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RESEARCH ARTICLES

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Quickly tapping targets that are flashed during smooth pursuit reveals perceptual mislocalisations

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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 mislocalisations. Thus the lack of systematic errors in Hansen's study is not a general property of fast motor responses.

Keywords Visuomotor · Spatial vision · Localisation · Smooth pursuit

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 and Wiersma 1924; Mita et al. 1950; Mitrani et al. 1979; Mateeff et al. 1981; Mitrani and Dimitrov 1982; Mateeff and Hohnsbein 1989; van Beers et al. 2001; Brenner et al. 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 et al. 2001). If the mislocalisation has such a fundamental origin, it should be found in any task that one examines. However, Hansen (1979) found no systematic mislocalisation 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 et al. 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 et al. 2000). In judgement tasks people are indeed known to be influenced by events that take place well after the flash (Mitrani et al. 1979). We therefore examined whether the same lack of mislocalisation that Hansen found for his hammer blows would also be found in a different fast motor task.

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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.

Materials and 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 (120×158 cm) that was tilted 20 degrees with respect to horizontal. A CRT projector (Sony, VPH 1271QM, 800×600 pixels, 120 Hz) projected the stimuli via a mirror from the rear onto the central part (70×55 cm) of this screen. The projector received its input from an Apple Macintosh G4. The subject was standing in front of the screen (Fig. 1).

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.

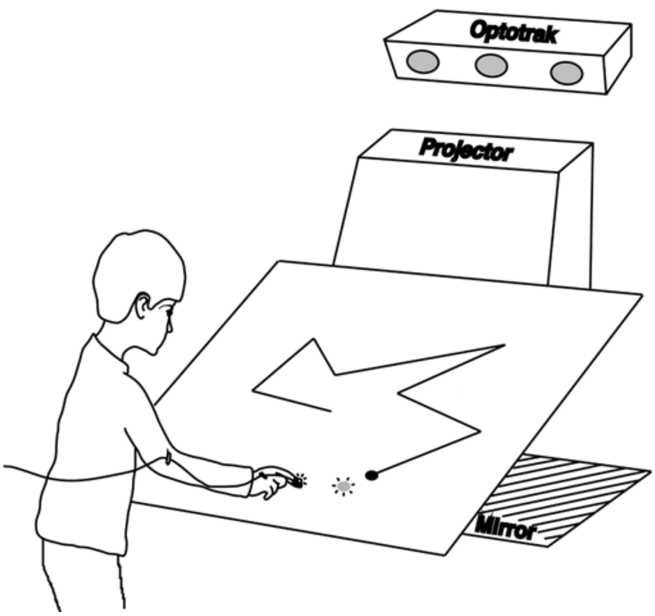


Fig. 1 Schematic drawing of the set-up. A flash (grey disk) is just being presented to the subject. The connected line segments indicate a piece of the path that the pursuit disk (black disk) followed; the subject never saw this. In this case the flash is presented ahead of the pursuit target

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 task 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 and Dimitrov 1982; van Beers et al. 2001). We want to compare our results with those to see whether those perceptual effects are also found here. Flashes were presented at five 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 five 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 counterclockwise) 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 localisation bias. A positive value means that it was in the direction in which the pursuit disk was moving. To express the localisation 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 counterclockwise 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 localisation 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 localisation bias is caused by combining afferent retinal signals with efferent eye movement signals without considering neural delays (Brenner et al. 2001). If so, the localisation 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 localisation bias indeed did not depend on the velocity of the pursuit disk when it was expressed as a timing error (Hazelhoff and Wiersma 1924; Mita et al. 1950) but another one did find a slight decrease of the timing error as velocity increased (Brenner et al. 2001). To see whether there was such a dependency in our experiment we checked the correlation coefficient between the localisation 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 localisation bias.

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 1,171 ms for the slowest subject. None of the subjects had a significant correlation (at α=0.05) between the localisation bias (in temporal units) and the target velocity. The spatial errors in the tapped positions are shown in Fig. 2. The subjects had a systematic bias to tap too far (30 mm) in the direction of pursuit.

Subjects' mean localisation biases at the different relative flash positions are shown in Fig. 3. The localisation 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

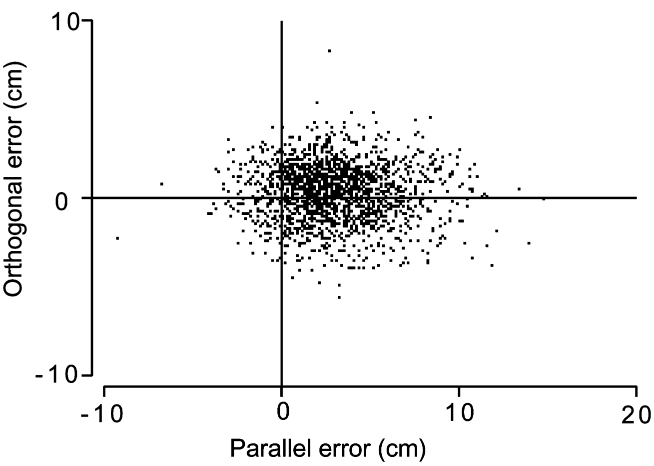


Fig. 2 Errors in tapped positions in experiment 1 (1,731 points)

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 localisation 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.

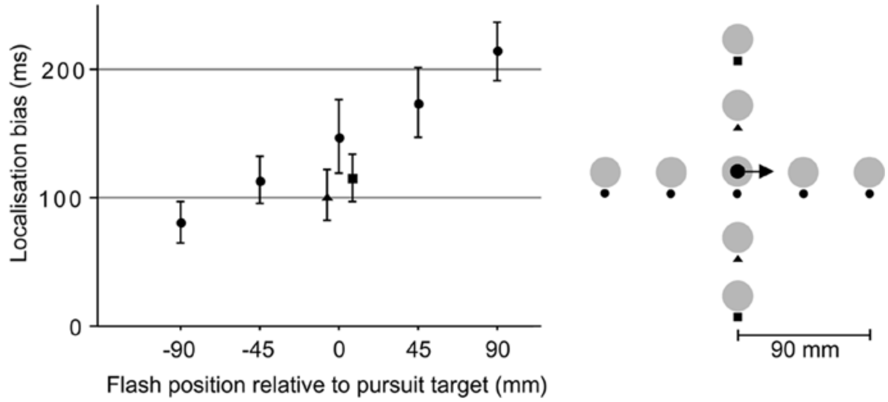
Discussion

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 localisation 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 and Dimitrov 1982; van Beers et al. 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 localisation bias (a similar but smaller dependency on motion direction has been found during fixation, so this expansion may be a totally independent effect; Watanabe et al. 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 mislocalisation 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

Fig. 3 Results of experiment 1. The average and standard error of the ten subjects' mean localisation biases (mislocalisation 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 localisation bias is in the direction of the *arrow*)



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 Fig. 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 Fig. 3, but at a negative value. If so, the timing error at the fovea is smaller than the value suggested by Fig. 3. One can deduce from Fig. 3 that the error would be zero at about –200 mm. Thus this effect is too small to challenge the existence of a localisation 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.

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.

Materials and 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 1,000 and 1,400 ms. Again the pursuit disk kept moving, so the experiment was one long pursuit trail with many tapping targets.

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 localisation bias (in temporal units) and the target velocity was significantly different from zero when the error was expressed in temporal units (at α=0.05). These three correlation coefficients were all negative as in Brenner et al. (2001). The slopes were: −2.5, −4.8 and −3.8 ms per

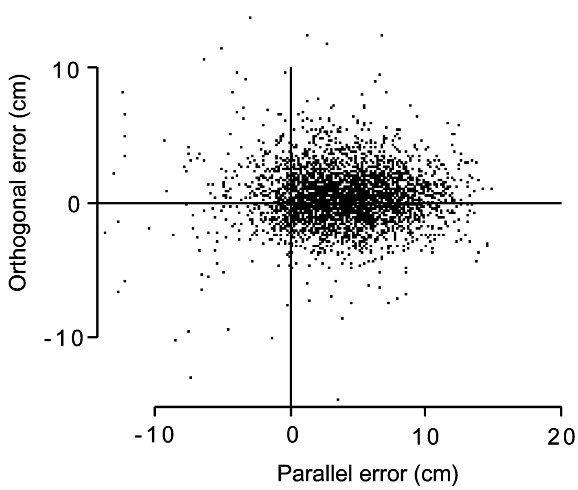


Fig. 4 Errors in tapped positions in experiment 2 (3,355 points)

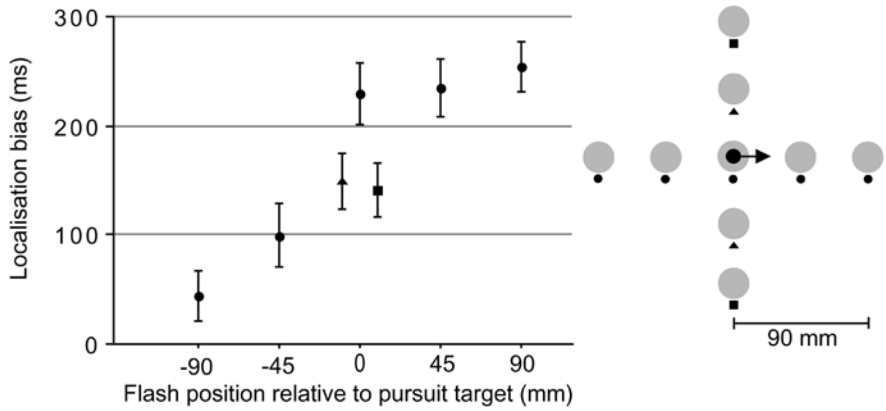


Fig. 5 Results of experiment 2. The average and standard error of the ten subjects' mean localisation biases (mislocalisation along the pursuit disk's path) as a function of the flash position relative to the pursuit target. The relative positions of the flashed targets and the symbols used for the different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

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 Fig. 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 localisation 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 localisation biases at the different relative flash positions are shown in Fig. 5. The mean localisation 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, $p_{\text{two-tailed}}$<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, $p_{\text{two-tailed}}$< 0.01). These slopes were not significantly different from each other (t_{176}=0.91, $p_{\text{two-tailed}}$=0.18). The within-subject standard deviation of the localisation 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.

Discussion

In this experiment subjects made tapping movements that were a lot quicker than those in experiment 1. Still the localisation bias is more comparable with those found in judgement tasks than with those of Hansen (1979), who found no localisation 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, 2000). If so, speeding up the movements in our study should have resulted in more veridical responses. We can reject this hypothesis because the localisation bias in experiment 2 is even a bit larger than that in experiment 1, while the subjects reacted faster. The standard deviation of the localisation 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 localisation bias in front of the pursuit disk and that behind the pursuit disk is caused by an overall tendency to overestimate retinal eccentricity.

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 and Wiersma 1924; Mita et al. 1950; Mitrani et al. 1979; Mateeff et al. 1981; Mitrani and Dimitrov 1982; Mateeff and Hohnsbein 1989; van Beers et al. 2001; Brenner et al. 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 et al. (2001) have shown that a structured background can reduce the localisation 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 mislocalisation of targets that were flashed at different positions relative to the pursuit disk was comparable to that found in judgement tasks. Van Beers et al. (2001) found large differences between the mislocalisation 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 mislocalised further than those that were presented behind the pursuit target. Mitrani and Dimitrov (1982) also report that the mislocalisation 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.

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