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8

Intercepting moving objects: do eye movements matter?

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Summary

Due to neuromuscular delays and the inertial properties of the arm people must consider where a moving object will be in the future if they want to intercept it. We previously proposed that people automatically aim ahead of moving objects they are trying to intercept because they pursue such objects with their eyes, and objects that are pursued with the eyes are mislocalized in their direction of motion. To test this hypothesis we examined whether asking subjects to fixate a static point on a moving target's path, rather than allowing them to pursue the target with their eyes, makes them try to intercept the target at a point that the target has already passed. Subjects could not see their hand during the movement and received no feedback about their performance. They did tend to cross the target's path later – with respect to when the target passed that position – when not pursuing the target with their eyes, but the effect of fixation was much smaller than we predicted, even considering that the subjects could not completely refrain from pursuing the moving target as their hand approached it. Moreover, when subjects first started to move, their hands did not aim farther ahead when pursuing the target than when trying to fixate. We conclude that pursuing the target with one's eyes may be important for interception, but not because it gives rise to localization errors that predict the target's displacement during the neuromuscular delay.

8.1 Introduction

It takes tens of milliseconds for visual stimulation of the retina to give rise to activity in the brain (Schmolesky et al. 1998), even longer for neural activity within the brain to result in the contraction of muscles in the arm, and longer yet for the arm to move to its goal. Due to neuromuscular delays and the inertial properties of the arm one must aim ahead of a moving object if one wants to intercept it. How far ahead should depend on how long one expects it to take one's hand to reach the object, and on the object's position and velocity. Surprisingly, making the object appear to move faster by moving the background in the opposite direction does not make people aim farther ahead, and making it appear to move more slowly does not make them aim less far ahead (Smeets & Brenner 1995; Brouwer et al. 2002). To explain this we proposed that the perceived velocity might not be used to predict the point of interception at all (also see Brenner & Smeets 1996). When one wants

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to intercept a moving object one follows it with one's eyes. If the position of an object pursued with the eyes were judged to be farther in the direction of ocular pursuit than it really is, then aiming for this position would make one aim ahead of the moving object (Brouwer et al. 2002; Rotman et al. 2005). But why should the perceived position of a moving object be misjudged in such a manner?

Targets that are flashed while subjects are pursuing a moving object with their eyes tend to be mislocalized in the direction of the eye movement (Hazelhoff & Wiersma 1924; Mita et al. 1950; Mitrani et al. 1979; Mateeff et al. 1981). The retinal stimulation by the flash is probably associated with an eye orientation at a later time (Matin et al. 1970; Matin 1986; Schlag & Schlag-Rey 2002). We have proposed that the origin of this misalignment in time is that signals arising from retinal stimulation (some time earlier) are combined with eye movement *command* signals (that will soon give rise to a change in the orientation of the eye) without considering any of the associated neuromuscular delays (Brenner et al. 2001). Pointing tasks reveal a mislocalization that corresponds with an asynchrony of more than 100 ms (Rotman et al. 2004a,b, 2005; Kerzel et al. 2005). This is all for *flashed* targets, but a study showing that the relative positions of flashed and moving targets are not misperceived during pursuit (Nijhawan 2001) suggests that moving targets are mislocalized in a similar manner as flashed ones (although relative positions may be judged independently; Brenner & Cornelissen 2000).

If eye-movement related mislocalization of a moving target is essential for intercepting the target, then we would expect subjects to always hit behind moving targets if they do not move their eyes. But do they? Of course, if they realize that they do so they will compensate for this on subsequent trials. Moreover, the position of the hand may also be misperceived when the eyes are moving, so asking subjects not to pursue the target may not only affect judgments of the target's position, but also that of the hand. To avoid such issues we asked subjects to hit moving targets in an experiment in which they could not see their hand and were not informed about whether they had hit the target. We compared their movements when asked to pursue the moving target with their eyes (which is what they would naturally do) with their movements when asked to fixate a point near where we expected them to intercept the target. If compensating for delays with eye-movement related mislocalization is the only reason for pursuing the target, then except for the hand passing behind the target when fixating, movement trajectories should be similar when fixating and pursuing the target.

8.2 Methods

Thirteen subjects took part in the experiment. Two were the authors. The other eleven were unaware of the hypothesis under study. Each subject took part in one session of 200 trials. There were eight types of trials (twenty-five each) and they were presented in random order. The trials differed in the eye movement that the subject was expected to make (pursuit or fixation), the target velocity (30 or 40 cm/s), and the position at which we expected the subject to hit the target (left or right). The task was always to hit the target as quickly as

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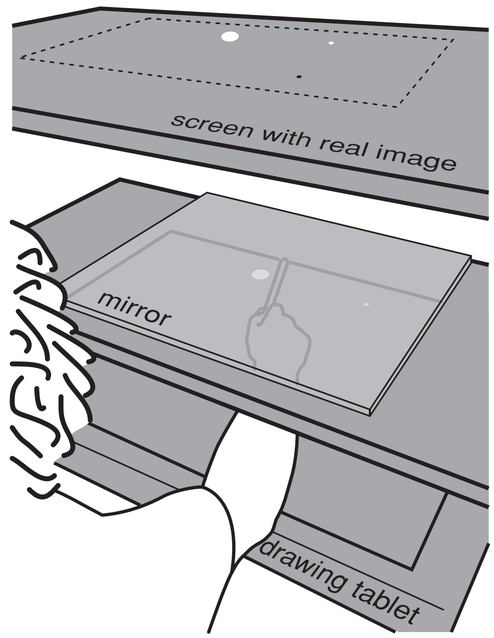

Fig. 8.1 The setup. The white starting point (*represented here by the black disk*), green target (*large white disk*), and red fixation point (*small white disk*) were back-projected from above onto a screen that the subject viewed by way of a mirror. The target always moved rightward. The fixation point was only presented on trials in which the subject was expected to fixate. The image in the mirror was precisely aligned with the surface of a drawing tablet across which the subject moved a pen. The task was to move the tip of the pen *through* the target as quickly as possible. The subject's hand is shown under the mirror to clarify the setup, but the subject could not see his or her hand during the experiment.

possible. To do so subjects moved a "pen" across a large (WACOM A2) drawing tablet. The experiments were conducted in a dimly illuminated room.

Figure 8.1 is a schematic depiction of our setup. The distance between the mirror and the screen (and that between the mirror and the drawing tablet) was 20 cm. The target was a 4-cm diameter green disk that always moved from left to right. On fixation trials a 1-cm diameter red disk was visible on the target's path, 8 cm to the right of the center of the drawing tablet. The pen's starting point was a 1-cm diameter white disk that was 30 cm closer to the subject than the target's path and was also 8 cm to the right of the center of the drawing tablet. Between trials a 1-cm diameter blue disk indicated where the pen was, to help the subject bring his or her hand to the starting position.

Subjects recognized fixation trials by the fact that the red disk appeared slightly to the right of the center of the tablet. On pursuit trials a similar disk appeared at the position at which the target would later appear, unmistakably to the left of the center of the tablet. This position was not fixed but was determined for each trial on the basis of the time it took the subject to reach the target's path on the previous trial of that condition. By doing

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so we tried to make the subjects hit the targets near two selected positions, irrespective of their movement times, so that the interception points of trials with different eye movement instructions would be comparable even if the movement times differed. We used two positions rather than a single position to discourage people from simply always making the same movement. The red disk appeared as soon as subjects held the pen motionless at the starting position. The moving target appeared between 500 and 1000 ms later. On pursuit trials the red disk disappeared when the moving target appeared (at the same position). On fixation trials the red disk remained visible throughout the trial; it occluded part of the target as the target crossed it, but the target always remained visible because it was much larger than the fixation point.

Hand movements (i.e., movements of the tip of the pen) were recorded at 200 Hz. The movements of both eyes were recorded at 250 Hz (Eyelink, SensoMotoric Instruments, Teltow, Germany). The subjects' eyes were about 55 cm from the targets' paths so that the targets' velocities were about 30 and 40 deg/s. Each session began with a calibration of the eye movement recordings. To motivate the subjects we gave points for each hit (in inverse proportion to the time it took them to hit the target) and displayed the outcome after the experiment. Because we were looking for small variations in subjects' arm movements we did not want to restrain the subjects in any way. This made it impossible to determine whether the subject's gaze was directed exactly at the moving target or at the fixation point because the subject could move his or her head and body, whereas the Eyelink recorded the orientation of the eye in the head. However, because our hypothesis specifically relates to eye velocity (rather than gaze position) this does not matter. Similar mechanisms to those that we propose could also apply to head and body movements, but the influence that differences in head or body movement speed between the conditions can have on the velocity at which the gaze position changes is presumably negligible in comparison to the influence of differences in eye velocity.

8.3 Results

Fifty-two of the 2600 trials (about 2%) were discarded because the pen did not reach the target's path within 1000 ms of the target appearing or because the data acquisition failed for technical reasons. Tables 8.1 and 8.2 show the average reaction time and movement time for each condition. We first determined the mean value for each subject in each condition and then averaged the thirteen subjects' values for each condition and calculated the standard error of this average. We also subjected the values to a repeated measures analysis of variance with the eye movement task, target speed, and position as variables. The reaction time was slightly shorter for the targets that were hit further to the right ($p = 0.002$) and for ones that moved more slowly ($p = 0.046$). The movement time was also slightly shorter for the targets that were hit further to the right ($p = 0.003$). No other differences were significant.

We manipulated the position at which the target appeared to ensure that subjects would hit the targets at about the same position when fixating as during pursuit. This precaution

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Table 8.1 *Reaction time in ms (means and standard errors of the thirteen subjects' average values)*

Target Speed	Position	Eyes Fixating Static Point	Eyes Pursuing Target
30 cm/s	Left	291 (20)	309 (30)
	Right	268 (14)	271 (20)
40 cm/s	Left	303 (20)	345 (28)
	Right	274 (17)	281 (19)

Table 8.2 *Movement time in ms (means and standard errors of the thirteen subjects' average values)*

Target Speed	Position	Eyes Fixating Static Point	Eyes Pursuing Target
30 cm/s	Left	369 (35)	379 (31)
	Right	344 (30)	352 (31)
40 cm/s	Left	368 (35)	360 (30)
	Right	347 (32)	354 (32)

turned out to be superfluous because the reaction and movement times did not depend on the eye movement task. We tried to make subjects hit the targets when they were at two positions (which we refer to as the left and right positions) that were 4 cm apart. In fact, the average distance between the targets at the moment they were hit (which was defined as the moment at which the hand crossed the target's path) was 3.9 cm for the fixation trials and 3.7 cm for the pursuit trials. The overall average target positions were also similar for the two eye movement tasks (on average the target was 0.2 cm further to the right when it was hit during ocular pursuit).

Although the targets at the left and right positions were almost 4 cm apart (on average) when the hand crossed their paths, the difference between the average positions of the hand was only 2.3 cm when pursuing the target and 1.5 cm when fixating. This can partly be explained by subjects tending to aim toward a similar position as on the previous trial, because on average they hit 0.5 cm further to the right if the previous target was hit on the right ($p = 0.0001$; as evaluated by a similar analysis of variance to that described in the next paragraph, with *previous target position* as an additional variable). The tendency to aim toward a similar position as on the previous trial was slightly stronger (0.6 vs. 0.4 cm) when there was a fixation point, but the difference was not significant ($p = 0.42$). Subjects probably also considered the positions on earlier trials and may also tend to aim toward where they are fixating (moving targets appear to be closer to fixation than they really are; Brenner et al. 2006).

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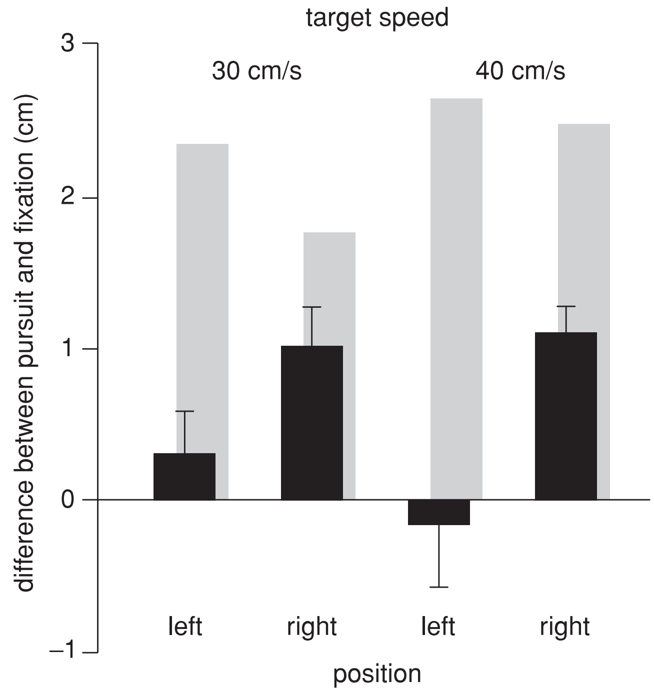

Fig. 8.2 How much further in the target's direction of motion the pen crosses the target's path (relative to the target's position at the time) during ocular pursuit than when trying to fixate (black bars; means and standard errors of the thirteen subjects' average values). The gray bars indicate the minimal extent to which we expected subjects to hit further in the direction of target motion when pursuing the target, considering the eye movements they made.

For a direct evaluation of our proposal we examined the systematic errors that subjects made. How far ahead or behind the target does the pen cross the target's path? There was considerable variability between subjects (average values between –0.2 cm and 5.2 cm) with an overall average value of 2.8 cm (whereby a positive value indicates passing ahead of the target center). A repeated measures analysis of variance showed that the tendency to hit ahead of the target was larger for targets on the left than on the right (3.8 vs. 1.9 cm; in accordance with the tendency mentioned in the previous paragraph; $p < 0.0001$) and was slightly larger for the faster targets (3.0 vs. 2.6 cm; $p = 0.003$). Most importantly, it was slightly larger during pursuit than during fixation (3.1 vs. 2.5 cm; $p = 0.03$), especially on the right ($p = 0.0009$ for the interaction between position and eye movement task). The extent to which subjects hit further ahead during pursuit is shown in Fig. 8.2.

Figure 8.3 shows the average pen movement paths for the two eye movement instructions. These paths were constructed by resampling the lateral position of the pen for fifty equidistant sagittal steps from the pen's starting position to the target's path (using linear interpolation). The resampled positions for individual movements were then first averaged across trials for each subject and condition, and then across subjects. The average paths

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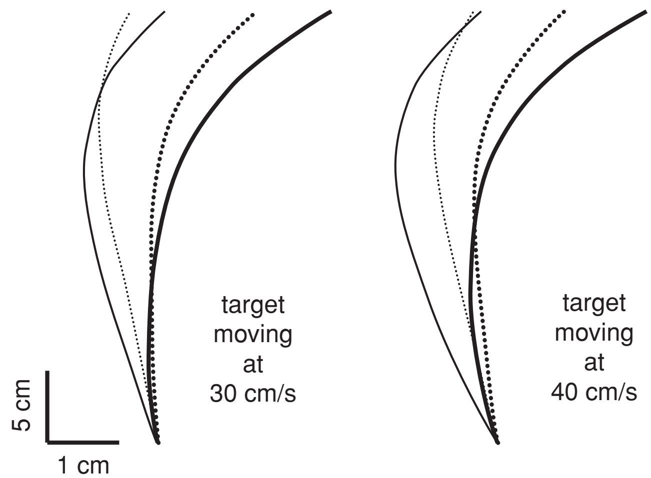

Fig. 8.3 The average path of the hand (pen) in each of the eight conditions. Thick curves are for the target that was to be hit on the right and thin ones for the target that was to be hit on the left. Solid curves are for movements while the subject pursued the target with his or her eyes. Dotted curves are for movements while the subject tried to fixate a static disk near where he or she was expected to hit the target. The lateral movement has been exaggerated for clarity (see different scales).

are slightly curved. This curvature differs systematically between the two eye movement tasks. Contrary to our prediction, the subjects' hands initially appear to have been heading less far ahead of the target when the subject was pursuing the target with his or her eyes, rather than further ahead. This too may be caused by a tendency to underestimate the retinal eccentricity of the target (judging it to be closer to where one is fixating).

Figure 8.4 shows the average velocity of the eye and hand near the moment that the hand passed the target's path. The orientations of the two eyes were first averaged and smoothed with a Gaussian with a standard deviation of 8 ms. Velocities of eye and hand were determined by dividing the distance between consecutive samples by the time interval between them. These values were attributed to the moment between the two samples. The velocities were then averaged across trials for each subject and condition. The mean velocity profile (curve) and standard error across subjects (shaded area) are shown for each condition. When the task was to pursue the target with their eyes (solid curves), the subjects' eyes moved at about the same velocity as the target (indicated by the dashed horizontal lines) during the last 200 ms before the hand passed the target's path (top panels). When the task was to fixate (dotted curves) the eye gradually accelerated as the target and hand approached the fixation point. The hand decelerated in the sagittal direction as it approached the target's path (bottom panels of Fig. 8.4) and accelerated to the right (central panels). The hand moved faster to the right near the time of the hit when the target was on the right (thick curves) and when the subjects were following the target with their eyes (solid curves).

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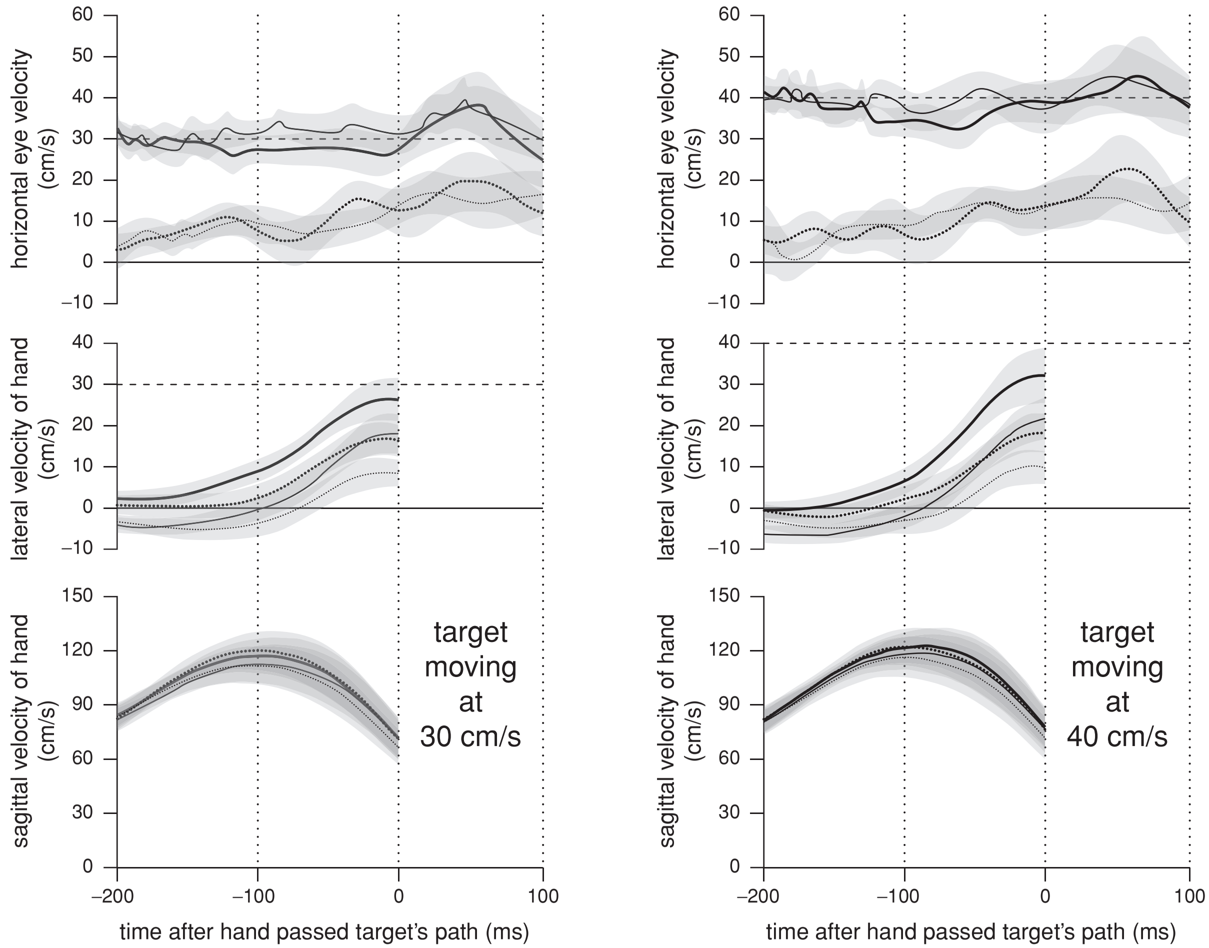

Fig. 8.4 The average velocity of the eye and hand (pen) near the moment that the subjects tried to intercept the target. Thick and thin curves are for movements in which we expected the target to be hit on the right and left, respectively. Solid curves are for movements while the subject tried to pursue the target with his or her eyes. Dotted curves are for movements while the subject tried to fixate a static disk near where the target was to be hit. The shaded areas indicate the standard errors across subjects.

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The critical question was whether subjects would hit further back along the target's path if they were forced to fixate while hitting. We initially expected them to hit at least 3 or 4 cm behind the target when forced to fixate. These are the distances that the targets move during 100 ms, and we anticipated that pursuing the targets gives rise to a localization error that corresponds with the targets' displacement during at least 100 ms. However, because subjects also pursued the targets with their eyes to some extent when trying not to do so, we have to refine our expectation. Our refined estimate of the expected effect depends on the difference between the extent to which subjects pursue the target on pursuit and fixation trials, which changes during the movement. The minimal difference that could be considered consistent with the proposal that mislocalizing targets during pursuit overcomes neuromuscular delays is 100 ms times the difference in the velocity of pursuit at the moment that the hand passed the target's path. This is the prediction shown by the gray bars in Fig. 8.2. It is clear that the tendency to hit further along the target's path when pursuing the target with the eyes than when fixating is much weaker than we predicted. Moreover, the extent to which individual subjects hit further ahead on pursuit trials than on fixation trials was not significantly correlated with the extent to which their average eye movement velocity differed between the two kinds of trials.

On average, subjects crossed the target's path further ahead of the target during pursuit than during fixation, but the extent to which they did so was only 25% of the predicted effect. Because our prediction did not distinguish between pursuit and saccades, we averaged the eye movements irrespective of whether saccades were made or not. To make sure that our conclusion would not have been different if we had restricted ourselves to *smooth* pursuit, we also selected the trials in which there was certainly no saccade near the critical moment: when the velocity of the eye did not exceed 100 deg/s during the last 100 ms before the target was intercepted. For those trials (92% of fixation trials and 89% of pursuit trials) the extent to which subjects hit further ahead of the target during pursuit was 30% of the predicted effect. This is slightly more than we found when we included all trials. The increase is mainly caused by the fact that the *predicted* effect is smaller (on average by 0.16 cm) if trials with saccades are excluded, which is not too surprising because 85% of the saccades during pursuit trials were in the direction in which the target was moving, whereas only 51% of the saccades in the fixation trials were in the direction of target motion (for the left position on fixation trials most saccades were to the left, opposite the direction of target motion). The tendency to hit further ahead of the target during pursuit was (on average) 0.065 cm larger on trials without saccades. Although these differences may be interesting, it is clear that excluding trials with saccades does not change our main conclusions.

8.4 Discussion

Apart from disproving our hypothesis about the relationship between manual interception and the mislocalization of targets flashed during pursuit, this study reveals two

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interesting phenomena. The first is that the hand's path toward the target depends on the eye movements the subject makes (Fig. 8.3). The hand's sagittal velocity hardly differs between the conditions (Fig. 8.4). It decreases as the hand approaches the target, but that is probably just the result of the hand reaching full extension and the end of the drawing tablet. The acceleration to the right, however, does differ between the conditions (Fig. 8.4). In all cases the hand curves slightly to move along with the target near the moment of interception (perhaps to reduce the influence of errors in judging one's own sagittal movement; Brenner & Smeets 2005), but when there was a static fixation point the path was less curved than when the eyes pursued the target (Fig. 8.3).

The difference between the paths could be explained by subjects underestimating the moving target's retinal eccentricity (Brenner et al. 2006), because if so subjects will initially aim closer to the fixation point when not pursuing the target, and because they are fixating a point that the target is still to pass this means they will initially aim further ahead of the target. If the retinal eccentricity of the moving target is systematically underestimated then the target's apparent position will change more rapidly during pursuit than when fixating. This could explain why the hand ended up moving faster to the right during pursuit (Fig. 8.4), and perhaps even why the final position was slightly further ahead of the target in that case (Fig. 8.2). Thus the different curvatures of the paths, different final lateral velocities of the hand, and different positions at which the hand crossed the target's path may all result from underestimating the retinal eccentricity of the moving target. Alternatively, subjects may tend to move their hand toward where they are looking for some other reason, or they may just underestimate the target's velocity during pursuit (e.g., Dichgans et al. 1975; Sumnall et al. 2003), either of which could also account for the difference between the paths.

The second interesting phenomenon is that subjects were unable to maintain fixation near the moment they hit the target. This is not simply a reflexive response of the eye to the target crossing the fixation point because the eye did not speed up earlier or more strongly when the target was to be hit on the right, although such targets crossed the fixation point 133 or 100 ms earlier (for targets moving at 30 and 40 cm/s, respectively). It also cannot be considered proof that the eye and hand are functionally linked during interception, supporting the many examples of failures to independently move the eye and hand (e.g., Lunenburger et al. 2000; Neggers & Bekkering 2001, 2002; Horstmann & Hoffmann 2005), because subjects also fail to fixate when performing tasks that require that one attends to a moving object without moving one's hand toward it (Khurana & Kowler 1987). It is interesting that the eye even seems to rotate to the right, in the same direction as the target and the hand, when the target is hit to the left of the fixation point (thin dashed lines in top panel of Fig. 8.4; note that we did not remove the occasional leftward saccades when calculating these average paths). For a better understanding of these eye movements we need to have more complete information about the direction of gaze.

The relationship between the eye and hand movements was not as we predicted. Even considering the failure to fixate, subjects did not hit even nearly as much further ahead of

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the targets during pursuit as we had predicted. The predictions shown in Fig. 8.4 are low estimates for the expected difference because the mislocalization during pursuit usually corresponds to more than 100 ms of target motion, and the difference in eye velocity would be larger if we were to consider an earlier moment before passing the target's path (remember that our proposal applies to the whole movement). Moreover, the movement paths curved differently when fixating than when following the target with the eyes, which would not be so if subjects only consistently misjudged the target's position in its direction of motion. Thus we conclude that eye movements play a role in interception, but that this role is not mediated by the perceptual mislocalization that is revealed when targets are flashed during eye movements.

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