misjudged positions when our eyes are moving. Thus the lack of systematic errors in Hansen's study is not a general property of fast motor responses.

4

Mislocalization of targets flashed during smooth pursuit depends on the change in gaze direction after the flash[3]

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[3] This chapter has been published in Journal of Vision (2004) 4:564-574.

Abstract

Subjects mislocalise the position of a target that is flashed while they are making pursuit eye movements. This mislocalization is in the direction of pursuit. However, it is not clear whether it is the movement of the eyes or the movement of the pursuit target that matters. Neither is it clear whether it is the movement after the flash or the movement before the flash that matters. To resolve these issues, we asked subjects to pursue a disk that regularly changed its movement direction. Each change was followed by a change in the direction of gaze movement. Subjects were asked to tap targets that were flashed close to the moment at which the pursuit disk changed direction. We measured the movements of the eyes, head, and index finger. Subjects did not make saccades to the position they tapped but kept pursuing the disk. We compared the direction of the mislocalization with the changes in gaze and in target position during different intervals relative to the flash. We found that the mislocalization is related to the change in gaze after the flash.

4.1 Introduction

When human subjects are asked to localize flashes that are shown to them shortly before or during an eye movement, they make systematic errors. Such errors can be understood by assuming that visual information from the retina is combined with information concerning eye orientation at a moment that does not exactly correspond with the moment of the retinal stimulation. This is a reasonable assumption because transmission delays make it difficult for the brain to determine the orientation of the eyes exactly at the moment that the light strikes the retina. The mislocalizations might, therefore, reveal how information concerning eye orientation is combined with information from the retina.

Most studies in which subjects had to judge the position of targets that were flashed prior to a saccade, or during smooth pursuit eye movement, show that subjects misjudge the position of the flashes in the direction of the eye movement (for a review, see Schlag & Schlag-Rey, 2002). A possible explanation for this is that retinal information is combined with the commanded eye orientation without accounting for transmission delays (Brenner, Smeets, & van den Berg, 2001). If so, the mislocalization of targets during pursuit should be highly correlated with the eye movement during some interval after the flash. On the other hand, there are also studies that do not involve eye movements in which motion signals were found to influence the perceived position of briefly visible targets (Nishida & Johnston, 1999; Whitney & Cavanagh, 2000; Honda 2001; Watanabe, Sato, & Shimojo, 2003). This suggests that the target motion might be the main factor in mislocalization. If so, the mislocalization should be highly correlated with some aspect of target movement. In the studies in which targets were flashed during pursuit eye movements, the eye movements were so strongly related to the target motion that it is impossible to distinguish between the two when interpreting the data. It is not even clear whether it is the eye (or target) movement *after* the flash or before the flash that determines the errors, because the movement after the flash was very similar to that before the flash in these studies.

To be able to distinguish between the use of information from before and after the flash, we presented a stimulus that ensured that the information before and after the flash was different. This was achieved by having the pursuit disk follow a path that has turns in it, and flashing targets around the moment of the turns. The subjects were asked to follow the pursuit disk with their eyes. By doing this, we got the subjects to make eye movements that changed direction somewhere close in time to the flash. Because the change in eye movement direction occurs later than that in the direction of target movement, this also allows us to determine whether the eye movement or the target movement is critical. We measured the movement of the subjects' eyes, head, and hand and compared the direction of the localization errors with the movement directions of gaze and target both before and after the flash. Because we did not want to have to deal with possible influences of retinal eccentricity (Rotman, Brenner, & Smeets, 2004), we always flashed the target where we expected the subject to be looking (i.e., at the same position as the pursuit disk). Flashing targets at the same position as the pursuit disk also encourages subjects to pursue the disk. To minimize possible effects of memory, we asked the subjects to tap the flashed target with their index finger as soon as they saw the flash. Subjects were completely unrestrained, so they were free to pursue the target naturally, with any combination of eye and head movements.

4.2 Methods

4.2.1 Experimental set-up

Subjects were seven members of our department, including one of the authors. Except for the author, the subjects were naïve about the purpose of the experiment. Stimuli were projected on a large screen (113 x 84 cm) that was tilted 20° with respect to horizontal. A CRT projector (Sony, VPH 1271QM, 800 x 600 pixels, 120 Hz) projected the stimuli via a mirror from the rear onto this screen. We used only the central part of the screen (70 x 55 cm, 500 x 400 pixels). The projector received its input from an Apple Macintosh G4. The subject was standing in front of the screen (Figure 1). The room was dimly lit so the subjects could see the screen and their hands. Having a visible background has the additional advantage of ensuring that subjects will not dramatically underestimate their pursuit velocity (e.g. Festinger, Sedgwick, & Holtzman, 1976; Mack & Herman 1978).

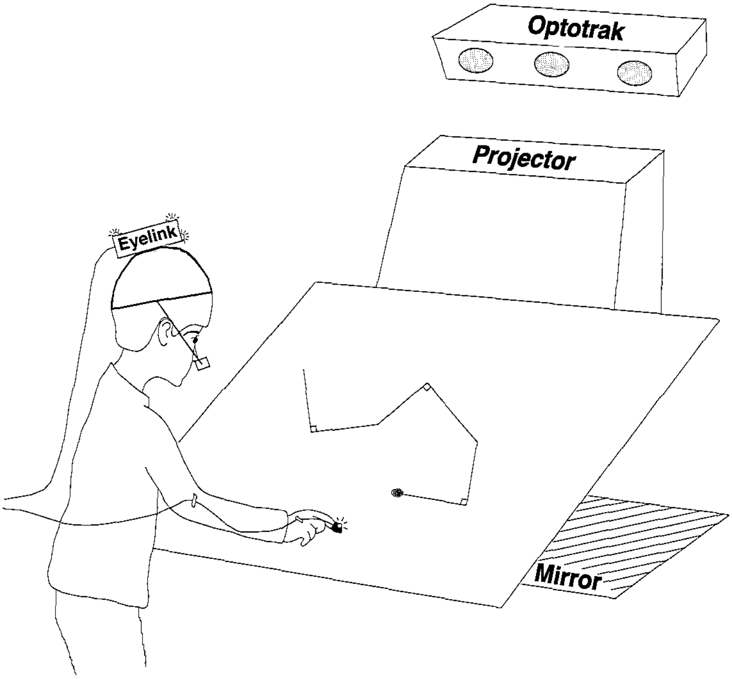


Figure 1: Schematic drawing of a subject performing the task. A moving pursuit disk is projected from the back onto the screen (via a mirror). An EyeLink measures the subject's eye movements. An Optotrak measures the subject's head movements and the position of the subject's finger. The grey disk in the drawing represents the red pursuit disk. The lines show part of the pursuit disk's path (subjects never saw these lines), including three right angle turns.

A red 15-mm diameter pursuit disk (2 cd/m^2) moved along a path of connected line segments. The subject was asked to pursue this disk with his eyes. We varied the parameters of the disk's motion to make its movement unpredictable for the subject. The disk traveled along each segment for a random period between 500 and 700 ms. The change in movement direction from one line segment to the next was chosen at random for half of the turns. For the other half, the pursuit disk made a right angle turn (either in the clockwise or in the counter-clockwise direction) to have a repeated event that we could analyze. The right angle and random angle turns alternated. The speed of the pursuit disk changed when the pursuit disk made a random angle turn. It was chosen at random from between 16 and 32 cm/s. When the pursuit disk made a right angle turn, its speed did not change. If the combination of the randomly drawn period and direction would lead the pursuit disk outside the central part of the screen, a new period and direction were chosen at random until a pair was found that fit.

A target was flashed around the time of the right-angle turn. Flashes were presented for one frame either 200, 100, or 50 ms before the pursuit disk made its turn, at the time that the pursuit disk made its turn, or 50, 100, or 200 ms after the pursuit disk had made its turn. There were 30 flashes for each of these seven moments. The flashes were green 30-mm diameter disks (8 cd/m^2). They were centered at the position of the pursuit disk, so they looked like a green ring surrounding the red pursuit disk. The subjects were instructed to quickly tap the position of the flash with their index finger.

4.2.2 Measurements

The position of the tip of the subject's right index finger was monitored at 250 Hz by a movement analysis system (Optotrak 3010; Northern Digital) that tracked an infrared emitting diode (IRED) that was attached to the nail of the subject's index finger. On one of its analog input channels, the Optotrak measured the blue video signal from the computer. This was done to be able to synchronize the measured IRED positions with the flashes: The flashes were drawn in green as well as in blue but only the green output was connected to the projector.

Eye movements were measured with an EyeLink system (EyeLink I; SensoMotoric Instruments, Teltow, Germany). Three IREDS were attached to the EyeLink's headbands, so we could measure the head's position and orientation in space using the Optotrak. This was needed to convert the EyeLink's (eye in head) data into gaze positions on the screen (i.e., to determine where the subject was looking).

To determine the spatial relationship between the EyeLink's measurements and those of the Optotrak, a calibration procedure was conducted before each experiment. The calibration consisted of two steps. First, we determined the vector between each eye and the IREDS on the head, so that we could later calculate the position of each eye on the basis of the measured IRED positions. Once we knew the position of the eyes, we could determine the function that relates the direction of gaze in the EyeLink's reference system to a direction of gaze relative to the positions of the IREDS on the head. With this we could later transform EyeLink data and measured IRED positions to a gaze position on the screen.

To determine the temporal relationship between the EyeLink's measurements and those of the Optotrak, we used a pulse generator. The pulses from the pulse generator were measured by one of the analog input channels of the Optotrak and via the parallel port of the "operator PC" of the EyeLink system. The relative timing of these synchronization signals was calibrated using a model eye: a cylinder with a hole (simulated pupil) in it. The model eye was connected to a potentiometer. Rotating the model eye (by hand) changed the voltage over the potentiometer. An analog input channel of the Optotrak measured this voltage. At the same time, the EyeLink measured the changing position of the simulated pupil. The data measured by the EyeLink were shifted in time by various amounts and correlated with data measured by the Optotrak. The shift of the EyeLink data that gave the highest correlation coefficient told us how to synchronize the measurements. We found that the data point at the moment of the pulse in the Optotrak data file corresponded to the data point 5 ms after the pulse in the EyeLink data file.

4.2.3 Data analysis

We defined the tapped position as the first position after the start of the movement at which the velocity of the finger came below 6 cm/s and the IRED was less than 2 cm from the screen (the finger was closer because the IRED was attached to the nail). In some cases no tapped position could be determined because the subject did not move (presumably because he missed the flash) or because the subject turned his hand so that he Optotrak could not see the IRED. To quantify the mislocalization, we calculated tapping errors: vectors connecting the positions of the flashes to the tapped positions.

We determined the position of gaze on the screen for both the left and the right eye, and then averaged them. Sometimes the subject turned his head so that the Optotrak could not see one of the IREDS. Sometimes the eye could not be seen by the EyeLink (presumably because the subject blinked). In both cases, the missing parts of the gaze path were not used in the analysis, but the parts that were not missing were used.

Parts of the gaze path were synchronized with respect to the moment at which the pursuit disk changed movement direction (right angle turns). The parts with a flash at the same moment relative to the turn were averaged. Because the pursuit target moved in a random direction and at a random velocity during each part, we could not simply average these parts. Before averaging them, the paths were rotated so that motion in the direction of the pursuit disk's movement before the turn was to the right. If the disk turned clockwise, we also flipped the paths, so that the direction of the pursuit disk's movement after the turn was always upward. Finally, each gaze path was scaled by the velocity of the pursuit disk during that time interval (distances from the turn were divided by the velocity to give a "distance" in time), and these scaled paths were averaged. The position that the subject tapped was obviously rotated, scaled, and flipped in the same way as the corresponding gaze path.

To get a measure of the direction and speed of the gaze movement, the trace of gaze positions (after having been scaled, turned, and/or flipped) was convolved with the first derivative of a normalized Gaussian. This procedure removed noise and gave us (smoothed) gaze velocity vectors for each sample. The amount of smoothing depends on the width of the Gaussian. We used a width of 8 ms.

To find out what kind of saccades the subjects made, we determined the direction and the amplitude of all the saccades that were made between 400 ms before and 700 ms after the pursuit disk's turn. We defined saccades on the basis of an angular velocity threshold of 40°/s. We added 8 ms of eye movement before and after the periods during which the angular velocity exceeded 40°/s to be sure to include the beginning and the end of the saccade, and consider the total change in gaze during this period as the saccade. To calculate the mean smooth pursuit component of the eye movement, we averaged all remaining eye movements.

4.3 Results

The tapped position could be determined for 94.5 % of the taps. For one subject, the right eye had not been calibrated correctly, so only the data of the left eye were used; 99.8% of the gaze data could be used.

4.3.1 Eye movements

On average, gaze turned 130 ms later than the pursuit disk (Figure 2a; at that time the average direction of gaze movement was 45 deg). This delay means that there is more than 100 ms during which gaze and the pursuit disk move in different directions. The subjects showed quite consistent pursuit behavior, as can be seen from the abrupt change of the average direction of gaze movement. Although we averaged all 1,470 pursuit movements of the seven subjects, with targets moving in various directions and at various angular velocities, the transition from 0° to 90° still occurred within a period of only about 60 ms. The speed of gaze is shown in Figure 2b; there are differences between the speed of gaze and the speed of the pursuit disk. This was the case because the pursuit movement consisted of two components, a smooth component and a saccadic component. The smooth component was consistently slightly lower than the velocity of the pursuit disk (the ratio was between 0.4 and 0.8, see Figure 2b). The saccadic component made gaze move much faster than the pursuit disk so that both components together prevent the position of gaze from moving too far from the position of the pursuit disk. The scaled total gaze velocity is on average larger than one because the eye moves over a longer distance than the target due to the overshoot at the turn.

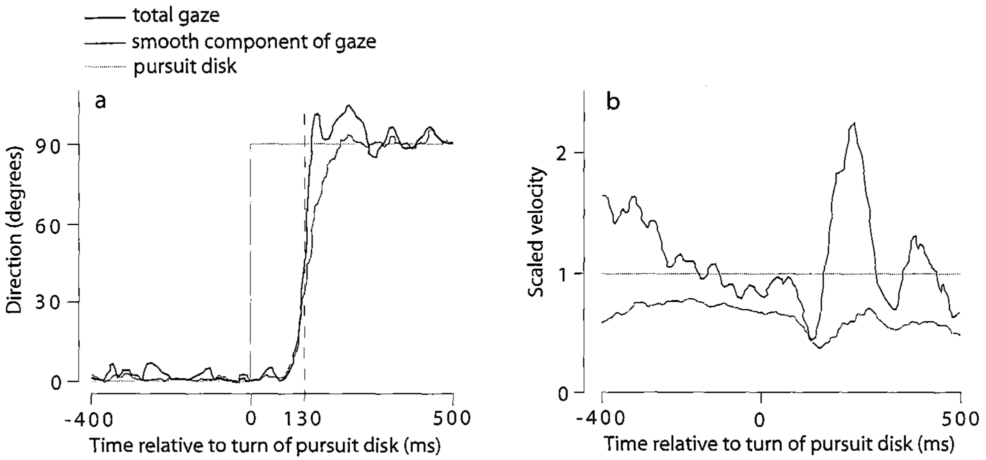


Figure 2: Response of the eyes to a 90-deg change in the direction of the pursuit disk's movement. The direction of the eye movement is shown in panel a, and the speed in panel b. The eye changes movement direction (i.e., the average movement direction is 45 deg) about 130 ms after the pursuit disk changed direction. This is accompanied by a reduction in smooth component velocity, and followed by an increased total velocity due to catch-up saccades.

4.3.2 Tapping movements

Subjects made systematic errors when tapping the flashed targets. There were some differences between the amplitudes of tapping errors (the distance from the flash to the tap) for targets flashed at different moments (Figure 3a, $p = .003$ repeated measures ANOVA with subject as repeated measure). The variability in the magnitude of the tapping error also depended on the moment of the flash (Figure 3b, $p = .03$ repeated measures ANOVA with subject as repeated measure). The average interval between the flash and the tap was 540 ms. This interval depended on the moment of the flash relative to the turn of the pursuit disk (Figure 3c, $p < .0001$ repeated measures ANOVA with subject as repeated measure): Subjects were slower if the target appeared long before the turn, perhaps because the flash was then sooner after the previous tap.

A positive linear correlation that was found between the amplitude of the errors in spatial units and the disk's velocity could explain 6% of the variance in the errors. A negative correlation between the amplitude of the errors in temporal units and the disk's velocity could explain 1% of the variance. Thus, it is not completely certain that the mislocalization should be interpreted as a temporal error, but because the dependency on velocity was considerably stronger when the errors were expressed in spatial units, a large part of the tapping errors is probably the result of temporal errors. For this reason, the paths and errors were expressed in time units before averaging (scaling described in "2.3 Data analysis"). The average error expressed in time units was 133 ms.

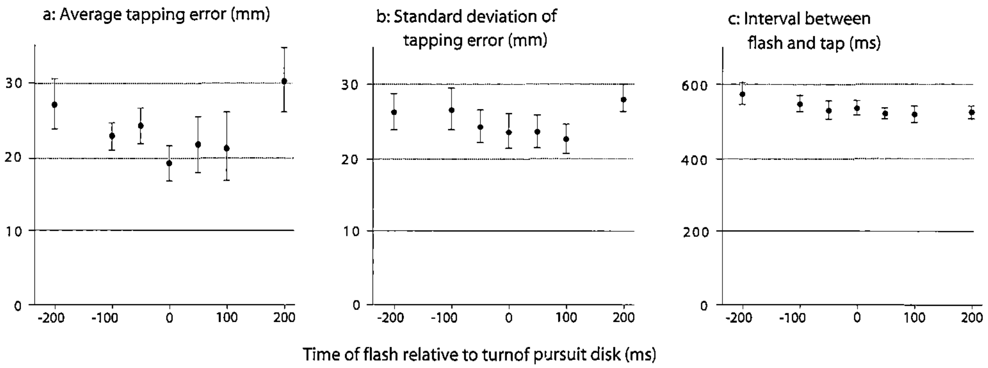


Figure 3: The average of the seven subjects' mean tapping errors (i.e., the distance from the flash to the tap (a), the standard deviations in their tapping errors (b), and the intervals between flash and tap (c), as a function of the time of the flash). Error bars show the standard error across subjects.

4.3.3 Comparison of eye movements and tapping movements

Figure 4 shows the averages of the scaled gaze and pursuit disk paths together with all the tapped positions. This figure shows that the taps are more evenly distributed around the gaze paths than around the pursuit disk path: The distribution of the taps is shifted from the pursuit disk's path in the same direction as the gaze paths.

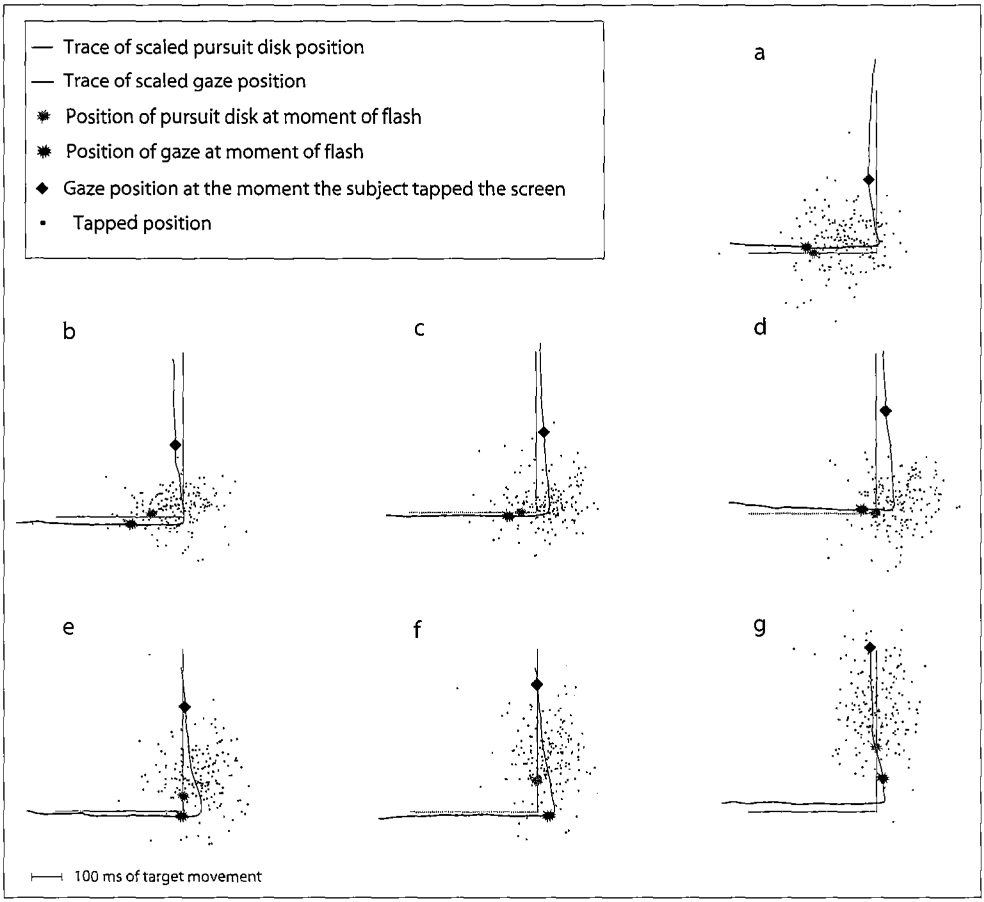


Figure 4: Comparison of gaze movement, target movement, and the tapped positions, split by the seven intervals between the flash and the turn of the pursuit disk (a-g). The grey traces show the path of the pursuit disk and the black traces the average paths of gaze. The scaled gaze paths are shown from 400 ms before the pursuit disk's turn until 700 ms after the turn. The pursuit disk's paths from 400 ms before the turn until 500 ms after the turn. The dots show the tapped positions. The diamonds show the average position of gaze at the moment that the finger tapped the screen.

Figure 5 shows the relation between the pursuit disk and gaze paths and the average tapping error. The average of the tapped positions is closer to the gaze paths than to the pursuit disk's path. Various aspects of the timing are also indicated in Figure 5. From this, one can see that the position in the gaze path that is closest to the average tapped position is not always at the same moment after the flash. This point is usually about 200 ms after the flash, but in Figure 5b and 5c, it is considerably later.

Even when the flash occurred 200 ms before the pursuit disk's turn, the tapping error was biased slightly in the direction of the pursuit disk's movement after the turn (Figure 5a). As the flash gets closer to the turn of gaze, the direction of the average tapping error gets closer to the direction of gaze movement after the turn. When the flash is after the turn in gaze direction, the error is in the direction of gaze movement after the turn.

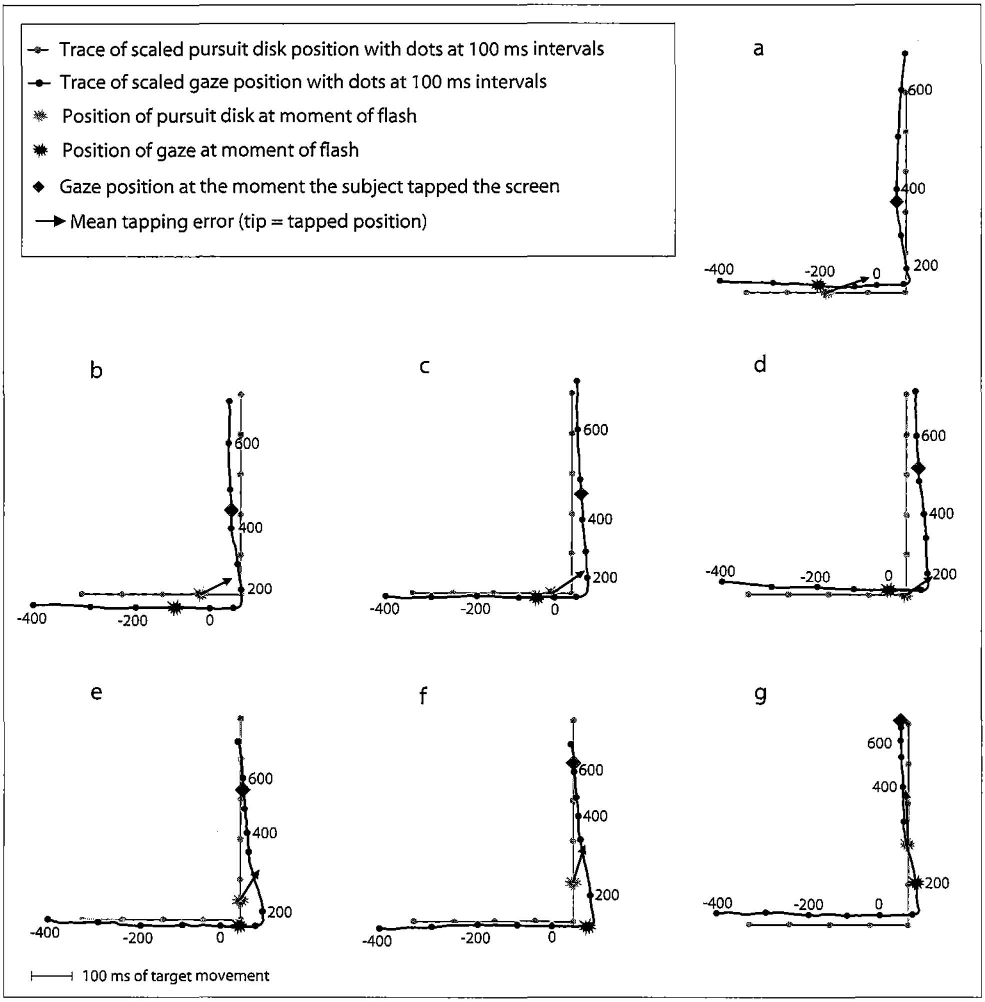


Figure 5: Summary of the experimental results, split by the seven intervals between the flash and the turn of the pursuit disk (a-g). The grey traces show the mean scaled paths of the pursuit disk and the black traces show the mean scaled gaze paths. The scaled gaze paths are shown from 400 ms before the pursuit disk's turn until 700 ms after the turn. Dots are drawn at 100-ms intervals. The numbers near the scaled gaze paths give the time relative to the turn of the pursuit disk. The arrows point from the position of the flash to the average tapped position. The diamonds show the average position of gaze at the moment that the finger tapped the screen.

If the velocity of gaze at some instant after the flash determines the tapping error, one would expect errors distributed around 0 or 90 degrees, because the eyes only move in those two directions. If the change in gaze position over a substantial time interval determines the tapping error, the errors would be distributed around intermediate values because the errors would be an average of movement in the 0° direction and movement in the 90° direction. To see whether the direction of the tapping errors shifts gradually or whether the gradual shift seen in Figure 5 is caused by averaging different combinations of tapping errors with directions of 0° and 90°, we made histograms of the direction of the tapping errors (Figure 6). Figure 6 shows that the tapping errors are distributed unimodally around the average directions that is indicated by the arrows in Figure 5.

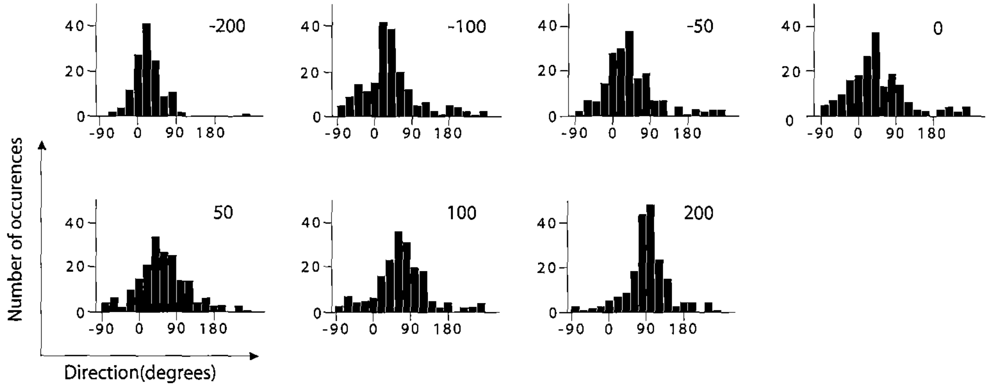


Figure 6: Histograms of the direction of the tapping errors (bin width 20°). The number at the top right of each histogram shows the time in milliseconds at which the flash was shown relative to the turn of the pursuit disk. Orientations of 0° and 90° correspond with the direction of the pursuit disk's movement before and after the turn, respectively. The distributions are all unimodal.

Because subjects pursued the disk with a combination of smooth eye movements and saccades, part of the mislocalization might be related to saccadic eye movements. Figure 7 shows the number of saccades that started at specific points in time relative to either the turn of the pursuit disk, the flash, or the tap. Many saccades started between 160 and 210 ms after the turn of the pursuit disk (Figure 7a). Thus, if saccadic eye movements had a strong influence on the tapping errors, we would expect to see a large change in tapping errors for targets that were flashed some time after the turn of the pursuit disk. We do not see large differences between the tapping errors for targets flashed at different times relative to the turn, but rather a smooth transition in the direction of the errors and small differences in their magnitudes.

There were no additional saccades around the time of the taps (Figure 7b). Moreover, the diamonds in Figure 5 indicate that on average the subjects did not look at the position that they tapped when they tapped it. It seems that the subjects never looked at the position that they were going to tap when they tapped. To see whether subjects made any saccades to look at the tapped position at all, we computed the directions of all saccades. Figure 8 shows the distribution of saccade directions and amplitudes separately for the saccades that started earlier than 100 ms after the turn of the pursuit disk, and for the ones that started later. The saccades that started more than 100 ms after the turn of the pursuit disk were almost all in the direction of the pursuit disk's movement after the turn, whereas the ones that started earlier were almost all in the direction of the pursuit disk's movement before the turn. The amplitudes of both groups of saccades are modest and have a similar distribution. The subjects never made saccades back to the position that they were going to tap. Almost all of the saccades appear to have been made to compensate for imperfect pursuit.

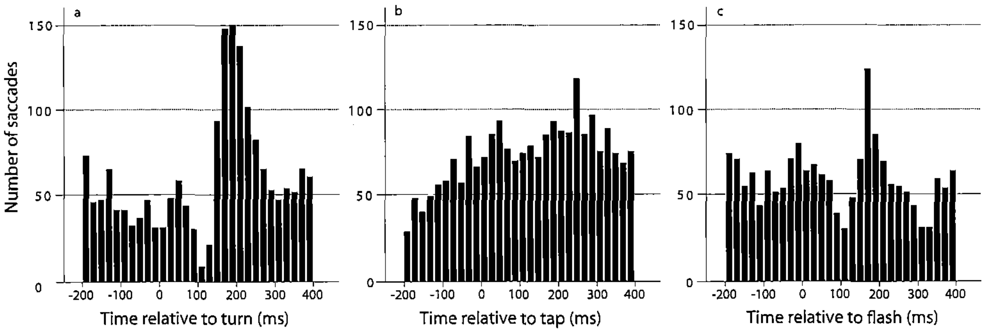
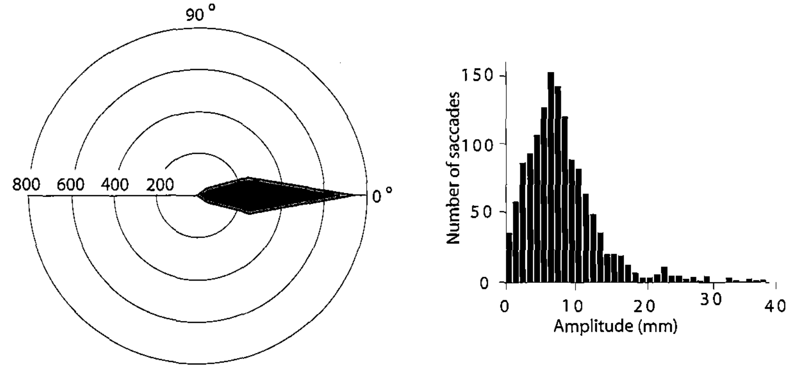


Figure 7: The number of saccades that started at different moments in time relative to the turn of the pursuit disk, the tap or the flash. The occurrence is most strongly related to the turn of the pursuit disk. The maximum number of saccades that could have been made at any moment was 1,470 (seven subjects, 210 flashes per subject). Bins are 20-ms wide.

a: Early saccades



b: Late saccades

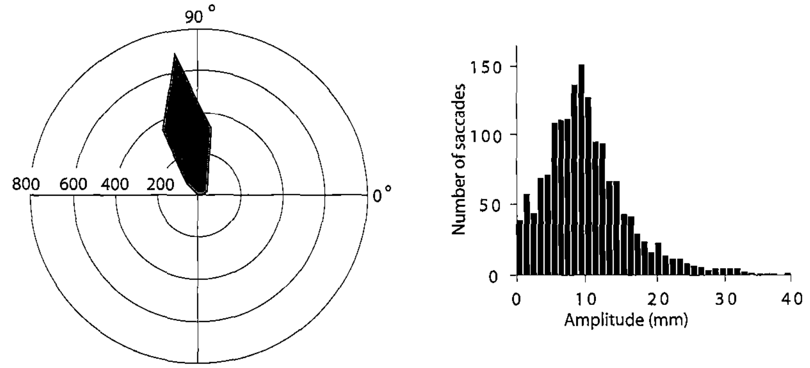


Figure 8: Distribution of saccade directions and amplitudes. Panel a shows the saccades that started between 300 ms before the turn and 100 after the turn (1,426 saccades). Panel b shows the saccades that started between 100 and 500 ms after the turn of the pursuit disk (1,687 saccades). The distance from the center in a given direction gives the number of saccades in that direction (20° bins). An orientation of 0° corresponds to the pursuit disk's movement direction before the turn and one of 90° to the movement direction after the turn. Saccades toward the position that the subject tapped would have shown up here as large, late saccades in a direction of about 270°. One can see that no such saccades were made.

4.4 Discussion

The tapped positions were not distributed around the flash but around positions that gaze and the pursuit disk had after the flash. They were closer to the path of gaze than to the path of the pursuit disk. The errors that were made when tapping the targets that were flashed before the eyes or the pursuit disk had made the turn were deflected in the direction of the movement after the turn. Thus, information acquired after the flash is required to account for the tapping errors.

Without additional assumptions, the hypothesis that the subjects aimed for a position of gaze at a constant time after the flash cannot explain the errors. This is evident from the fact that the time between the flash and the moment that gaze reached the position that was closest to the average tapped position was not the same in all conditions.

The condition in which the flash appears when the pursuit disk makes the turn is critical for making the distinction between the use of gaze movement or pursuit disk movement. In that condition, the pursuit disk and gaze moved in different directions for more than 100 ms after the flash. If the movement of the pursuit disk after the flash had been critical, the average tapping error would have been "upwards" in Figure 5d. It clearly is not. Even when the flash came 50 ms after the pursuit disk's turn, the average tapping error had a clear component in the original direction of pursuit (Figure 5e). When the flash came shortly (on average 32 ms) before the eyes made the turn (Figure 5f), the average tapping error was largely in the new direction of pursuit. When the target was flashed after the eyes had made the turn, the tapping error was "upwards" (Figure 5g). Thus, the eye movement after the flash is critical.

Brenner et al. (2001) suggested that a commanded eye orientation signal is combined with retinal information without considering neural delays. This would result in a timing error that is equal to the time that it takes for information about the flash to reach the brain, plus the time that it takes for a motor command to make the eyes move. The tapping error depends on the velocity and direction of the movement during the timing error. In our current experiment, the average tapping error (133 ms) is indeed close to the average response latency of the eyes (130 ms, Figure 2). However, the timing error should not be exactly equal to the tapping error because the direction of the eye movement changes. The amplitude of the tapping error that is predicted by the hypothesis that a commanded eye orientation signal is used, ignoring neural delays, is shown by the curve in Figure 9a. The amplitudes of the tapping errors that we found (dots in Figure 9a, corresponding to the lengths of the arrows in Figure 5) do not fall on this curve. They do bear some resemblance to the curve, but they are clearly larger than predicted.

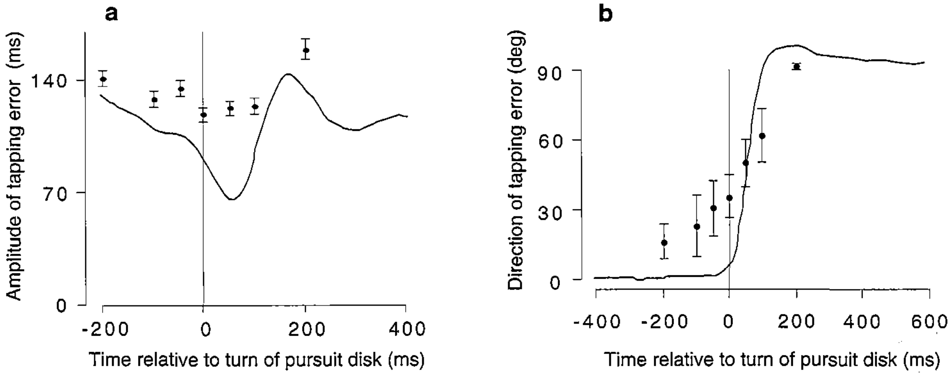


Figure 9: The amplitude (a) and direction (b) of the tapping error as a function of the moment of the flash. The curves show the prediction of the hypothesis that a commanded eye orientation signal is used and neural delays are ignored. The dots show the average measured amplitudes (i.e., the distance from the flash to the tap, divided by the velocity of the pursuit disk) and directions of the tapping errors. The bars indicate the standard errors across subjects

The curve in Figure 9b shows predictions based on the above-mentioned hypothesis for the direction of the tapping error. Again, there is some similarity with the data, but the directions that we measured do not fall on the curve. In particular, when examining the direction of the average tapping error, one can see that even when the target was flashed more than 300 ms before the turn of gaze, the direction of the tapping error was deflected a bit in the direction of the gaze movement after the turn (also see Figure 5a). In that case, the interval between the flash and the change in direction of gaze movement is much longer than the sum of the time that it takes for the flash to be detected and for a motor command to travel from somewhere within the brain to the extra ocular muscles and make the eyes move (less than 130 ms, Figure 2). Thus, ignoring neural delays when combining eye orientation information with retinal information (Brenner et al., 2001) cannot fully explain the tapping errors.

The time course of the directions of the tapping errors seems to correspond to a "damped" version of the predicted directions. The use of a "damped" representation of the eye orientation for visual localization has been proposed to explain the results of experiments in which subjects had to judge the position of targets that were flashed near saccades. (Honda 1991, 1993; Dassonville, Schlag, & Schlag-Rey, 1992, 1993; Bockisch & Miller 1999). The suggestion is that localization uses a coding of the (impending) saccade that is not exactly equivalent to the saccade itself. However, the time window over which the changes in gaze direction would have to be averaged to explain the error directions that we measured (Figure 9b) would have a width of about 400 ms, which predicts error lengths that are between 283 and 400 ms, which is much larger than what we found (Figure 9a). Thus, although we could get a better fit of the direction of the timing error by assuming a severe damping of the relevant eye movement signals, doing so would result in poor prediction of the amplitude of the errors. Moreover, a "damped eye orientation signal" cannot account for the tapping errors that we found, because the turn is not predictable in our experiment, so subjects could not have planned the eye movement long in advance (as they could have done in the experiments that flashed targets around the moment of a saccade).

The shallow slope of the change in the direction of the tapping error (Figure 9b) could result from variability in the timing of signals that are involved in the response (Boucher, Groh, & Hughes, 2001). It is not clear what factors vary enough within our study to possibly result in such a damped representation. Here we briefly discuss some obvious possibilities.

The mislocalization of flashes during pursuit is reduced when there are visible references (Brenner et al., 2001) and is increased when the flashes are hard to detect (Mita, Hironaka, & Koike, 1950). However, neither the availability of references nor the detectability of the flash varied much in our study (for stimuli that are well above detection, threshold factors such as luminance hardly appear to matter; Boucher et al., 2001). Predictability of the flash has also been shown to influence the localization error under some conditions (Mitrani, Dimitrov, Yakimoff, & Mateeff, 1979; Mateeff, Yakimoff, & Dimitrov, 1981; Rotman, Brenner, & Smeets, 2002), but that too hardly differed between flashes in our study, and would be expected to give rise to smaller errors for flashes after than for ones before the turn if it were an important factor (which is not what we see in Figures 3b and 9a). However, if the subjects were anticipating the unpredictable targets, this may have caused some of the variability in the results. Another factor that could introduce some variability is the retinal position of the flash (Mitrani & Dimitrov, 1982; van Beers, Wolpert, & Haggard, 2001). The different velocities of pursuit probably also gave rise to some variability, because the responses did depend on the velocity to some extent (see "4.3.2 Tapping movements").

Although variability in the signals that are involved in the timing of the response could cause a shallow slope, as in Figure 9b, none of the above-mentioned sources of variability can explain the early onset. Possibly two effects lead to the total pattern of the errors: one effect being responsible for the shallow slope, and another for the early onset.

Another interesting finding from this experiment is that the subjects did not look at the position that they were tapping. The eyes did not return to the position of the flash; they kept pursuing the disk. Almost all of the saccades that the subjects made seem to be made to catch up with the pursuit target. This shows that ocular gaze does not always have to stay at the target of an intended hand movement, as suggested by Neggers and Bekkering (2000, 2001, 2002). In the studies of Neggers and Bekkering, as well as in ours, the subjects were given instructions about the eye movements that they had to make. In more natural tasks, without eye movement instructions, both types of behavior are found. In an experiment by Pelz, Hayhoe, and Loeber (2001), subjects had to pick up and position colored blocks to copy a given model consisting of similar blocks. They found that in certain cases the eyes kept gazing at the target location until the hand had reached it, whereas in other cases, gaze left the target location 100 to 150 ms before the hand had reached it. Johansson, Westling, Bäström, and Flanagan (2001) found that when grasping a small bar, subjects direct their gaze somewhere near the grasp site before starting the grasp, but often deviate their gaze from this position 163 ms before the hand contacts the bar. In our study, subjects had always been looking at the position that they were going to tap only about 500 ms before the tap (Figure 3a). Apparently, looking at the target of a hand movement shortly before the hand's arrival is not a necessity. Thus, the coordination between the eyes and the hand is task dependent.

In the above, we regarded the tapping errors as temporal errors. Can we disregard the possibility that purely spatial errors play a role? The analysis of the eye movements showed that subjects were not looking where they tapped. This might have influenced the errors, because pointing toward eccentric positions can lead to systematic errors. Bock (1986) found that subjects overestimate the retinal eccentricity of a target when asked to point at it with the unseen hand. Enright (1995) found that pointing movements toward targets that were presented eccentrically relative to the head ended at more eccentric positions when the subject kept fixating straight ahead than when the subject made a saccade toward the target position. This happened irrespective of whether the target was still visible when the saccade was made or not. Exactly the same was found by van Donkelaar and Staub (2000). Henriques, Klier, Smith, Lowy, and Crawford (1998) also found that subjects overestimate the eccentricity when pointing toward targets seen in the retinal periphery. The Henriques et al. (1998) study contained a condition in which the target was presented briefly at the fovea, after which the subjects made a saccade to some eccentric position and then pointed to the remembered position of the target. In that condition, they found the same amount of overestimation of the eccentricity as when the target was presented eccentrically. That condition is the most similar to ours because in our experiment the eyes were also directed at the target when it flashed and also moved away from the position of the target before the subjects pointed at it.

The results from the four studies discussed in the previous paragraph suggest that pointing movements toward a retinally eccentric position will reach a position that is too far from the gaze position. We see an opposite trend in our data. Thus, we cannot explain the errors by assuming that the retinal eccentricity at some moment after the flash is overestimated, because if so the tapping errors in Figure 5 should have pointed away from the gaze trace after the flash and not toward it. Thus, although such effects in pointing could introduce variability, and thus contribute to the smooth transition of the tapping error, they cannot explain the bias that we find. If we assume that our subjects also have this tendency to point too far in the retinal periphery, we have to explain an even larger effect.

To explain the bias in terms of retinal eccentricity alone, we would have to assume an influence opposite to that mentioned above, namely that subjects underestimate the eccentricity. Underestimation of retinal eccentricity has been proposed to account for the results of other studies (van der Heijden, van der Geest, de Leeuw, Krikke, & Müsseler, 1999; Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999; Kerzel, 2001). Such underestimation could account for the smooth transition in our data. However, the studies that proposed underestimation of the eccentricity were less similar to ours than the ones that found overestimation, because the tasks that they used were not pointing tasks. Thus, before such a mechanism can be considered to be an explanation, we would have to understand why subjects would underestimate eccentricity in this study, whereas they overestimated it in other studies in which subjects responded by pointing. Perhaps pointing is different during pursuit.

4.5 Conclusion

We cannot yet fully account for the time course of the errors, but our results clearly suggest that the mislocalization depends on the eye movement rather than the target movement, and on the movement after the flash rather than on the movement before the flash.

5

Flashes are localised as if they were moving with the eyes[4]

Gerben Rotman, Eli Brenner & Jeroen B. J. Smeets

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[4] This chapter has been published in Vision Research (2005) 45:355-364.

Abstract

Targets that are flashed during smooth pursuit are mislocalised in the direction of the pursuit. It has been suggested that a similar mislocalization of moving targets could help to overcome processing delays when hitting moving objects. But are moving targets really mislocalised in the way that flashed ones are? To find out we asked people to indicate where targets that were visible for different periods of time had appeared. The targets appeared while the subjects' eyes were moving, and were either moving with the eyes or static. For flashed targets we found the usual systematic mislocalization. For targets that moved with the eyes the mislocalization was at least as large, irrespective of the presentation time. For static targets the mislocalization decreased with increasing presentation time, so that by the time the presentations reached about 200 ms the targets were not mislocalised at all. A simple model that combines smooth retinal motion with information about the velocity of smooth pursuit could account for the measured tapping errors. These findings support the notion that the systematic mislocalization of flashed targets is related to the way in which people intercept moving objects.

5.1 Introduction

The mechanisms by which people intercept moving objects are still far from being fully understood. One problem is that people must somehow anticipate where they will make contact with the object before the object reaches that position. This is necessary because the object is moving while the information flows through the visual and motor pathways to guide the limb to the interception point. This means that one must predict the object's future position. Such a prediction is relatively straightforward if one knows the object's velocity and how long it will take to reach the object's path. However, Brouwer, Brenner and Smeets (2002) found that the perceived velocity of an object that one is trying to hit is not used to make such predictions. Nevertheless subjects can hit moving targets. Thus, they must account for the distance that the object moves as the hand approaches it without using the perceived velocity. This raises the question of how to predict the object's displacement during the final part of the action, when no on-line corrections are possible because of neuronal and muscular delays. When people are pursuing the object with their eyes, a way in which the object's displacement during this time interval could be predicted is by misperceiving the object's position in a velocity-dependent manner. Such mislocalization has often been reported (e.g. Hazelhoff & Wiersma, 1924).

The evidence that positions are mislocalised during pursuit comes from studies in which targets were flashed. Targets that are flashed during smooth pursuit are mislocalised in the direction of the pursuit (Hazelhoff & Wiersma, 1924; Mita, Hironaka & Koike, 1950; Mitrani, Dimitrov, Yakimoff & Mateeff, 1979; Mateeff, Yakimoff & Dimitrov, 1981; Mitrani & Dimitrov, 1982; Mateeff & Hohnsbein, 1989; van Beers, Wolpert & Haggard, 2001; Brenner, Smeets & van den Berg, 2001). The critical assumption in using this finding to explain how people intercept moving targets is that the same mechanism of mislocalization applies to moving targets that remain visible. The main reason to accept this assumption is that it would provide a functional explanation for the existence of such a systematic localization error within the visual system.

If all objects were mislocalised in the direction in which the eyes move, we would encounter problems in avoiding surrounding static objects whenever we move our eyes to pursue a moving object. To avoid such problems the mislocalization should only apply to the object that is moving. The information underlying the distinction between static and moving objects might be the motion in the retinal image. When the eyes move to pursue a target, that target's image is kept on the fovea, while most other objects' images move on the retina. Could the reason that flashed targets are mislocalised be related to the fact that their image does not move on the retina?

In order to test this hypothesis we examined whether “flashed” targets are mislocalised when their image does move on the retina. We presented targets for various time intervals. In order to be sure that the movement on the retina was critical, rather than the duration of presentation, we presented both static targets and ones that were moving with the pursuit disk. A complication that the longer presentation times introduce is that people may perceive the targets to be moving. We therefore asked our subjects to always indicate where the target first appeared. They indicated this position by tapping the screen.

5.2 Methods

5.2.1 Experimental set-up

Eight colleagues volunteered to take part in this study after being informed about what they would be required to do. Two of them were authors. The others were unaware of the hypothesis that was being tested. The research in this study is part of an ongoing research program that has been approved by the local ethics committee.

Stimuli were projected onto a large screen (120x158 cm) that was tilted 20° with respect to horizontal. A CRT projector with fast phosphors (Sony, VPH 1271QM, 800x600 pixels, 120 Hz) projected the stimuli via a mirror from the rear onto this screen. The 800x600 pixels covered an area of 110 by 85 cm. The projector received its input from an Apple Macintosh G4. The subject was standing in front of the screen (figure 1). The room was dimly lit so that the subjects could see the screen and their hands. The screen itself was white with little structure on it except for a few stains and some dust. The edges of the screen and other objects surrounding the screen were clearly visible.

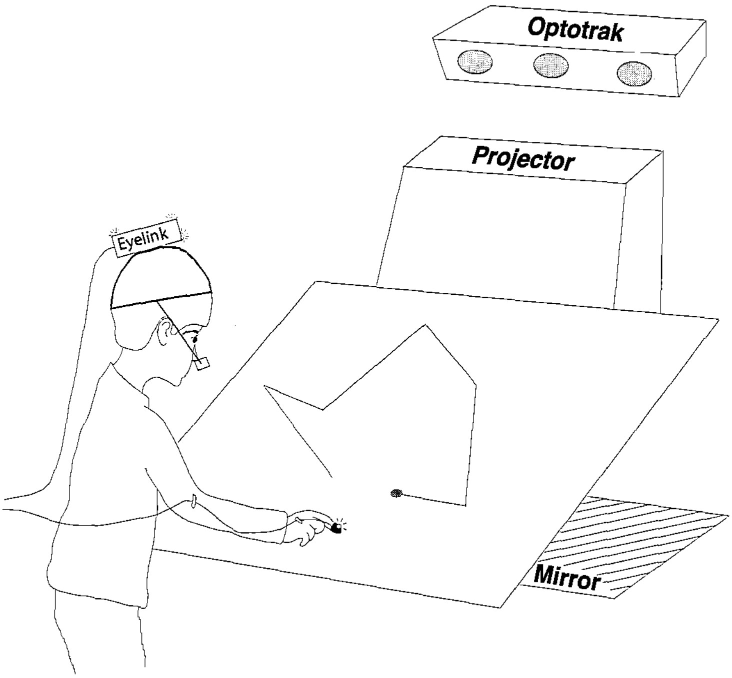

Figure 1: Schematic drawing of a subject performing the task. A moving pursuit disk is projected from the back onto the screen (via a mirror). An EyeLink measures the subject's eye movements. An Optotrak measures the subject's head movements and the position of the subject's finger. The grey disk in the drawing represents the red pursuit disk. The lines show part of the pursuit disk's path (subjects never saw these lines).

A red 15 mm diameter pursuit disk (2 cd/m^2) moved along a path of connected line segments. The subject was asked to pursue this disk with his eyes. At random moments a green disk was shown. The subjects were instructed to quickly tap the position of this green disk with their index finger. We call these green disks tapping targets. The average interval between two tapping targets was 4.5 seconds (the range was 2 to 9 seconds). The tapping targets were never presented close to the moment that the pursuit disk changed direction, or close to the edge of the screen. The duration of the line segments in which a tapping target was shown was chosen at random from between 800 and 1200 ms. The tapping target appeared after the pursuit disk had followed the line segment for a random interval between 300 and 500 ms. The direction in which the pursuit disk moved was chosen at random from all possible directions. The pursuit disk's velocity was chosen at random from between 16 and 32 cm/s. The pursuit disk's initial position on such segments was not constrained, but if the combination of the randomly drawn interval and direction would place the tapping target outside the central (84x41cm) part of the screen a new interval and direction were chosen at random. If necessary, this was repeated until an appropriate interval and direction were found.

The tapping targets were green 30 mm diameter disks (8 cd/m^2). They were presented for various durations: about 1, 43, 93 or 193 ms (1, 6, 12 or 24 frames at 120 Hz). When they were presented for more than one frame they were either stationary, so that they gave rise to movement of the retinal image, or moved with the pursuit disk, so that there would be little retinal movement if the gain of pursuit was close to one. In all cases the tapping targets were initially centred at the position of the pursuit disk, so that flashed targets and ones that moved with the pursuit disk looked like a bright green ring surrounding the red pursuit disk. The targets that were stationary were also initially centred at the position of the pursuit disk, but of course the pursuit disk moved away from this position. We instructed the subjects that if the tapping target moved they had to tap the position at which it first appeared. There were 15 tapping targets in each of the 7 categories. The experiment was divided into 5 blocks of trials that took about 1.5 minutes each, with a short break between the blocks. The tapping targets of each category were distributed evenly across the blocks.

5.2.2 Measurements

The position of the tip of the subject's right index finger was measured at 250 Hz by a movement analysis system (Optotrak 3020; Northern Digital) that tracked an infrared emitting diode (IRED) that was attached to the nail of the subject's index finger. On one of its analogue input channels the Optotrak measured the blue video signal from the computer. This was done in order to be able to synchronise the measured IRED positions with the moments that the tapping targets were visible: the tapping targets were drawn in green as well as in blue, but only the green output was connected to the projector.

Eye movements were measured with an EyeLink system (EyeLink I; SensoMotoric Instruments, Teltow, Germany). This is a fast video-based eye tracker with cameras attached to the subject's head with a headband (van der Geest & Frens 2002). In order to prevent the headband from slipping relative to the head we attached a bite board to the headband. Three IREDS were attached to the EyeLink's headband, so that we could measure the head's position and orientation in space using the Optotrak. This was needed to convert the EyeLink's (eye in head) data into gaze positions on the screen (i.e. to determine where the subject was looking).

The Eyelink provides information about the orientation of the eyes in the head. Since our subjects were free to move their heads this information has to be combined with measured head movements if we want to determine where the subject is looking (i.e. gaze position). In order to be able to do so a calibration procedure was conducted before each experiment. First, we determined the position of the eyes relative to the head (i.e. relative to the IREDS attached to the headset). We did this by asking the subjects to position their head so that they could look through three small tubes, first with their left eye and then with their right eye. We knew the position at which the lines through these tubes intersect, so the measured positions of the headband when subjects could see through all three tubes gives us the positions of the eyes relative to the headband. We next performed the Eyelink's standard 9-point calibration procedure, on a monitor that was part of the Eyelink system. After this calibration, the Eyelink gave us gaze positions on that monitor (assuming that the subject's head never moved). Since we knew where the monitor was during the calibration we could convert the output of the Eyelink into directions of gaze. With information about the position and orientation of the head, from the markers on the headband, and knowing where the screen is, the directions of gaze could be converted into positions on the screen. To confirm that these calculations revealed where the subject was looking, we presented a dot at the calculated position and asked the subjects to look around the screen while moving and turning their heads. All subjects reported that the dot remained near where they thought they were looking, but some reported a small systematic offset. We did not try to correct for such offsets because we were mainly interested in the direction and speed of the eye movements, rather than the precise direction of gaze, so small systematic offsets hardly matter.

To determine the temporal relationship between the EyeLink's measurements and those of the Optotrak we used a pulse generator. The pulses from the pulse generator were measured by one of the analogue input channels of the Optotrak and via the parallel port of the "operator PC" of the EyeLink system. The relative timing of these synchronisation signals was determined using a model eye: a cylinder with a hole (simulated pupil) in it. The model eye was connected to a potentiometer. Rotating the model eye (by hand) changed the voltage over the potentiometer. An analogue input channel of the Optotrak measured this voltage. At the same time, the EyeLink measured the changing position of the simulated pupil. The data measured by the EyeLink was shifted in time by various amounts and correlated with the data measured by the Optotrak. The shift of the EyeLink data that gave the highest correlation coefficient told us how to synchronise the measurements. We found that the data point at the moment of the pulse in the Optotrak file corresponded to the data point 5 ms after the pulse in the EyeLink data file.

5.2.3 Data analysis

We defined the tapped position as the first position after the start of the movement at which the IRED was less than 2 cm from the screen (the finger was almost touching the screen because the IRED was attached to the nail). In a few cases, no tapped position could be determined because the subject did not move (presumably because he did not notice the tapping target) or because the subject turned his hand so that the IRED on the finger could not be seen by the Optotrak. To quantify the mislocalization we calculated one-dimensional tapping errors: the distance along the direction of pursuit from the initial position of the tapping target to the position that was tapped. We divided this distance by the pursuit disk's velocity to express the tapping error in time units. The error in time units indicates how long it would take for the pursuit disk to move to the tapped position. This kind of mislocalization has generally been reported in time units. Originally, Hazelhoff and Wiersma (1924) did so because they assumed that the error reflected "perception time". Later this was done because most authors assumed that it has something to do with neural delays. Moreover, the error has been found to be less dependent on pursuit speed if it is expressed in time units (Mita, Hironaka & Koike, 1950). To check whether this is also the case in our experiment, we compared the slopes of the regression between the errors and the velocity of the pursuit disk when the errors are expressed in temporal units and when the errors are expressed in time units (all conditions were included in this analysis).

We determined the position of gaze on the screen for both the left and the right eye, and then averaged them. Occasionally the gaze position could not be determined, either because the subject turned his head so that the Optotrak could not see one of the IREDS on the headset, or because the EyeLink could not determine the eye orientation (presumably because the subject blinked). In both these cases the missing parts of the gaze path were not used in the analysis, but parts that were not missing were used.

In order to find out what kind of eye movements the subjects made we characterised the gaze movement that was made between 100 ms before and 500 ms after the onset of a tapping target. To get a measure of the direction and speed of the gaze movement, the gaze positions were convoluted with the first derivative of a normalised Gaussian, with a width of 8 ms. This gave us smoothed gaze velocity vectors. We used the length of these vectors to separate saccades from smooth pursuit.

We defined saccades as changes in gaze position that involve angular gaze velocities exceeding 40°/s (in any direction). If the period in which the angular eye velocity was above 40°/s was shorter than 3 samples (at 250 Hz) it was considered to be noise. If not, we added 8 ms of eye movement before and after the periods during which the angular velocity exceeded 40°/s to be sure to include the beginning and end of the saccade, and consider the total change in gaze during this period as the saccade. To calculate the mean smooth pursuit component of the eye movement at a certain moment (relative to tapping target onset) we averaged all remaining eye movements. For both saccades and smooth pursuit we report the component of the eye movement in the direction in which the pursuit disk moved.

5.3 Results

The tapped position could be determined for 98% of the tapping targets. On average, the finger tapped the screen 629 ms after the tapping target appeared. The average errors are shown in figure 2. When the tapping error was expressed in temporal units it did not depend significantly on the velocity of the pursuit disk for any of the subjects. On average, the tapping error decreased by 0.7 ± 1.3 ms (mean ± SE) for every cm/s increase in the velocity of the pursuit disk (mean slope of the regression described in the previous section; the decrease was not consistent across subjects t_7=0.5; p=0.62). When the tapping error was expressed in spatial units it depended significantly on the velocity of the pursuit disk for 4 of the 8 subjects ($p<0.05$). On average, the tapping error increased by 1.1 ± 0.3 ms for every cm/s increase in the velocity of the pursuit disk (the increase was consistent across subjects t_7=3.9; p=0.006). This justifies our choice to express the errors in time units.

The tapping target that was only visible for one millisecond was mislocalised by 175 ms in the direction of the pursuit. In spatial units this was 4.4 cm. The initial positions of the tapping targets that moved with the pursuit disk were mislocalised to about the same extent, except for the ones that were visible for a very long time (193 ms) which were mislocalised even further. The tapping targets that did not move with the pursuit disk were mislocalised less, especially if they were visible for a long period of time. The stationary tapping targets that were visible for 193 ms were not mislocalised at all.

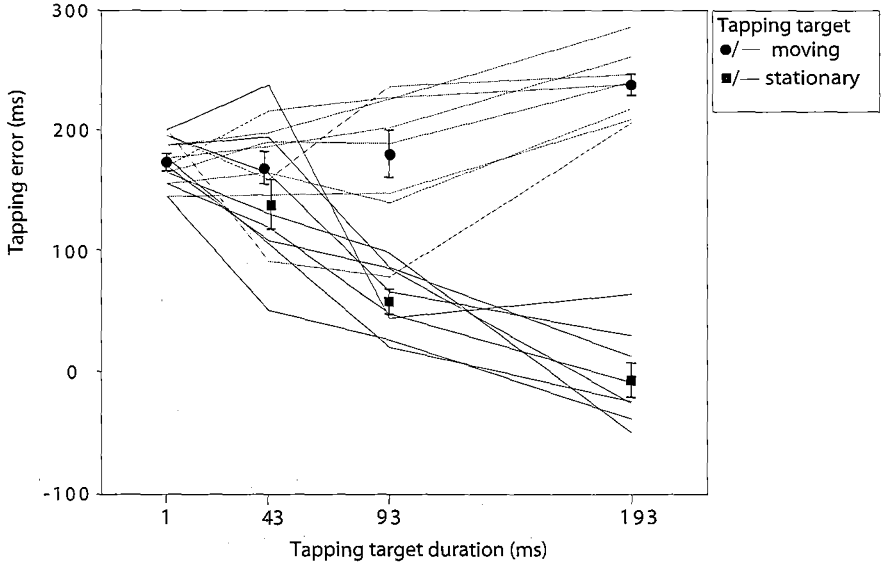

Figure 2: The tapping error as a function of the tapping target duration. The black symbols show the overall mean tapping error and the error bars indicate the between-subjects standard error. The thin lines connect the mean tapping errors of the individual subjects.

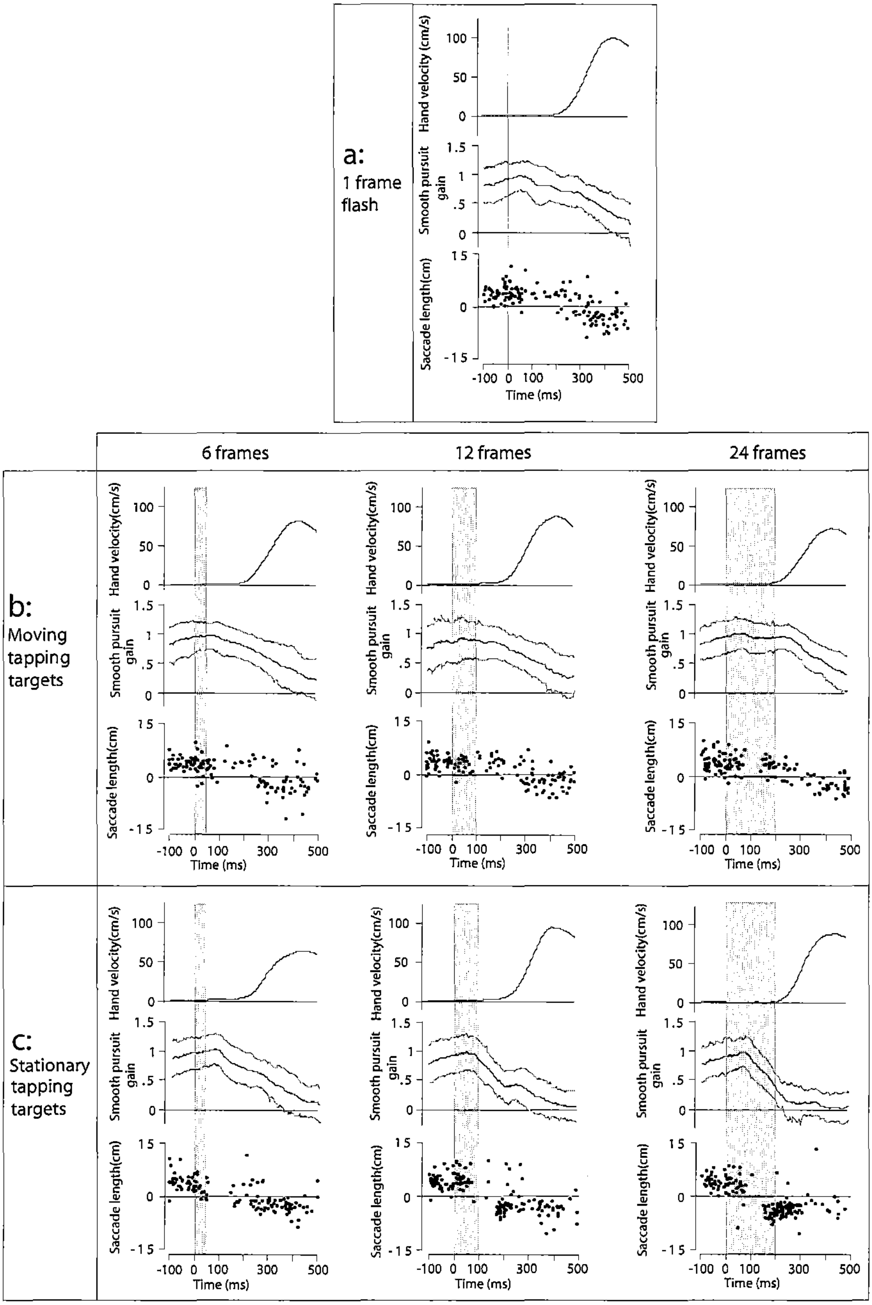

Figure 3: The hand velocity, the gain of smooth pursuit (black trace: average; grey traces: average plus or minus one standard deviation) and the lengths of the saccades, all as a function of the time relative to the moment that the tapping target appeared. The shaded area indicates the period when the tapping target was visible. Data for the 1 ms tapping targets (a), the tapping targets that were visible longer and were stationary (b), and the tapping targets that were visible longer and moved with the pursuit disk (c).

The eye movements that were made in the different conditions differed in several respects. The average pursuit gain is shown in the central parts of each panel in figure 3. The lengths of the components of the saccades that were in the direction of pursuit are shown in the lower parts of each panel in figure 3. The hand velocity (top part of each panel) is also shown to illustrate the relation between the eye movements and the hand movements. When the tapping target was stationary the smooth pursuit gain started to drop about 100 ms after the tapping target appeared. When the tapping target moved with the pursuit disk the pursuit gain remained high until after the tapping target disappeared.

Up to about 150 ms after the tapping target appeared most saccades were *forwards*, in the direction of pursuit (positive saccade lengths in bottom part of each panel in figure 3). These are presumably catch-up saccades that compensate for a too low gain of smooth pursuit. Their occurrence is independent of the duration of the flash (figure 4a). Most saccades that started later were *backwards*, in the opposite direction than pursuit, presumably redirecting gaze to the perceived position of the target in anticipation of the upcoming tap. The transition from *forward* to *backward* saccades occurred 100 ms later if the tapping target moved with the eyes. When the tapping targets were stationary, *backward* saccades appeared earlier and there were more of them (see figure 4b). The difference is particularly clear when comparing the two kinds of targets that were visible for 193 ms.

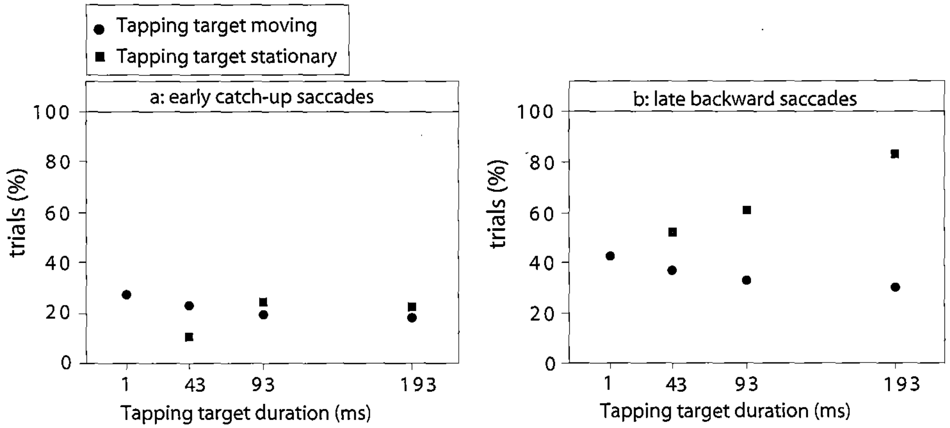

Figure 4: The percentage of trials in which a *catch-up* saccade started less than 152 ms after the onset of the tapping target (a) and the percentage of trials in which a *backward* saccade started between 152 and 500 ms after the onset of the tapping target (b), both as a function of the duration of the tapping target. 100 % corresponds to 120 trials.

Targets that are presented shortly in the temporal proximity of a saccade can be mislocalised in very complicated ways (for reviews see Schlag & Schlag-Rey (2002) or Ross, Morrone, Goldberg & Burr (2001)). To determine whether the tapping errors are specifically related to smooth pursuit, or whether pre-saccadic mislocalization is also important, we checked whether the *catch-up* saccades shortly after target onset influence the tapping errors. To do so we split the trials into ones with and ones without a *catch-up* saccade starting less than 152 ms after target onset (*catch-up* saccades started within this period in about 20% of the trials, see figure 4a). The presence of a *catch-up* saccade closely after target onset appears to have no influence on the errors (see figure 5a). Thus it appears that the errors are not influenced by saccades and do not depend on the total displacement of gaze after target onset. When a *catch-up* saccade was made the average displacement of gaze was 183% of the average displacement during this period when no *catch-up* saccade was made.

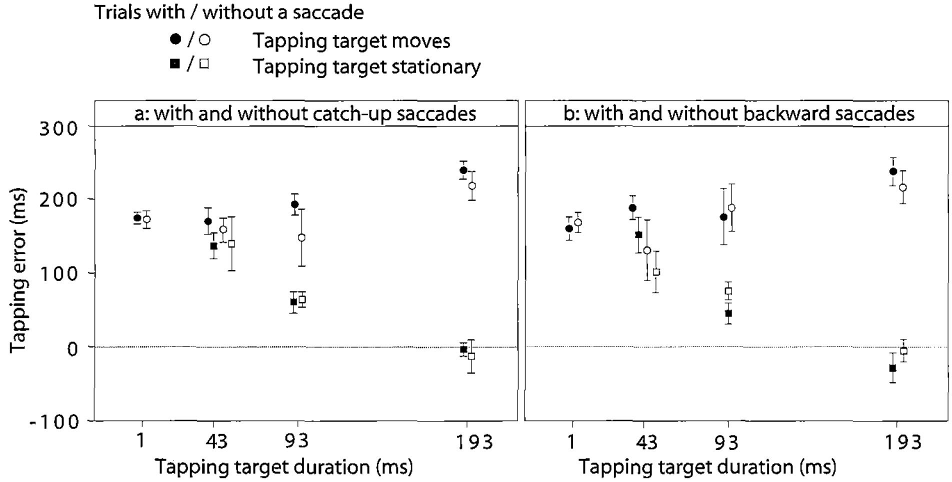

Figure 5: The tapping error as a function of tapping target duration, shown separately for trials with and without *catch-up* saccades that started less than 152 ms after target onset (a) and shown separately for trials with and without *backward* saccades that started between 152 ms and 500 ms after target onset (b). The error bars indicate the between-subjects standard error.

Comparing the percentage of *backward* saccades in figure 4b with the errors in figure 2 shows that the errors were smaller in the conditions in which the percentage of *backward* saccades was higher. One might therefore think that the presence of these *backward* saccades is responsible for the difference in the tapping errors. To examine this possibility we split the trials into ones with and ones without such saccades (between 152 ms and 500 ms after the onset of the tapping target). Figure 5b shows the tapping errors (as in figure 2) split by whether or not a *backward* saccade was made in that trial. Whether subjects made *backward* saccades appears to have no influence on the tapping error (see figure 5b). It also had no influence on the timing of the tap: the interval between the flash and the tap was not different when subjects made a *backward* saccade than when they did not (paired t-test: t_{49}=0.93, p=0.36).

5.4 Discussion

We confirmed that targets that are presented for short periods of time (i.e. *flashed*) during smooth pursuit are mislocalised in the direction of the eye movement. Moreover, we show that if the target is visible at a single position for a longer period of time, the amount of mislocalization is reduced. If the target is visible for the same period but moves with the pursuit disk, its initial position is mislocalised at least as much as flashed targets are. This shows that the reduced mislocalization is not caused directly by the duration of target presentation.

Asking subjects to localise moving targets always introduces complications, because it is difficult to separate timing errors from spatial errors. We asked subjects to indicate where the target appeared. A possible explanation for the difference between the responses to the moving and the static targets could be that subjects did not tap the initial position of the target. The reason for that might be that the lack of movement of the retinal image removed the sense that the position changed over time (Mack 1970), so that subjects judged the position at a later time than target onset. However even the most extreme possibility, that subjects tapped the position at which the targets disappeared, could not account for the difference between the mislocalization of the stationary and the moving targets (figure 6). To make the difference disappear we would need to assume that subjects judged positions beyond the position of target offset.

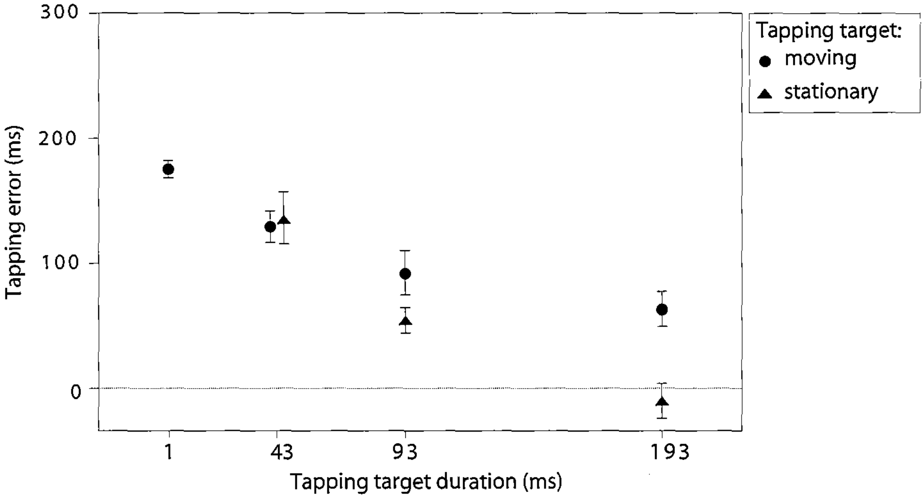

Figure 6: The tapping error when it is calculated relative to the final position of the tapping target as a function of the tapping target duration. The error bars indicate the between subjects standard error. Note that the task was to indicate the target's initial position. For stationary targets it makes no difference whether the error is calculated relative to the initial or the final position, but we reproduce the errors here for comparison.

In the introduction we predicted a difference in tapping error between static and moving targets on the basis of the proposal that targets are only mislocalised if no retinal motion is detected. In figure 2 one can see that for a 93 ms presentation of a stationary target subjects make an error that is about half of the magnitude of the error that is made when there is hardly any retinal motion (93 ms presentation of a moving target). This argues against our simple proposal, because we expect the retinal motion either to be detected or not. However, since this is an average value, it could be that the retinal motion is close to the threshold so that subjects sometimes do and sometimes do not detect it. If so, the distribution of errors for this condition should be bimodal. Figure 7 shows this not to be the case. Thus the dependence of the mislocalization on the retinal motion is unlikely to be a matter of detecting the presence or absence of motion.

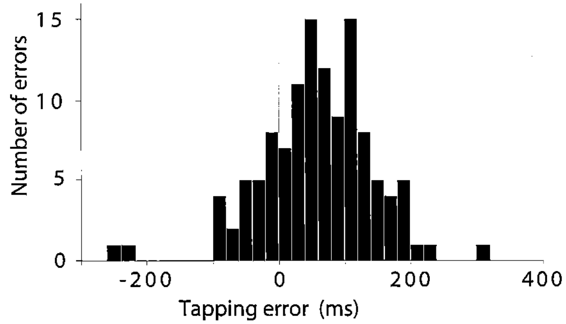

Figure 7: Histogram of tapping errors when tapping the position of a stationary target that was presented for 93 ms. The distribution is clearly unimodal (bin width: 20 ms).

Even when fixating a stationary point people can make systematic errors. These errors depend on the retinal eccentricity of the target's image. Both compression towards the fovea (Müsseler et al. 1999; van der Heijden et al. 1999) and expansion away from the fovea (Bock 1986; Enright 1994; Henriques, et al. 1998) have been found. Kerzel (2002) proposed that since the eyes move past the final position of a pursued target, compression towards the fovea might explain the forward mislocalization of the final position. In our experiment the eyes also moved on after target onset, and the retinal eccentricity of the position that had to be tapped changed differently in trials with than in trials without a backward saccade. However, in figure 5b we saw that it did not matter for the tapping error whether a *backward* saccade was made after target onset or not. From this we can conclude that the retinal eccentricity of the position that one is tapping (just before or at the moment of the tap) is irrelevant. As we saw in figure 5a, the presence of catch-up saccades shortly after target onset did not matter either. This suggests that the smooth pursuit component of the eye movement is critical for the localization error, rather than the total shift of gaze.

We rejected the proposal that the mislocalization depended on whether retinal motion was detected or not. Could the mislocalization depend on the retinal motion in a more complicated way? Our new proposal is that the perceived position depends on the sum of the pursuit signal and the retinal motion, integrated over some time. We reasoned that there is no need to explicitly detect whether targets are stationary, because stationary targets will yield retinal motion that exactly matches the pursuit signal but with an opposite sign. Integrating the retinal motion and the pursuit signal over time gives an estimate of the target's displacement over the integration period. This is very similar to using a velocity signal, and is therefore suitable for predicting future target positions.

This new hypothesis is qualitatively consistent with our results. Flashed targets and ones that are moving with the eyes produce little retinal motion. Consequently, their position is misperceived by an amount that depends on the speed of pursuit, because the pursuit signal is integrated over some time, and there is no retinal motion to cancel it. Stationary targets do produce retinal motion that counteracts the integrated pursuit signal, but this only cancels the integrated pursuit completely if the target remains visible during the whole integration time.

Quantitatively, this hypothesis predicts that the tapping error is the sum of the gaze displacement caused by pursuit and the displacement of the retinal image during some time interval. We tried to predict the tapping errors by integrating the sum of those two signals for different periods of time. Because we found that the errors did not depend on whether or not a saccade was made closely after target onset we assume that the error only depends on the smooth pursuit signal and on retinal motion when the eyes move smoothly. Thus, our model has two components the integrated smooth pursuit and the integrated smooth image movement. Both of these can be extracted from our data. We started the integration at the moment of target onset. It turned out that the error was predicted best if we integrated over 200 ms. The integration was done according to the following equation:

$$\text{error} = \int_{0}^{200} (G_p V_{pd} + V_r)\, dt$$

In this equation V_{pd} is the pursuit disk's velocity and G_p is the gain of smooth pursuit, so their product is the velocity of the smooth displacement of the gaze direction. V_r is the velocity of the target's image across the retina. Integrating these values gives the total smooth change in gaze and displacement of the retinal image during the 200 ms after target onset. The velocity of the retinal motion (V_r) is considered positive if the image moves in the direction in which the retina is moving, so that during pursuit it is negative for stationary targets (and the two components of the equation cancel each other). It is zero when no target is visible or when the retinal motion is extremely fast (i.e. during saccades).

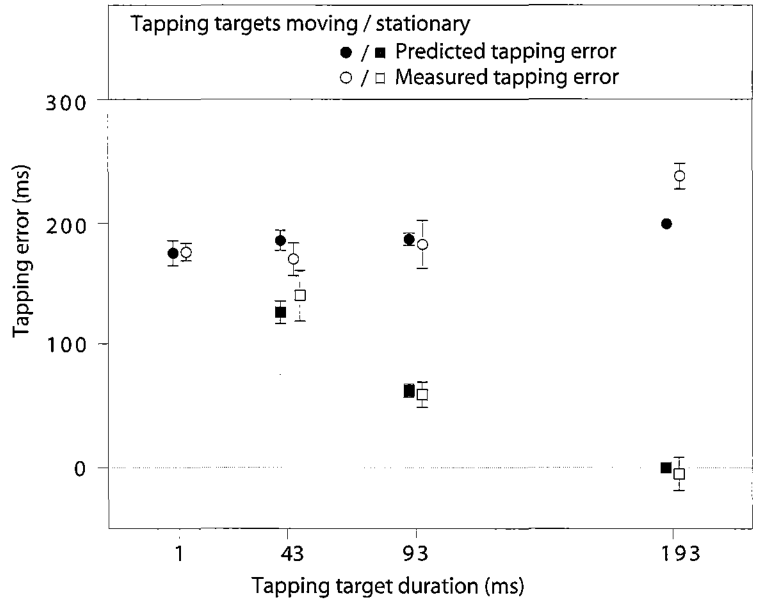

Figure 8: The tapping error as predicted by adding gaze displacement caused by smooth pursuit and smooth retinal motion for 200 ms after target onset. To make it easy to compare the prediction (solid symbols) with the measured errors, we reproduced the latter as open symbols (data from figure 2). The prediction was based on individual trials, so we can also give an error measure that is equivalent to that for the measured data.

This model is consistent with the measured errors (figure 8). Note that the model is not equivalent to saying that the subjects tapped where they were looking 200 ms after target onset. Firstly, the model does not consider saccadic eye movements, but only smooth eye movements. Secondly, in addition to the smooth *eye* movement, smooth *retinal* movement is also considered. The fact that a model that ignores saccadic eye movements reproduces the tapping errors so well suggests that the brain uses prior knowledge that objects in our surroundings never move at saccadic speeds. This is probably an essential part of predicting the target's future position on the basis of short periods of retinal motion and eye movements. It ensures that (catch up) saccades will not result in sudden perceived displacements, and eliminates the necessity to deal with the stringent temporal requirements, and the high retinal speeds, which would otherwise make it difficult to evaluate motion signals near the fast and abrupt changes that are characteristic of saccades.

The duration of 200 ms is longer than most of the times that were previously suggested. Early studies that measured the length of the error in time units called this the “perception time” (Hazelhoff & Wiersma 1924; Mita Hironaka & Koike 1950). Later studies suggested that the mislocalization was related to the way in which retinal information and information about eye orientation are combined (Mateeff, Yakimoff & Dimitrov 1981; Brenner, Smeets & van den Berg 2001), and examined factors that can influence the mislocalization (Mateeff & Hohnsbein 1989; Mitrani & Dimitrov 1982; Rotman, Brenner, Smeets 2002). Various factors can do so. The value of 200 ms in our model is not directly equivalent to the mislocalization in time units, because our model predicts less mislocalization if the eyes follow the target with a combination of smooth pursuit and catch-up saccades. However, it is not likely that there were many saccades in the mentioned studies, because the experimenters carefully tried to evoke smooth pursuit eye movements. Therefore, the value of 200 ms is probably not fixed, but depends on the experimental conditions.

Our main conclusion is that flashes are mislocalised because they produce no retinal motion. The evidence for this is that our subjects mislocalised the flashed targets in the same way as they did the other targets that produced no retinal motion: the moving targets. Stationary targets did produce retinal motion, and they were not mislocalised if they were present long enough. A simple model that combines the smooth retinal motion with a pursuit signal can account for the tapping errors quite well. According to the model these signals are integrated during a short interval (about 200ms) to predict the target's position a fixed time later. The model implies that *any* target that moves relative to oneself will be mislocalised in its direction of motion, because when a target moves there must be either a pursuit signal or retinal motion. When the subject does not pursue the target, there is retinal motion that will be integrated for 200 ms after target onset, and when the subject does pursue the target, there is a pursuit signal that will be integrated for 200 ms after target onset. The only instance in which the model predicts no mislocalization is when the target is stationary (and visible for longer than the integration period). In that case there is either no motion at all, or else the pursuit signal and the retinal motion are equal in magnitude and opposite in sign so that they cancel each other.

It has often been suggested that when the eyes are not moving, targets that are moving are judged to be further in the direction of their motion than they really are (giving rise to the flash-lag effect; Nijhawan 1994). The flash-lag effect has been shown to depend on the (retinal) motion after the flash (Brenner & Smeets 2000). The onset of motion is also often judged to have occurred further in the direction of motion than it really had (e.g. Fröhlich 1923). When targets are flashed during smooth pursuit they are generally mislocalised in the direction of pursuit. We here show that during pursuit, subjects misjudge the positions at which moving targets appeared in a similar manner. We propose that not only the initial position is misperceived, but that moving targets are constantly judged to be further along their path than they really are. This proposition is supported by the finding that the flash-lag effect disappears when the moving target is pursued (Nijhawan 2001). We propose that this is because the flash and the pursued target are then both mislocalised. Such localization errors could be useful, because the control of any fast action that is aimed at a moving target must include some mechanism for dealing with neuronal and muscular delays. The existence of such a mechanism presumably gives rise to the mislocalization of flashed targets that we (and others) have found. This would provide a functional significance for the mislocalization, which would explain why such a systematic error has not been corrected during evolution or during the individual's development.

6

Summary and conclusions

The experiments that are described in this thesis were designed to get more information on the spatial localization abilities of human subjects. Subjects had to indicate the position of visual targets. The targets were shown to them while their eyes were moving in order to pursue another target. It is not known how the human nervous system accomplishes such a task. The subjects make errors when performing this task. Many questions can be asked about what happens between the moment when the image of the target strikes the retina and the moment when the position where the nervous system located the target is indicated. We focussed on which information sources influence the error and on how the error depends on those information sources. We considered two sources of information as of key importance for localization: the retinal information and the information specifying the orientation of the eyes.

In all the studies that are described in this thesis a task was used in which the orientation of the eyes was changing constantly. This means that in order to determine the exact position where the target was presented, a registration of the position of the target's image on the retina has to be combined with the orientation of the eyes at the moment of that registration. If this is not the case the localized position will not be the same as the position where the target was presented. But do people locate visual targets at the exact position that the targets have when their image strikes the retina? When the target is presented for a long time and does not move they usually do, but when the target is presented briefly they often misjudge its position. We have assumed that the process of combining retinal information and eye orientation information is primarily responsible for these misjudgements. The results of the experiments that are reported in this thesis have made it more likely that this is indeed the case.

We have also tried to argue for a functional relevance of the misjudgements. It may seem counter intuitive that misjudgements can be functional. However, we did not try to argue that they are functional in this task. We argued that, although the judgements are wrong in respect to the task the subjects where asked to do, they may be suitable in more natural tasks. Presumably the misjudgements of flashed targets are the result of the fact that our localization abilities are not adapted to targets that are only visible for a short time. However, the misjudgements are the result of certain neural mechanisms, and these mechanisms presumably do have a function that in a more natural setting would be beneficial. The misjudgements can therefore be used to gain insight into these mechanisms. We proposed that the misjudgements are the result of mechanisms that are responsible for our ability to deal with moving objects, be it either to come in contact with the object as in intercepting or to avoid coming into contact with it. This is a very beneficial ability because whenever we move all the stationary objects in our surroundings move relative to us, and also during evolutionary history it has probably been very important to be able to intercept certain fast moving animals and to avoid others. The reasoning that has led us to this proposition is as follows. When an object moves relative to us, the position of the object at the time that its image strikes our retinas may not be the most useful information in order to successfully interact with it. It is more useful to locate a moving object at a position that it will have a little later. In particular, so much later that an action that is started in response to the retinal stimulation could have started. The located position might be the reference signal towards which (or away from which) a neural control system tries to move the body or a part thereof. Stated differently, the perceived position may be a specification of where the chosen action should be aimed at and not a measurement of the real physical position at the moment the light strikes the retina (Jordan 1999).

In the following previous work on mislocalization and the results of the experiments that are the topic of this thesis are summarized. After the summary more discussion of the results will follow.

6.1 Localization errors

A finding that motivated the studies that are reported in this thesis is that human subjects misjudge the position of targets that are flashed during pursuit eye movement (e.g. Hazelhoff & Wiersma 1924). These judgements are biased in the direction of the pursuit. Other kinds of mislocalization are the misjudgement of the position of a target that is flashed prior to a saccadic eye movement (e.g. Dassonville, Schlag & Schlag-Rey 1992) and the misjudgement of the relative positions of a flashed and a moving target while fixating (e.g. Nijhawan 1994), the latter is often called the flash-lag effect. The mislocalization during pursuit eye movements and the mislocalization of a target that is flashed prior to a saccade can both be explained by the hypothesis that retinal information is combined with eye orientation information that concerns actual eye orientation somewhat later. The flash-lag effect cannot be explained in this way because the eyes do not move.

In relation to our ability to interact with moving objects, the mislocalization during smooth pursuit is probably most relevant, because when we intend to interact with something we look at it (Pelz, Hayhoe & Loeber 2001). This means that when the object moves, our eyes will have to pursue the object. Oudejans, Michaels, Bakker and Davids (1999) showed that we pursue a moving ball when we try to catch it. It also means that when we move and want and interact with some stationary object we will have to pursue the stationary object. Land and Hayhoe (2001) showed that when walking towards a teakettle, that will be picked up in order to transport it to the sink where it will be filled with water, we will fixate the kettle when walking towards it. As far as we know there are no reports in the literature of people fixating some other stationary object when trying to intercept a moving object. Of course in real life situations you often have to deal with multiple objects. For example, you may run to intercept something while at the same time you must take care not to bump into obstacles. In such a case you will probably look intermittently at one and the other. Moreover, you will probably not have to deal with both at exactly the same time (i.e. you will first encounter the obstacle and then the object you want to intercept), so that you can pursue each at the time that that it is most relevant. Nonetheless, the results of tasks in which subjects are required to localise moving targets when they are instructed not to pursue the targets (as in flash-lag studies) may say something about the underlying mechanisms that would allow us to accurately intercept the targets if we were allowed to pursue them. We will come back to this in the general discussion and remarks (section 6.3).

Because the experiments reported in this thesis were all concerned with the localization of targets that were flashed during pursuit eye movement we will now briefly summarise previous results of mislocalization during pursuit eye movement. All the studies reported a systematic bias in the direction of the pursuit movement, this bias will be called: localization bias.

Early studies suggested that the localization bias corresponds to the amount of time needed for the flash to be perceived (Hazelhoff & Wiersma 1924; Mita, Hironaka & Koike 1950), they called this "perception-time". Mateeff, Yakimoff and Dimitrov (1981) criticised the idea of perception-time and claimed that there should also be a "time" for an eye orientation signal, in addition to the time for the retinal signal (i.e. perception time). Brenner, Smeets and van den Berg (2001) suggested that the eye orientation information that is used is the commanded eye orientation. This could account for the bias being forwards (i.e. in the direction in which the eye was commanded to go). The localization bias appears to depend on many factors. Mitrani and Dimitrov (1982) and van Beers, Wolpert and Haggard (2001) found that flashes in front of the pursuit target are misjudged more than those on or those behind the pursuit target are. The localization bias can be reduced by the availability of visual references (Mateeff & Hohnsbein 1989; Brenner, Smeets & van den Berg 2001). In two studies in which a visible ruler was shown along the path of pursuit the errors depended systematically on the position along the ruler at which the target was flashed (Mitrani, Dimitrov, Yakimoff & Mateeff 1979; Mateeff, Yakimoff & Dimitrov 1981). It is not clear what the critical variables resulting in these responses were.

6.2 Experiments in this thesis

6.2.1 Chapter two

In the experiment that is described in chapter two we investigated whether making the appearance of the flashed target more predictable could reduce the localization bias. This was motivated by the findings of Mitrani, Dimitrov, Yakimoff & Mateeff (1979) and of Mateeff, Yakimoff & Dimitrov (1981). They found that the localization bias was smaller in certain situations, but it was not clear what aspects of those situations were critical. The authors suggested that the predictability of target appearance might have influenced the localization bias. We therefore tried whether different forms of predictability would influence the localization bias. We used stimuli in which different kinds of predictions were possible. We found that some of our manipulations influenced the subject's settings considerably. We did not interpret this as an effect of predictability but as an effect of the target appearing at a spatially cued position. We concluded that a spatial cue can reduce the mislocalization of targets that are flashed during pursuit eye movements. The cue does not have to be exactly at the same position as the flash.

6.2.2 Chapter three

The study described in chapter three compares different ways of indicating the location of the target. There is only one study (Hansen 1979) that we know of in which subjects were not biased in their localization of a target that was flashed during pursuit eye movement. An obvious difference between that study and the others was the way of indicating the position of the flashed targets. In Hansen's study the subjects were instructed to strike the targets with a quick hammer blow. In the other studies the subjects responded by indicting the position of the target in much slower ways. We examined whether the difference between Hansen's result and the results of the others was because of the quick motor response as opposed to the much slower ways of responding in the other studies. Because of the way of responding these studies are often called perceptual judgement studies. We reasoned that perhaps there is a fundamental difference between the information that determines our perceptual judgements of a target's position and the information that is used to guide our hand to a similar target. In order to see whether the quick motor response versus the slow judgements was critical, we instructed our subjects to quickly tap the targets with their index finger. We found that they systematically tapped ahead of the position of the flash, in similar ways as in the perceptual judgement tasks. We concluded that the lack of systematic errors in Hansen's study is not due to a general property of fast motor responses.

6.2.3 Chapter four

The study described in chapter four was aimed at making clear which movement was critical for the localization bias. In previous studies the movement of the eyes and the pursuit disk was very similar, and also the movement before the flash was very similar to that after the flash. Therefore it was neither clear whether it is the movement of the eyes or the movement of the pursuit target that matters nor was it clear whether the movement after the flash or the movement before the flash mattered. In order to resolve these issues we asked subjects to pursue a disk that regularly changed its movement direction. Each change was followed by a change in the direction of gaze movement. Subjects were asked to tap targets that were flashed close to the moment at which the pursuit disk changed direction. We compared the direction of the mislocalization with the changes in gaze and in target position during different intervals relative to the flash. We found that the movement of the eyes after the flash is critical. It was also interesting to see that the subjects did not make saccades to the position they tapped but kept pursuing the disk.

6.2.4 Chapter five

In the study described in chapter five we investigated whether flashing the target (i.e. having it visible very short) was crucial for the localization bias. The study was motivated by the suggestion that a localization bias of moving targets, similar to that of the flashes, could help to overcome neural and muscular delays when intercepting moving objects. We examined whether moving targets and flashed ones are indeed mislocalised in a similar way. We did this by asking people to indicate where targets that were visible for different periods of time had appeared. The targets appeared while the subjects' eyes were moving, and they were either moving with the eyes or stationary. We found the usual systematic mislocalization of flashed targets and a similar mislocalization for targets that moved with the eyes. Stationary targets that were visible for 200 ms were not mislocalised. These findings support the notion that the systematic mislocalization of flashed targets is related to our ability to intercept moving objects. A simple model that combines smooth retinal and extra-retinal motion can explain the errors.

6.2.5 Conclusions of the experiments in this thesis

- A spatial cue can reduce the mislocalization of a target that is flashed during pursuit eye movements. The cue does not have to be exactly at the same position as the flash. (chapter 2)
- The systematic mislocalization of targets flashed during pursuit eye movement as found in many perceptual experiments, is also evident in a fast motor response. (chapter 3)
- The systematic mislocalization of targets flashed during pursuit eye movement is related to the movement of the eyes, rather than to the movement of the pursued target, and rather to the movement after the flash than to that before the flash. (chapter 4)
- During a hand movement a human subject may look at other positions than the position that is the goal of the hand movement. (chapter 4)
- Targets that are flashed during pursuit eye movement are localised as if they were moving with the eyes. The position of targets that are moving with the eyes is systematically mislocalised in the direction of the movement. (chapter 5)
- Saccades made during the pursuit do not influence the localization bias. (chapter 5)

6.3 General conclusions and remarks

Our results confirm that during pursuit eye movement human subjects systematically mislocalise flashed targets in the direction of the pursuit movement. We also showed that during the pursuit the position of a target that is moving with the pursued target is mislocalised in a similar way (at least their start position is). Our results are the first to show that these mislocalizations do influence fast motor responses. These findings support the notion that the mislocalization might be the result of mechanisms that are responsible for our ability to intercept moving objects. This possibility has recently also been suggested by others (Kerzel & Gegenfurtner 2003; Ashida 2004).

We have presented a model of how the mislocalization could arise by using the information that is available to the nervous system. Two information sources would be used. One information source is concerned with the orientation of the eyes. This information could be obtained from either an efferent copy of the motor commands for the extra-ocular muscles or from afferent information from muscle spindles and/or Golgi tendon organs in the extra ocular muscles and associated tendons. The second information source is the movement of the target's retinal image. This information can only be obtained from the afferent information coming from the retina. The way in which the information from these two sources is combined will have consequences for the position at which objects are located. Therefore, looking at the way in which the nervous system locates targets allows us to propose how the nervous system combines eye orientation information with retinal information. Obviously a proposal will be stronger if it is not only in agreement with the results on which the model is based but also with other findings. Furthermore, a proposal about information processing in a living organism will also be supported by arguments that argue for adaptive advantages of processing the information like it is proposed. Therefore, in the following sections we will discuss how our findings and the model that we proposed to explain these findings relate to other kinds of mislocalization and finally how such mislocalization could be useful when dealing with moving objects.

6.3.1 Relation with pre-saccadic mislocalization

Pre-saccadic mislocalization refers to the finding that subjects mislocalize a target that is flashed shortly before a saccade. They mislocalize such targets in the direction of the saccade (e.g. Dassonville, Schlag & Schlag-Rey 1992). This mislocalization can be explained by assuming that the retinal information concerning the position of the flash is combined with information concerning the eye orientation some time after the flash, when the eyes have moved in the direction of the saccade. This information can already be there when the flash is presented in the form of a motor command that is to be send to the extra ocular muscles in order to make the saccade. As described in chapter four we found that the mislocalization of flashes presented during smooth pursuit eye movement depends on information about eye orientation some time after the flash. Therefore both these findings can be explained by the assumption that the eye orientation information that is used for localization is efferent in origin. However, we found in chapter five that during smooth pursuit eye movement the mislocalization is not influenced by saccades that are made during the pursuit. We have argued there that only the smooth component of the pursuit contributes to the mislocalization. This seems to indicate that, although in both cases efferent information is probably used, the sources of this efferent information are different. When engaged in smooth pursuit the eye orientation information comes purely from the pursuit system while during fixation it comes from the saccade system or from a higher level closer to the motor units that drive the eyes. It is well known that the pursuit system and the saccade system are separated systems. Although they do overlap to some extent (Krauslitz 2004), it would certainly be possible to tap into the system to get either pure saccade related information or pure smooth pursuit related information. The reason that during pursuit the saccadic signals do not influence the mislocalization may be as follows. During pursuit a combination of the efferent pursuit signal and retinal information gives an accurate prediction of where the target is. This prediction is the signal that is used for any goal directed movement towards the target, be it an interceptive hand movement or a saccade. Moreover, the pursuit information is related to the pursued object's movement, while the saccadic information is not related to object movement but is presumably only used to replace the retinal information to a position (i.e. the fovea) where it can be tracked more accurately.

6.3.2 Relation with the flash-lag effect

The flash-lag effect refers to the finding that subjects misjudge the relative position of the flashed and the moving target. The mislocalization is consistent with the moving target being shifted in its direction of motion (e.g. Nijhawan 1994). The major difference between the flash-lag effect and the mislocalization during smooth pursuit is that in flash-lag studies the eyes do not move. While the mislocalization during smooth pursuit depends on both the retinal information and the eye orientation information, the flash-lag effect depends only on the retinal information. Like the mislocalization during smooth pursuit the flash-lag effect depends on information from after the flash. Difference authors have reported that the flash-lag effect depends on the direction of the moving target after the flash (Eagleman & Sejnowski 2000; Whitney, Murakami & Cavanagh 2000) and that it depends on the speed after the flash (Brenner & Smeets 2000; Whitney, Murakami & Cavanagh 2000). The model that we proposed in chapter 5 to account for the mislocalization during smooth pursuit also uses retinal information from after the flash. Our model can therefore also account for the flash-lag effect. In the model (efferent) eye orientation information is combined with retinal information from just after the flash. In a flash-lag study the eyes do not move, so the eye orientation information does not change. Therefore, using eye orientation information that corresponds to the actual eye orientation somewhat later does not lead to any error, it specifies the same position all the time. The retinal position of the flash does not change either. However, the retinal position of the moving target does change, so our model that samples this information after the flash and combines it with the non-changing eye orientation information will predict a mismatch between the flashed target and the moving target, exactly as is found in the flash-lag studies. Namely a mismatch that is consistent with the moving target being shifted forwards along its path of motion. Moreover, the proposal that retinal information is sampled after the flash onset is also sufficient to explain the "lag" of other attributes of the retinal image that are constantly changing, like colour (Seth, Nijhawan & Shimojo 2000). Murakami (2001) has shown that the results of almost all the previous flash-lag studies can be explained by averaging the moving target's position for some time after the flash. The time over which it needs to be averaged is however shorter than the time over which we had to average to explain the mislocalization during smooth pursuit.

Nijhawan (2001) did a variation on the flash-lag paradigm in which he instructed his subjects to pursue the moving target and found that this eliminated the flash-lag effect (i.e. the relative position of the flash and the moving target were judged correctly). Our model also predicts this. In this case the retinal position of neither the flash nor the moving target changes, so sampling the moving target's retinal position after the flash does not lead to any mismatch. Nonetheless, the use of eye orientation information corresponding to the actual eye orientation somewhat later will lead to a forward mislocalization of both the flashed and the moving target, which accounts for the usual localization error of flashes during smooth pursuit. This finding also supports the notion that the pursued object is mislocalised to a similar extent as the flash.

6.3.3 Relation with mislocalization of eccentric targets

Several studies have shown that targets that are presented at eccentric positions (i.e. at some distance from the fixation point) are mislocalized. This happens even when there is neither movement of the eyes nor any movement in the retinal image. When subjects were asked to point to targets that were briefly flashed at eccentric positions during steady fixation they pointed too far in the periphery (Bock 1986; Enright 1994; Henriques et al. 1998). During smooth pursuit there is also an effect of eccentric presentation. Targets that are presented ahead of the pursuit target are mislocalized more than targets that are presented behind the pursuit target. This happens irrespective of whether the target is indicated immediately when it is seen (chapter 3) or whether the position of the target is indicated later after the pursuit movement (Mitrani & Dimitrov 1982; van Beers et al. 2001). This effect of eccentric presentation during smooth pursuit is consistent with the overestimation of retinal eccentricity during fixation. When the flash is presented ahead of a pursued target the forward mislocalization due to the pursuit eye movement is in the same direction as the mislocalization due to an overestimation of eccentricity. For a target that is presented behind a pursued target, the overestimation of eccentricity will be against the direction of the forward mislocalization due to the pursuit eye movement. Combining the mislocalization due to the pursuit eye movement with the mislocalization due to the eccentricity of target presentation, would therefore lead to a larger mislocalization of targets that are presented ahead of a pursued target and to a smaller mislocalization of targets presented behind a pursued target. However, in one of the experiments described in chapter three the differences in the localization bias between targets at different eccentricity along the path of pursuit were too large to be explained in this way. The localization biases in the second experiment described in chapter three could be explained like that. It is therefore not clear whether the mislocalization of eccentrically flashed targets and that of targets flashed during smooth pursuit are two totally independent effects. Moreover, there have also been reports of underestimation of eccentrically presented targets during fixation (van der Heijden et al. 1999; Müsseler et al. 1999). A presumably important difference of these studies with the studies that found overestimation of eccentricity is the way in which subjects reported the positions of the targets. In the studies that found overestimation of eccentricity the subjects pointed to the perceived position, while in the others the subjects had to compare different structures in the retinal periphery.

6.3.4 Relation with interception

When a target is flashed or when subjects are asked to indicate the position where a moving target started to move it appears they make mistakes and do not indicate the right position. How could these mistakes result from a mechanism that is responsible for intercepting moving targets? The reason can be very simple: if you have to intercept a moving target you should not move your hand to the position that the target has when you decide to start the interception movement but rather to the position that the target has when you end the interception movement. The biases presumably show us that the nervous system locates moving targets at a position that is useful. The explanation for the subjects mislocalising a *flashed* target would be that they treat a flashed target in the same way as they treat a moving target, which is what they do as we showed in chapter 5. Flashed targets are probably treated like moving targets because they do not produce movement in the retinal image (like moving targets), while the image of a target that is not moving should move over the retina. In case of a flash and in case of a target that is pursued there will be no movement of the target's retinal image, and the mislocalization will only depend on the eye movement information. The image of a stationary target will move over the retina and the information about its retinal image's movement will counteract the information about the eye movement, and therefore such targets will not be mislocalised. We showed in chapter five that a combination of these two information sources could explain our subjects' mislocalization of moving and flashed targets, as well as their accurate localization of stationary targets. It may seem problematic that this model requires retinal image movement from after target onset. However, this would be no problem for a mechanism that exists to support our ability to intercept moving objects. We need to see some movement before we can use it to predict what will be a good position to intercept the object at. There is always a certain reaction time before a human subject starts a movement in order to hit a moving target, the sampling of some retinal movement may be what happens during the first period of the reaction time.

The model also explains why we can interact with moving objects without using the perceived velocity (Brouwer, Brenner & Smeets 2002). Our model does not use the perceived velocity to determine a suitable interception point. The model is only concerned with the perceived position and simply implies that a moving target is located at a position that already predicts a future position of the pursued target. It is easy to understand that this would be a better solution than using the perceived velocity in order to predict a future target position, because the perceived velocity depends strongly on movement of the background (known as the Duncker illusion). Directly using the perceived velocity would therefore make accurate interaction with moving objects impossible in many situations. Comparing our model with other models of interception is not straightforward. As described in the introduction, most other models focus on the temporal aspects of the interception, and try to find variables that are used to control the timing. They are not concerned with how the interception point is determined. Our model is specifically concerned with the localization. It combines temporal and spatial aspects of interception by having the localized position always specify the (predicted) actual position a little later, which makes this located position a useful control signal.

6

Samenvatting en conclusies

De experimenten die in dit proefschrift beschreven zijn zijn ontworpen om meer inzicht te geven in de lokalisatie capaciteiten van mensen. Proefpersonen werden gevraagd om de positie van visuele doelen aan te geven. Deze doelen werden getoond terwijl hun ogen bewogen om een ander doel te volgen. Het is niet bekend hoe het menselijk zenuwstelsel zo'n taak volbrengt. Proefpersonen maken fouten als ze deze taak uitvoeren. Vele vragen kunnen gesteld worden over wat er gebeurd tussen het moment dat het beeld van het doel op de retina (het netvlies) valt en het moment waarop de positie waar het zenuwstelsel het doel gelokaliseerd heeft aangegeven wordt. Wij hebben ons gericht op de vraag welke informatiebronnen de fouten beïnvloeden en hoe de fouten van deze informatiebronnen afhangen. We hebben aangenomen dat twee informatiebronnen van primair belang waren: de retinale informatie and the informatie betreffende de oriëntatie van de ogen.

In alle studies die beschreven zijn in dit proefschrift is een taak gebruikt waarin de oriëntatie van de ogen constant veranderde. Dit betekent dat om de exacte positie van het doel te bepalen een registratie van de positie van het beeld van het doel op de retina gecombineerd moet worden met de oriëntatie van de ogen op het moment van die registratie. Als dit niet gebeurd zal de gelokaliseerde positie niet dezelfde zijn als de positie waar het doel gepresenteerd werd. Maar lokaliseren mensen de positie van een visueel doel wel precies op de plek waar het gepresenteerd werd? Als het doel lang genoeg gepresenteerd wordt en niet beweegt dan doen ze dat normaal gesproken wel, maar als het doel erg kort gepresenteerd wordt beoordelen ze de positie vaak fout. Wij hebben aangenomen dat voornamelijk het combineren van de retinale informatie met informatie over de oriëntatie van de ogen hiervoor verantwoordelijk is. De resultaten van de experimenten beschreven in dit proefschrift hebben het waarschijnlijker gemaakt dat dit inderdaad het geval is.

We hebben ook geprobeerd om te beargumenteren dat de mislokalisatie een functie zou kunnen hebben. Het lijkt misschien vreemd dat mislokalisatie nuttig kan zijn. Echter, we hebben niet geprobeerd te beargumenteren dat ze nuttig waren in deze taak. We hebben beargumenteerd dat, alhoewel het fouten zijn met betrekking tot deze taak, ze toch passend zouden kunnen zijn in een meer natuurlijkere taak. Waarschijnlijk is de mislokalisatie van geflitste doelen het gevolg van het feit dat onze lokalisatie capaciteiten niet aangepast zijn aan het lokaliseren van doelen die slechts kort zichtbaar zijn. Echter, de mislokalisaties zijn het gevolg van bepaalde neurale mechanismen en deze mechanismen hebben vermoedelijk een functie die in een meer natuurlijke situatie nuttig zou zijn. De lokalisatiefouten kunnen daarom gebruikt worden om inzicht te krijgen in deze mechanismen. Wij hebben voorgesteld dat de lokalisatiefouten het gevolg zijn van mechanismen die verantwoordelijk zijn voor onze capaciteiten om met bewegende doelen om te gaan, zij het om in contact te komen met een bewegend doel, bijvoorbeeld om het te onderscheppen, of om een bewegend doel te vermijden. Het is erg belangrijk en nuttig om dit te kunnen omdat elke keer dat wijzelf bewegen alle objecten in onze omgeving relatief ten opzichte van onszelf bewegen. Bovendien is het gedurende de evolutionaire geschiedenis waarschijnlijk erg belangrijk geweest om in staat te zijn bepaalde snel bewegende dieren te kunnen vangen en andere te ontwijken. De redenering die ons tot dit voorstel bracht is als volgt. Als een object beweegt is de positie op het moment dat het beeld van het object de retina bereikt niet de meest nuttige informatie om een succesvolle interactie met het object aan te gaan. Het is nuttiger om het object te lokaliseren op een positie die het net iets later zal hebben. En wel zoveel later dat een actie die is gestart als reactie op de retinale stimulatie gestart zou kunnen zijn. De gelokaliseerde positie zou een controle signaal kunnen zijn waar naar toe (of waar van af) een neuraal controle systeem het lichaam of een deel daarvan probeert te sturen. Anders verwoord, de waargenomen positie zou een positie kunnen zijn waarop de gekozen actie gericht dient te worden en niet een registratie van de werkelijke fysieke positie op het moment dat het licht op de retina valt (Jordan 1999).

In het nu volgende zal eerder werk betreffende mislokalisatie en de resultaten van de experimenten die het onderwerp van dit proefschrift vormen samengevat worden. Na de samenvatting zal verdere discussie van de resultaten volgen.

6.1 Lokalisatiefouten

De studies die beschreven zijn in dit proefschrift werden gemotiveerd door de bevinding dat mensen de positie van een doel dat geflitst wordt tijdens volgbewegingen van de ogen mislokaliseren (Hazelhoff & Wiersma 1924). Ze mislokaliseren de doelen in de richting van de volgbeweging. Andere vormen van mislokalisatie zijn de mislokalisatie van doelen die geflitst worden vlak voor een saccade (bijv. Dassonville, Schlag & Schlag-Rey 1992) en de mislokalisatie van de relatieve posities van een geflitst en een bewegend doel tijdens fixatie (bijv. Nijhawan 1994). De laatstgenoemde vorm van mislokalisatie wordt vaak het "flash-lag" effect genoemd. De mislokalisatie tijdens volgbewegingen van de ogen en de mislokalisatie van een doel dat vlak voor een saccade geflitst wordt kunnen beide verklaard worden door de hypothese dat retinale informatie gecombineerd wordt met oogoriëntatie informatie die overeen komt met de werkelijke oogoriëntatie net iets later. Het flash-lag effect kan niet op deze wijze verklaard worden omdat de ogen in dat geval niet bewegen.

In relatie met onze capaciteiten om met bewegende doelen om te gaan is de mislokalisatie tijdens volgbewegingen van de ogen het meest relevant, want als we van plan zijn iets met een object te doen dan kijken we ernaar (Peltz, Hayhoe & Loeber 2001). Dit betekent dat we het object met onze ogen moeten volgen als het beweegt. Oudejans, Michaels en Bakker (1999) hebben aangetoond dat we een bal volgen met onze ogen als we het proberen te vangen. Het betekent ook dat wanneer we zelf bewegen en iets willen doen met een stilstaand object dat we dat dan met onze ogen moeten volgen. Land en Hayhoe (2001) hebben aangetoond dat wanneer we op een ketel af lopen om die op te pakken en te vullen met water dat we dan de ketel blijven fixeren. Voor zover wij weten zijn er geen verslagen in de literatuur die aangeven dat mensen een ander stilstaand object fixeren wanneer ze een bewegend object proberen te onderscheppen. In het dagelijks leven hebben we natuurlijk vaak te maken met meerdere objecten. Bijvoorbeeld als je rent om iets te onderscheppen moet je opletten om niet op obstakels te botsen. In zo'n geval zul je waarschijnlijk afwisselend van het ene naar het andere object kijken. Bovendien zul je waarschijnlijk niet op hetzelfde moment met beide rekening hoeven te houden (je komt het obstakel eerst tegen en pas later het doel), zodat je elk object kunt volgen wanneer dat object het meest relevant is. Niettemin, kunnen de resultaten van studies waarin proefpersonen doelen moesten lokaliseren terwijl hun ogen niet bewogen (zoals flash-lag studies) wel wat zeggen over de mechanismen die ons in staat stellen om accuraat objecten te onderscheppen wanneer we de doelen wel zouden volgen. We komen hierop terug in de algemene discussie en opmerkingen (sectie 6.3).

Omdat de experimenten die beschreven zijn in dit proefschrift allemaal te maken hebben met het lokaliseren van geflitste doelen tijdens volgbewegingen van de ogen zullen we nu eerst kort samenvatten wat er eerder gevonden is met betrekking tot mislokalisatie tijdens volgbewegingen van de ogen. Alle eerdere studies vonden een systematische fout in het lokaliseren in de richting van de volgbeweging. Deze lokalisatie fout tijdens volgbewegingen van de ogen wordt vanaf nu simpelweg lokalisatie fout genoemd.

Vroege studies suggereerden dat de lokalisatie fout overeen kwam met de tijd die nodig was om het geflitste doel waar te nemen (Hazelhoff & Wiersma 1924; Mita, Hironaka & Koike 1950), men noemde het de “waarnemingstijd”. Mateeff, Yakimoff en Dimitrov (1981) bekritiseerden het idee van de waarnemingstijd en stelden dat er ook tijd nodig was voor het gebruik van een oogoriëntatie signaal, naast een tijd voor het retinale signaal (de waarnemingstijd). Brenner, Smeets en van den Berg (2001) suggereerden dat de oogoriëntatie informatie die gebruikt wordt het stuursignaal is voor de spieren die de ogen bewegen. Dit zou kunnen verklaren dat de lokalisatiefout in voorwaartse richting is (in de richting waarin het oog gestuurd werd). The lokalisatie fout lijkt van vele factoren afhankelijk te zijn. Mitrani en Dimitrov (1982) en van Beers, Wolpert en Haggard (2001) hebben gevonden dat doel die voor het gevolgde doel geflitst worden meer gemislokaliseerd worden dan doelen die op of achter het gevolgde doel geflitst worden. De lokalisatie fout kan verminderd worden door de aanwezigheid van visuele referentie punten (Mateeff & Hohnsbein 1989; Brenner, Smeets & van de Berg 2001). In twee studies waarin een zichtbare meetlat langs het pad van de volgbeweging werd getoond hing de lokalisatie fout systematisch af van de positie langs de meetlat waar het doel geflitst werd (Mitrani, Dimitrov, Yakimoff & Mateeff 1979; Mateeff, Yakimoff & Dimitrov 1981). Het is niet duidelijk wat de kritieke variabelen resulterend in al deze bevindingen waren.

6.2 De Experiment in dit proefschrift

6.2.1 Hoofdstuk twee

In het experiment dat beschreven is in hoofdstuk 2 hebben we onderzocht of de lokalisatie fout zou verminderen als de verschijning van de flits meer voorspelbaar gemaakt werd. De aanzet hiertoe waren bevindingen van Mitrani, Dimitrov, Yakimoff en Mateeff (1979) en van Mateeff, Yakimoff & Dimitrov (1981). Zij hadden gevonden dat de lokalisatie fout kleiner was in bepaalde situaties, maar het was onduidelijk welke aspecten van die situaties van kritiek belang waren. De auteurs suggereerden dat de voorspelbaarheid van het verschijnen van de flits wellicht de lokalisatie fout beïnvloed had. Daarom hebben wij geprobeerd of verscheidene vormen van voorspelbaarheid de lokalisatie beïnvloeden. We hebben stimuli gebruikt waarin verschillende soorten voorspellingen mogelijk waren. We vonden dat sommige van onze manipulaties de lokalisatie fout behoorlijk beïnvloeden. We hebben dit niet geïnterpreteerd als een effect van voorspelbaarheid maar als een gevolg van het verschijnen van het doel in een ruimtelijk aangeven gebied. We concludeerden dat een ruimtelijk sein betreffende de plaats waar het doel zal komen de mislokalisatie van doelen die geflitst worden tijdens volgbewegingen van de ogen kan verminderen. Het ruimtelijke sein hoeft niet precies op dezelfde positie te zijn als de flits.

6.2.2 Hoofdstuk drie

De studie beschreven in hoofdstuk drie vergelijkt verschillende manieren om de positie van de flits aan te geven. Er is maar een studie (Hansen 1979) voor zover wij weten waarin proefpersonen geen fout maakten tijdens het lokaliseren van een doel dat geflitst werd tijdens volgbewegingen van de ogen. Een duidelijk verschil tussen die studie en de andere studies was de manier waarop de positie van de flits aangegeven werd. In de studie van Hansen werden de proefpersonen gevraagd de positie van de flits aan te geven met een snelle hamerslag. In de andere studies gaven de proefpersonen de positie van de flits aan op veel langzamere wijze. Wij hebben onderzocht of het verschil tussen de resultaten van Hansen en die van de anderen het gevolg was van het gebruik van een snelle motorische response in vergelijking met de veel langzamere manier van reageren in de andere studies. Vanwege de manier waarop de waargenomen positie wordt aangegeven worden deze laatst genoemde studies vaak perceptuele beoordelingsstudies genoemd. We namen aan dat er wellicht een fundamenteel verschil zou zijn tussen de informatie die onze perceptuele oordelen van een positie bepalen en de informatie die gebruikt wordt om onze hand naar een positie te sturen. Om te testen of de snelle motorische response versus de langzame beoordeling het kritieke verschil was instrueerden wij onze proefpersonen om de positie van de flits aan te geven door middel van een snelle tik van de wijsvinger. We vonden dat ze systematisch voor de positie van de flits tikten, op een vergelijkbare manier als in de perceptuele beoordelingstaken. We hebben geconcludeerd dat het gebrek aan systematische fouten in de studie van Hansen (1979) niet het gevolg is van een algemene eigenschap van snelle motorische reacties.

6.2.3 Hoofdstuk vier

De studie beschreven in hoofdstuk vier was erop gericht te verduidelijken welke beweging van belang is voor de lokalisatie fout. In eerdere studies was de beweging van het gevolgde doel en die van de ogen erg vergelijkbaar en ook was de beweging voordat het doel geflitst werd erg vergelijkbaar met de beweging erna. Daarom was het niet duidelijk of de beweging van het gevolgde doel of die van ogen van belang was en het was ook niet duidelijk of de beweging voor de flits of de beweging na de flits van belang was. Om dit op te helderen hebben wij proefpersonen gevraagd om met hun ogen een bewegende schijf te volgen die regelmatig van richting veranderde. Elke verandering in de bewegingsrichting van de schijf werd gevolgd door een verandering van de richting waarin de ogen bewogen. De proefpersonen waren gevraagd om doelen die geflitst werden in de buurt van het moment waarop de gevolgde schijf van richting veranderde snel aan te tikken. We hebben de richting van de lokalisatie fouten die zij maakten vergeleken met de richting waarin de schijf en de ogen bewogen gedurende verschillende tijdsintervallen relatief ten opzichte van de flits. We vonden dat de beweging van de ogen na de flits van kritiek belang was. Verder was het ook interessant om te zien dat de proefpersonen geen saccades maakten naar de positie die ze aantikten maar gewoon de schijf bleven volgen.

6.2.4 Hoofdstuk vijf

In de studie beschreven in hoofdstuk vijf hebben we onderzocht of het flitsen van het doel (het erg kort zichtbaar zijn van het doel) van cruciaal belang was voor de lokalisatie fout. Deze studie werd gemotiveerd door de suggestie dan een lokalisatie fout van een bewegend doel vergelijkbaar met de lokalisatie fout van geflitste doelen nuttig zou kunnen zijn om neuronale en musculaire vertragingen te compenseren. We hebben onderzocht of bewegende doelen en geflitste doelen op een zelfde wijze gemislokaliseerd worden. We deden dit door proefpersonen te vragen om aan te geven waar doelen die zichtbaar waren voor verschillende periodes voor het eerst verschenen. De doelen werden getoond terwijl de ogen van de proefpersonen bewogen. De doelen bewogen met de ogen mee of stonden stil. We vonden de gebruikelijke systematische lokalisatie fout van de geflitste doelen en een vergelijkbare lokalisatie fout voor de doelen die met de ogen mee bewogen. Stilstaande doelen die 200 milliseconden zichtbaar waren werden niet gemislokaliseerd. Deze bevindingen ondersteunen de veronderstelling dat de systematische mislokalisatie van geflitste doelen gerelateerd is aan onze capaciteit om bewegende doelen te onderscheppen. Een simpel model dat retinale beweging en oog beweging combineert kan de lokalisatie fouten verklaren.

6.2.5 Conclusies van de experimenten in dit proefschrift

- Een ruimtelijk sein kan de mislokalisatie van een doel dat geflitst wordt tijdens een volgbeweging van de ogen verminderen. Het sein hoeft niet op precies dezelfde plaats te zijn als de flits. (hoofdstuk 2)
- De systematische mislokalisatie van een doel dat geflitst wordt tijdens een volgbeweging van de ogen zoals gevonden in vele perceptuele studies is ook aanwezig in snelle motorische reacties. (hoofdstuk 3)
- De systematische mislokalisatie van een doel dat geflitst wordt tijdens een volgbeweging van de ogen is meer gerelateerd aan de beweging van de ogen dan aan de beweging van het gevolgde doel, en meer aan de beweging na de flits dan aan de beweging voor de flits. (hoofdstuk 4)
- Tijdens een handbeweging kan een menselijke proefpersoon naar andere posities kijken dan het doel van de handbeweging. (hoofdstuk 4)
- Doelen die geflitst worden tijdens een volgbeweging van de ogen worden gelokaliseerd alsof ze met de ogen mee bewegen. De positie van een doel dat met de ogen mee beweegt wordt systematisch gemislokaliseerd in de richting van de beweging. (hoofdstuk 5)
- Saccades die gemaakt worden tijdens een volgbeweging van de ogen beïnvloeden de lokalisatie fout niet. (hoofdstuk 5)

6.3 Algemene conclusies en opmerkingen

Onze resultaten bevestigen dat mensen tijdens volgbewegingen van de ogen een geflitst doel systematisch mislokaliseren in de richting van de volgbeweging. We hebben ook aangetoond dat doelen die met de ogen mee bewegen tijdens de volgbeweging op een zelfde wijze gemislokaliseerd worden (in ieder geval hun start positie). Onze resultaten zijn de eerste die laten zien dat deze lokalisatie fout ook snelle motorische reacties beïnvloedt. Deze bevindingen ondersteunen het idee dat deze mislokalisaties het gevolg zijn van mechanismen die verantwoordelijk zijn voor onze capaciteit bewegende doelen te onderscheppen. Dit is onlangs ook door anderen voorgesteld (Kerzel & Gegenfurtner 2003; Ashida 2004).

We hebben een model voorgesteld dat aangeeft hoe deze lokalisatie fouten zouden kunnen ontstaan gebruikmakend van informatiebronnen die beschikbaar zijn voor het zenuwstelsel. Twee informatiebronnen zouden hiervoor nodig zijn. Een informatiebron geeft informatie over de oriëntatie van de ogen. Deze informatie kan ofwel komen van een kopie van de uitgaande stuursignalen voor de spieren die de ogen bewegen of van de binnen komende signalen van de spierspoeltjes en/of de Golgi pees lichaampjes in de spieren die de ogen sturen en de geassocieerde pezen. De tweede informatiebron is de beweging van het retinale beeld van het doel. Deze informatie kan alleen maar komen van de binnen komende signalen van de retina. De manier waarop de signalen van deze twee informatiebronnen gecombineerd worden, heeft consequenties voor de positie waarop het doel gelokaliseerd wordt. Vandaar dat kennis van de wijze waarop het zenuwstelsel doelen lokaliseert ons de mogelijkheid biedt veronderstellingen te maken over hoe het zenuwstelsel oogoriëntatie informatie met retinale informatie combineert. Vanzelfsprekend is een model sterker als het niet alleen in overeenstemming is met de resultaten waarop het gebaseerd is maar ook met ander bevindingen. Verder wordt een voorstel over informatieverwerking in een levend wezen ondersteund door argumenten die aangeven dat het op de voorgestelde wijze verwerken van de informatie adaptieve voordelen biedt. Daarom zullen we in het volgende aangeven hoe onze bevindingen en het model dat we hebben voorgesteld andere vormen van mislokalisatie kan verklaren en hoe deze vorm van mislokalisatie nuttig kan zijn in het omgaan met bewegende objecten.

6.3.1 De relatie met pre-saccadische mislokalisatie

Pre-saccadische mislokalisatie verwijst naar het fenomeen dat proefpersonen een doel dat vlak voor een saccade geflitst wordt mislokaliseren. Ze mislokaliseren zulke doelen in de richting van de saccade (bijv. Dassonville, Schlag & Schlag-Rey). Deze vorm van mislokalisatie kan verklaard worden door aan te nemen dat retinale informatie over de flits gecombineerd wordt met informatie over de oriëntatie van de ogen iets later, wanneer de ogen bewogen zijn in de richting van de saccade. Deze informatie kan al aanwezig zijn als de flits gepresenteerd wordt in de vorm van een stuursignaal dat nog naar de ogen gestuurd moet worden om de saccade te maken. Zoals beschreven in hoofdstuk vier hebben wij gevonden dat de mislokalisatie van flitsen tijdens volgbewegingen van de ogen afhangt van informatie over de oogbeweging na de flits. Daarom kunnen beide bevindingen verklaard worden door de aanname dat de oogoriëntatie informatie die gebruikt wordt afkomstig is van de uitgaande stuursignalen naar de spieren die de ogen zullen bewegen. Echter we hebben in hoofdstuk vijf beschreven dat de mislokalisatie tijdens volgbewegingen van de ogen niet afhangt van saccades die gemaakt worden tijdens het volgen. We hebben beargumenteerd dat alleen de gladde component van de volgbeweging bijdraagt aan de mislokalisatie. Dit lijkt aan te geven dat, alhoewel in beide gevallen waarschijnlijk uitgaande informatie wordt gebruikt, deze informatie een verschillende oorsprong heeft. Als we iets volgen met onze ogen komt de oogoriëntatie informatie van het volg systeem terwijl het tijdens fixatie van het saccade systeem komt of van een niveau dichter bij de spieren die de ogen bewegen. Het is bekend dat het volg systeem en het saccade systeem gescheiden systemen in het zenuwstelsel zijn. Alhoewel ze voor een deel overlappen (Krauslitz 2004), is het zeker mogelijk om ergens informatie af te tappen zodat er een puur volg signaal of een puur saccadisch signaal verkregen wordt. De reden dat tijdens volbewegingen de saccadische signalen niet gebruikt worden zou als volgt kunnen zijn. Tijdens een volgbeweging van de ogen kan een combinatie van een retinaal signaal met een signaal gerelateerd aan de volgbeweging voorspellen waar het doel is. Deze voorspelling is het signaal dat gebruikt wordt voor elke doelgerichte beweging zij het een arm beweging of een saccade. Bovendien is de informatie over de volgbeweging gerelateerd aan de beweging van het doel dat gevolgd wordt, terwijl de saccade geen relatie heeft met de beweging van het gevolgde doel en er waarschijnlijk slechts voor zorgt dat het beeld verplaatst wordt naar een positie (de fovea) waar het goed gevolgd kan worden.

6.3.1 De relatie met het flash-lag effect

Het flash-lag effect verwijst naar de bevinding dat de relatieve positie van een geflitst en een bewegend doel gemislokaliseerd wordt. De relatieve mislokalisatie is consistent met een verschuiving van het bewegende doel in de richting waarin het beweegt (Nijhawan 1994). Het grote verschil tussen het flash-lag effect en de mislokalisatie tijdens volgbewegingen van de ogen is dat bij het flash-lag effect de ogen niet bewegen. Terwijl de mislokalisatie tijdens volgbewegingen van de ogen afhangt van retinale informatie en van oogoriëntatie informatie, hangt het flash-lag effect alleen van retinale informatie af. Net zoals mislokalisatie tijdens volgbewegingen van de ogen hangt het flash-lag effect ook af van beweging na de flits. Verscheidene auteurs hebben beschreven dat het flash-lag effect afhangt van de richting waarin het doel beweegt na de flits (Eagleman & Sejnowski 2000; Whitney, Murakami & Cavanagh 2000) en van de snelheid waarop het beweegt na de flits (Brenner & Smeets 2000; Whitney, Murakami & Cavanagh 2000). Het model dat wij hebben voorgesteld in hoofdstuk 5 ter verklaring van mislokalisatie tijdens volgbewegingen van de ogen maakt ook gebruikt van retinale beweging na de flits. Ons model kan daardoor ook het flash-lag effect verklaren. In ons model wordt informatie over de oogoriëntatie net na de flits gecombineerd met informatie over retinale beweging net na de flits. In een flash-lag studie bewegen de ogen niet en dus zal de oogoriëntatie informatie niet veranderen. Daarom zal het gebruik van informatie die de oogoriëntatie net iets na de flits specificeert niet tot een fout leiden; het specificeert dezelfde positie de gehele tijd. De retinale positie van de flits verandert ook niet. Echter, de retinale positie van het bewegende doel verander wel, dus ons model dat deze beweging van net iets na de flits gebruikt en dat combineert met de niet veranderende oogoriëntatie informatie voorpelt een mislokalisatie van de relatieve posities van de flits en het bewegende doel precies zoals die gevonden is in flash-lag studies. Namelijk een relatieve mislokalisatie die consistent is met een verplaatsing van het bewegende doel in de richting van zijn beweging. Bovendien kan de aanname dat retinale informatie van net iets na de flits gebruikt wordt ook de beoordelingsfout van de staat die andere aspecten van het retinale beeld, zoals kleur, hebben op het moment van een flits (Seth, Nijhawan & Shimojo 2000). Murakami (2001) heeft aangetoond dat de resultaten van bijna alle flash-lag studies verklaard kunnen worden door het integreren van de positie van het bewegende doel over enige tijd na de flits. De tijd waarover geïntegreerd dient te worden is echter wel wat korter dan de tijd waarover wij moesten middelen om de mislokalisatie tijdens volgbewegingen van de ogen te verklaren.

Nijhawan (2001) heeft een variatie op de een flash-lag studie gedaan, hierin instrueerde hij zijn proefpersonen om het bewegende doel met hun ogen te volgen. Hierdoor verdween het flash-lag effect; de relatieve positie van de flits en het bewegende doel werden correct beoordeeld. Ons model voorspelt dit. In dit geval zullen de retinale positie van de flits en die van het bewegende doel beide niet veranderen en dus zal het gebruiken van de retinale positie van het bewegende doel net na de flits niets uit maken. Niettemin, zal het gebruikmaken van de informatie over de oogoriëntatie van net na de flits wel zorgen voor de voorwaartse mislokalisatie van zowel de flits als het bewegende doel: de gebruikelijk mislokalisatie tijdens volgbewegingen van de ogen. Deze bevinding ondersteunt de aanname dat de flits en het gevolgde object op dezelfde wijze gemislokaliseerd worden.

6.3.1 De relatie met de mislokalisatie van excentrische doelen

Verscheidene studies hebben aangetoond dat doelen die werden gepresenteerd op excentrische posities (op enige afstand van het fixatiepunt) gemislokaliseerd worden. Dit gebeurt zelfs als er geen beweging in het het retinale beeld noch beweging van de ogen is. Toen proefpersonen gevraagd werd naar doelen te wijzen die gepresenteerd werden op excentrische posities tijdens fixatie wezen zij te ver in de periferie (Bock 1986; Enright 1994; Henriques et al. 1998). Tijdens volgbewegingen van de ogen is er ook een effect van excentrische presentatie. Doelen die voor het gevolgde doel gepresenteerd worden worden verder gemislokaliseerd dan doelen die achter het gevolgde doel gepresenteerd worden. Dit gebeurt zowel als de positie van het doel onmiddellijk aangegeven wordt (hoofdstuk 3) als wanneer de positie van het doel later, nadat de volgbeweging van de ogen is afgelopen, wordt aangegeven (Mitrani & Dimitrov 1982; van Beers et al. 2001). Dit effect van excentrische presentatie tijdens volgbewegingen van de ogen is consistent met de overschatting van de excentriciteit tijdens fixatie. Als de flits voor het gevolgde doel gepresenteerd wordt is de voorwaartse mislokalisatie ten gevolge van de volgbeweging in dezelfde richting als de mislokalisatie ten gevolge van een overschatting van de excentriciteit. Voor een doel dat achter het gevolgde doel gepresenteerd wordt is de mislokalisatie ten gevolge van een overschatting van de excentriciteit in een richting tegengesteld aan de voorwaartse mislokalisatie ten gevolge van de volgbeweging van de ogen. Het combineren van de mislokalisatie ten gevolge van de excentriciteit met de mislokalisatie ten gevolge van de volgbeweging van de ogen zou daardoor dus leiden tot een grotere mislokalisatie van doelen voor het gevolgde doel en tot een kleinere mislokalisatie van doelen achter het gevolgde doel. Echter, in een van de experimenten beschreven in hoofdstuk 3 waren de verschillen in de mislokalisatie van de doelen die gepresenteerd waren op verschillende excentriciteit te groot om op deze wijze verklaard te kunnen worden. De lokalisatie fouten in het tweede experiment dat beschreven is in hoofdstuk drie kunnen wel op deze wijze verklaard worden. Het is daarom nog niet duidelijk of de mislokalisatie van doelen tijdens volgbewegingen van de ogen en de mislokalisatie van excentrische doelen twee totaal onafhankelijke effecten zijn. Bovendien zijn er ook verslagen van het onderschatten van de excentriciteit van excentrisch gepresenteerde doelen tijdens fixatie (van der Heijden et al. 1999; Müsseler et al. 1999). Een waarschijnlijk belangrijk verschil tussen deze studies en de studies die overschatting van de excentriciteit vonden is de manier waarop de proefpersonen de posities van de doelen aangaven. In de studies die een overschatting van de excentriciteit vonden wezen de proefpersonen naar de doelen en in de studies die een onderschatting vonden moesten de proefpersonen verschillende structuren in de periferie vergelijken.

6.3.1 De relatie met interceptie

Als proefpersonen gevraagd wordt de positie van een doel dat geflitst wordt tijdens een volgbeweging van de ogen of de positie waar een bewegend doel verscheen tijdens een volgbeweging aan te geven blijken ze fouten te maken en geven ze niet de juiste positie aan. Hoe kunnen deze fouten het gevolg zijn van een mechanisme dat verantwoordelijk is voor het onderscheppen van bewegende doelen? De reden kan simpel zijn: als je een bewegend doel wilt onderscheppen moet je je hand niet naar de positie sturen die het doel heeft op het moment dat je beslist de beweging te beginnen maar naar de positie die het doel heeft aan het eind van de interceptiebeweging. De lokalisatie fouten laten wellicht zien dat het zenuwstelsel het doel lokaliseert op een positie die nuttig is. De reden dat ze een flits mislokaliseren is waarschijnlijk dat een flits behandelt wordt als een bewegend doel, wat zoals beschreven in hoofdstuk 5 het geval lijkt te zijn. Geflitste doelen worden waarschijnlijk net zo behandeld als bewegende doelen omdat ze geen beweging in het retinale beeld veroorzaken (zoals bewegende doelen), terwijl het beeld van een doel dat niet met de ogen mee beweegt over de retina zou moeten bewegen. In het geval van een geflitst doel en in het geval van een doel dat met de ogen mee beweegt is er geen beweging van het beeld over de retina en zal de mislokalisatie volledig afhangen van de beweging van de ogen. Het beeld van een stilstaand object zal over de retina bewegen en de informatie over de beweging van dit beeld zal tegengesteld zijn aan de informatie over de beweging van de ogen en daarom zullen zulke objecten niet gemislokaliseerd worden. We hebben in hoofdstuk vijf laten zien dat een combinatie van deze twee informatiebronnen de mislokalisatie van de geflitste en de bewegende doelen en ook de accurate lokalisatie van de stilstaande doelen kon verklaren. Het zou problematisch kunnen lijken dat het model informatie over beweging in het retinale beeld na de flits gebruikt. Dit hoeft echter geen probleem te zijn voor een mechanisme dat verantwoordelijk is voor het onderscheppen van bewegende doelen. We moeten wat beweging zien voordat we kunnen beslissen wat een goede positie zou kunnen zijn om het doel te onderscheppen. Er is altijd een zekere reactie tijd voordat een proefpersoon een beweging start om een bewegend doel te onderscheppen, het meten van wat retinale beweging zou kunnen gebeuren tijdens deze reactietijd.

Het model verklaart ook waarom we in staat zijn met bewegende doelen om te gaan zonder de waargenomen snelheid te gebruiken (Brouwer, Brenner & Smeets 2001). Ons model gebruikt de waargenomen snelheid niet om een mogelijk interceptiepunt te bepalen. Het model gaat alleen over de waargenomen positie en impliceert simpelweg dat de waargenomen positie al een voorspelling is van een toekomstige positie van het doel. Het is makkelijk te begrijpen dat dit een betere oplossing is dan gebruik te maken van de waargenomen snelheid om een toekomstige positie te voorspellen, want de waargenomen snelheid hangt sterk af van de beweging van de achtergrond (bekend als de Duncker illusie). Gebruik maken van de waargenomen snelheid zou daardoor in vele situaties accurate interceptie van bewegende doelen onmogelijk maken. Het vergelijken van ons model met andere modellen van interceptie is niet zo makkelijk. Zoals beschreven in de introductie richten de meeste andere modellen zich op de timing van de interceptie, en proberen ze variabelen te vinden die gebruikt worden om de timing te controleren. Ons model is specifiek gericht op de lokalisatie. Het combineert de temporele en de ruimtelijke aspecten van interceptie door er voor te zorgen dat de gelokaliseerde positie altijd de (voorspelde) werkelijke positie iets later is. Dit maakt dat dit een geschikt controle signaal kan zijn voor interceptiebewegingen.

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9 Curriculum Vitae

I was born on December 17th, 1975 in Zwolle, the Netherlands. After secondary school I started studying biology at the University of Utrecht in 1995. I did my master's thesis at the department of neuroethology, which is now called the department of functional neurobiology. The thesis was about directional/distance hearing in fish and was done under the supervision of Dr. F. Bretschneider. It concerned heart rate conditioning experiments in simulated soundfields on cod. I received my master's degree in biology in 1999. After that I started on a PhD student project at the Erasmus University Rotterdam under supervision of Dr. E. Brenner and Dr. J.B.J. Smeets at the former physiology department which is now part of the department of Neuroscience. The results of this project are the subject of this thesis.

10 Publications

Chapter 2

Rotman G., Brenner E., Smeets J.B.J. (2002), Spatial but not temporal cueing influences the mislocalization of a target flashed during smooth pursuit. Perception 31: 1195-1203.

Chapter 3

Rotman G., Brenner E., Smeets J.B.J. (2004). Quickly tapping targets that are flashed during smooth pursuit reveals perceptual mislocalizations. Experimental Brain Research 156: 409-414.

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Chapter 5

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