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Perceived localizations and eye movements with action-generated and computer-generated vanishing points of moving stimuli

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When observers localize the vanishing point of a moving target, localizations are reliably displaced beyond the final position, in the direction the stimulus was travelling just prior to its offset. We examined modulations of this phenomenon through eye movements and action control over the vanishing point. In Experiment 1 with pursuit eye movements, localization errors were in movement direction, but less pronounced when the vanishing point was self-determined by a key press of the observer. In contrast, in Experiment 2 with fixation instruction, localization errors were opposite movement direction and independent from action control. This pattern of results points at the role of eye movements, which were gathered in Experiment 3. That experiment showed that the eyes lagged behind the target at the point in time, when it vanished from the screen, but that the eyes continued to drift on the targets' virtual trajectory. It is suggested that the perceived target position resulted from the spatial lag of the eyes and of the persisting retinal image during the drift.

When an observer is asked to judge the vanishing point of a moving target, the indicated position is displaced in movement direction (e.g., Freyd & Fincke, 1984; Hubbard & Bharucha, 1988). Accounts of this mislocalization are often conceptualized in terms of *representational momentum*—the notion that the dynamics of the external environment have been incorporated into the dynamics of cognitive representations (for an overview see Hubbard, 1995). Given that internal representations, just as external events, have dynamic properties that cannot simply be brought to a halt, stimulus representations are assumed to

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continue for some time following stimulus offset. It is the momentum of these representations from which the localization error at the end of the movement is assumed to emerge.

Recent studies indicated, however, that not only the momentum of mental representations but also the pursuit eye movements contribute to the localization error. In representational momentum experiments, observers are often free to move their eyes. It is known that the eyes continue to drift in the direction of target motion if a pursued target suddenly disappears (Mitrani & Dimitrov, 1978; Mitrani, Dimitrov, Yakimoff, & Mateeff, 1979). One consequence of this drift could be that it moves the persisting image of the target in the direction of movement and that, from this drift, the perceived mislocalization emerges (Kerzel, 2000).

Kerzel and co-workers investigated systematically the role of eye movements in representational momentum. With smooth linear target motions, Kerzel, Jordan, and Müsseler (2001) observed a clear localization error in movement direction only with pursuit eye movements. With fixation, only foveopetal movements lead to a small mislocalization in movement direction (see also Aschersleben & Müsseler, 1999, Exp. 1; Brenner, Smeets, & Van den Berg, 2001), while a displacement opposite movement direction occurred with foveofugal movements. Moreover, Kerzel (2000) was able to demonstrate with a relative judgement task that 11 ms after target offset the judged position was already displaced in the movement direction and that this displacement increased up to 250 ms after target offset. A further conclusion of this study was that the retinal image, which seems to persist for about 60 ms, is indeed shifted with the eye in movement direction.

The studies of Kerzel and co-workers clearly showed that eye movements play an important role in representational momentum. In order to pursue the target, eye movements have to be planned and executed continuously. This task requires coordinating present positions of the eye with future positions of the moving target. However, the question is whether the localization error resulted exclusively from the planning and the generating of eye movements or if also other actions with respect to the moving target could modulate perceived target positions.

Jordan, Stork, Knuf, Kerzel, and Müsseler (2002) designed a series of experiments to address this question. To minimize the planning processes of eye movements, the main conditions of this study were carried out with fixation. The observers were asked to indicate the perceived final position of a target that moved on a circular trajectory around a central fixation point. Similar to the study of Kerzel et al. (2001) with fixation instruction and foveofugal movements, results revealed a general tendency for mislocalizations opposite the movement direction (for details and an explanation of this tendency see below). More important in the present context is that the perceived localization depended on the experimental conditions introduced in this study. The offset of the movement was produced by either an observer generated key press (action-generated vanishing condition) or the computer program (computer-generated vanishing condition). In the first case observers' action plan to press the key did not require continuous anticipation of future positions of the moving target (as it is the case with the control of eye movements), but the intended effect of the key press is the offset of the target at a certain position. In this situation, perceived locations were predicted to be attracted toward the position of the intended effect. This was indeed what the experiments showed with a high stimulus velocity of 30.8°/s. However, the effects on the localization judgements were small and were not observed with a slow stimulus velocity of 15.4°/s.

In the present study these action effects are further investigated. In addition to the study of Jordan et al. (2002) with eye fixation, observers were now asked to pursue the target with their eyes. Under these conditions one problem is whether and how key-press control over the vanishing point of the moving target exerts an influence on the trajectory of pursuit eye movements. Previous studies have already shown that the drift and the resulting overshoot of eye movements decreased when the target reached the end position of a target trajectory (Mitrani et al., 1979). Like the anticipations of future target positions, which enable the maintenance of ongoing pursuit, the anticipation of the target offset could be used to stop the eye movements more precisely. Further studies revealed that if the observer actively produced the target movement, the smooth pursuit behaviour of the eyes was largely improved in gain and phase (Lazzari, Vercher, & Buizza, 1997; Steinbach, 1969; Vercher, Lazzari, & Gauthier, 1997). More recently, Stork, Neggers, and Müsseler (2002) showed that the smooth pursuit eye movements were also improved by a key press, which terminated target movements. In other words, the overshoot in relation to the eye position at offset time was significantly reduced. So, modifications in the eye movement trajectories are to be expected with a key-press control over the vanishing point of the moving target.

Another problem is whether and how these modifications in the trajectories affect the perceived localization of the vanishing point. In other words, the question is whether the improved performance in eye-movement behaviour corresponds with the improvement in localization performance. Therefore, Experiments 1 and 2 compared the effects of action-generated and computer-generated target offsets on the perceived location with a pursuit and a fixation instruction. In Experiment 3, eye-movement parameters were gathered in order to compare them with the perceived locations.

EXPERIMENT 1

In this experiment the influence of action control over the vanishing point of a moving stimulus on stimulus localization was investigated in a localization task with pursuit eye movements. Pursuit eye movements aimed to follow the target, which is only possible by anticipating future target positions on the base of stimulus characteristics like velocity and movement trajectory. Two conditions were compared. In one condition the target disappeared unexpectedly (computer-generated vanishing point). In the other condition the target vanished intentionally with an observer's key press (action-generated vanishing point). The key press had all preconditions of an intentional action. The relationship between the action and its effect is systematic and could be experienced. As a result, the vanishing position of the target could be anticipated and this prediction could be used for the localization of the movement offset. Therefore, it was assumed that the localization error in movement direction with pursuit eye movements would be less pronounced in the action-generated condition than in the computer-generated condition.

Method

Participants. Eight female and two male individuals who ranged in age from 15 to 30 years (mean age of 22.7 years) were paid to participate in the experiment.

Apparatus and stimuli. The experiments were carried out on a Macintosh computer and the stimuli were presented on a 17-inch AppleVision colour monitor with black-on-white projection. The monitor had a refresh rate of 75 Hz and a luminance of approximately 40 cd/m^2. The rest of the room was dimly lit.

The moving stimulus was a dot of 0.5° visual angle (4.4 mm at a viewing distance of 500 mm) with a luminance of 13 cd/m^2. On each trial, the dot moved on a trajectory that circled around a fixation cross at a radius of 5.5° (Figure 1). The stimulus movement was induced by shifting the dot clockwise by 0.206° visual angle with every vertical retrace of the monitor (13.33 ms per frame), resulting in a velocity of 15.4°/s. This target velocity was well within the velocity range in which observers are able to accurately track a moving target (Robinson, Gordon, & Gordon, 1968). The movement started at the upper part of the circle (randomly in between ±20 degrees of rotation at the 12 o'clock position).

Design. Target offset was controlled either by the computer program (computer-generated vanishing point) or the key press of an observer (action-generated vanishing point). The two conditions were presented blockwise to each observer with the sequence of the blocks counterbalanced between participants. In total, the participants underwent 48 trials (i.e., 24 trials per condition). The experiment lasted approximately 30 min, including training trials and short breaks.

Procedure. At the beginning of each trial observers fixated the central fixation cross, which was visible throughout the experiment. Then an auditory warning signal was presented. After 300 ms the stimulus appeared and traced out

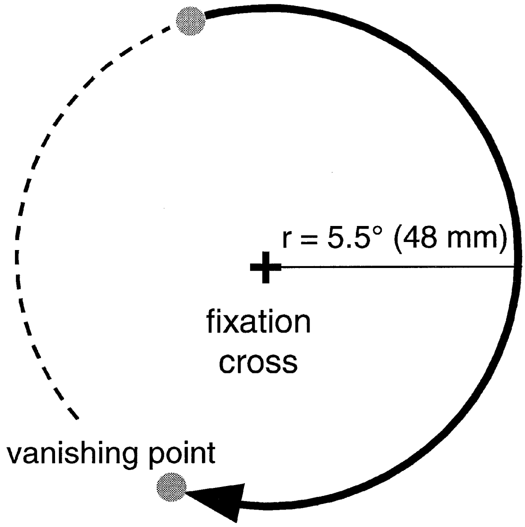

Figure 1. Stimulus presentation used in the experiments. A moving dot circled the central fixation cross at a radius of 5.5° visual angle. After presentation, the observer's task was to adjust a cursor to the perceived position where the moving stimulus vanished.

at least a quarter circle and at most a full circle. The instructions stressed the participants to immediately pursuit the target with their eyes.

Stimulus offset was either controlled by the computer or by an observers' key press with the right index finger. In the computer-generated vanishing condition, movement length varied randomly between 90 and 360 degrees of rotation with the absolute movement times of 560–2240 ms. In order to make conditions comparable, in the action-generated condition observers were instructed to stop the target not before a quarter circle or after a complete circle. If the observer pressed the key too early or too late, an error message was presented, and the trial was repeated immediately. Further, instruction stressed to distribute offset positions and not to stop the movement at recurrent salient positions (e.g., the 6 o'clock position).

500 ms after stimulus presentation an adjustment cursor appeared, which was identical to the moving target. Its starting position varied randomly on the circle's hemisphere opposite to the vanishing position. The cursor could be moved either clockwise or counterclockwise along the circle's trajectory by pressing a right or left key, respectively. Keys were mounted on a flat board in front of the observer. After having indicated the perceived position, pressing an ok-button confirmed the adjustment. Then the participants returned with their eyes to the fixation cross. The next trial was initiated with a programmed 1 s

delay. To familiarize participants with the task, training trials were presented at the beginning.

Results and discussion

Mean spatial deviations from the objective vanishing point were computed in visual angle (°) separately for every participant and each condition. Positive values indicate mislocalizations in movement direction beyond the target's final position; negative values indicate mislocalizations before the target's final position. The data of one observer were excluded from further analysis because the mean localization score exceeded the criterion of ±2 standard deviations between participants in the action-generated condition.

The deviation scores were then analysed with a *t*-test which revealed a significant difference between the computer-generated and action-generated condition, $t(8) = 5.18$, $SE = .10$, $p = .001$; cf. Figure 2 (left). This pattern of results showed that the anticipation of the target offset enabled by the action-generated key press offered the possibility to localize the movement offset accurately. In fact, in this condition no mislocalization different from zero was observed (0.12°), $t(8) = 0.91$, $SE = .13$, $p = .390$.

An additional analysis examined whether observers followed the instruction to equally distribute their stop positions between a quarter of circle and a full circle (see above). From the literature it is known that anticipating the moving

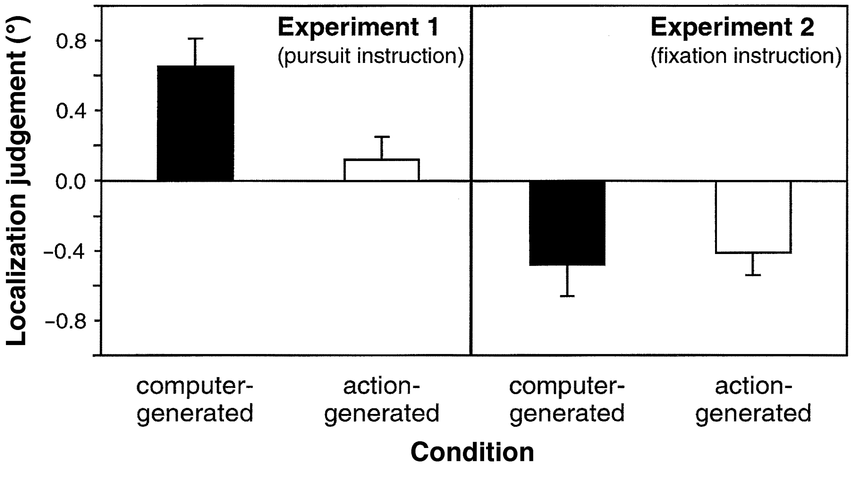

Figure 2. Mean mislocalizations in visual angle (and standard errors between participants) with pursuit instruction (left) and fixation instruction (right) as a function of condition (computer-generated vs. action-generated vanishing point). Positive values indicate displacements in movement direction, negative values opposite to movement direction (Experiments 1 and 2).

targets' position can be quite accurate at recurrent salient positions (e.g., the 6 o'clock position; for an overview see Fleury, Bard, Gagnon, & Teasdale, 1992). Therefore, improvements in localization accuracy could simply result from observers' strategy to preselect salient stop positions. A detailed analysis of the present data showed that all observers followed the instruction and varied the positions nearly equally over the whole trajectory. Accordingly, it can be concluded that the anticipation of the target offset, generated by the key press, lead to the more accurate localization judgements.

In contrast to the improvement in localization accuracy in the action-generated condition, a clear forward displacement different form zero occurred in the condition with a computer-generated offset (0.65°), $SE = .16$, $t(8) = 4.05$, $p = .004$. This result replicates previous findings with pursuit eye movements (cf. Kerzel et al., 2001). Kerzel and co-workers argued that with pursuit eye movements the persisting retinal image of the target drifts with the eye in the direction of movement and that from this drift, the perceived location emerged.

If Kerzel et al.'s (2001) suggestion is correct, an improvement of the eye-movement behaviour (i.e., in form of a reduction of the drift) could yield an improvement of localization judgements. The present experiment leaves open whether the high localization accuracy in the action-generated condition originated from an improvement of the eye-movement behaviour. The subsequent experiments address this issue. In Experiment 2 eye movements were eliminated by a fixation instruction and in Experiment 3 eye-movement trajectories were directly compared with the location judgements.

EXPERIMENT 2

In this experiment, we examine whether with an action-generated vanishing point localization accuracy is also improved with fixation. If in Experiment 1 the more accurate localizations originated from a reduced drift in the eye movements (induced by the action-generated anticipations of the vanishing point), an improvement should not occur with fixation. If the more accurate localizations stemmed from other factors than eye movements, an improvement is still expected. For example, it is possible that the prediction of the vanishing point allocates attention to that location, which might improve localization performance. Recent studies revealed that allocation of attention could indeed improve localization accuracy (e.g., Tsal, Meiran, & Lamy, 1995; for an overview see Tsal, 1999).

Method

Participants. Eight female and seven male students of the University of Munich who ranged in age from 21 to 37 years (mean age of 24.5 years) were paid to participate in the experiment.

Stimuli, design, and procedure. Stimulus presentation, design, and procedure were the same as in Experiment 1, except for the instruction that now emphasized to fixate the fixation cross during stimulus presentation.

Results and discussion

The data of one subject were excluded from further analysis because the mean localization score exceeded the criterion of ±2 standard deviations between participants. A *t*-test revealed no significant difference between the computer-generated and the action-generated vanishing condition, $t(13) = 0.50$, $SE = .14$, $p = .626$; cf. Figure 2 (right). There was a significant negative localization error with the computer-generated offset (–0.48°), $SE = .18$, $t(13) = 2.63$, $p = .021$, and the action-generated offset (–0.41°), $SE = .13$, $t(13) = 3.27$, $p = .006$.

Contrary to Experiment 1 with pursuit eye movements, the present experiment revealed a reliable mislocalization opposite the movement direction. Jordan and co-authors (2002) already speculated about a low-level explanation of this negative localization error. With fixation, retinal stimulation during one refresh frame overlaps with the stimulation of the previous frame(s). As a consequence, it is possible for stimulation to build up, simply as a function of the stroboscopic nature of presentation (for a similar idea in another context, see Ansbacher, 1944; Vierordt, 1868). Summation of stimulus information (cf. Bloch's law) caused by stimulation during successive frames may occur at all positions on the stimulus trajectory, save the final position. Given such summation, it may be the case that stimulation is less pronounced and consequently more often missed at the final position.[1]

In order to examine whether the negative localization error originated from the more pronounced stimulation of overlapping frames, the spatial amount of overlap was computed. The stimulus of 0.5° was rotated by an amount of 0.206° visual angle with every retrace frame of the monitor. Accordingly, when the stimulus vanished from the screen, the stimulus overlap was 0.294° considering two subsequent frames and 0.088° considering three subsequent frames. Or in other words, when the leading edge of the stimulus is considered as the zero point, the most pronounced stimulation was in between –0.206° and –0.5° (mean –0.353°, when considering two subsequent frames) or in between –0.412° and –0.5° (mean –0.456°, when considering three subsequent frames). Note, however, that the midposition of the adjustment cursor, which was identical in size to the

[1] Notice that a comparable negative displacement opposite movement direction, previously observed with linear and foveofugal movements (Kerzel et al., 2001), was attributed to a general tendency to judge peripheral targets more foveally than they actually are (cf. Müsseler & Van der Heijden, 2004; Müsseler, Van der Heijden, Mahmud, Deubel, & Ertsey, 1999). This tendency cannot account for the present data, because with circular movements displacements did not represent foveal tendencies at all.

target stimulus, determined the adjusted position. Consequently, when observers adjusted the midposition of the overlap, the values have to be reduced by another 0.25° (half of the size of the adjustment cursor). Thus, it is likely that the overlaps in stimulation of two or three successive frames cannot completely account for the observed localization error of –0.41° in the action-generated condition and of –0.48° in the computer-generated condition. But it possibly contributes to it.

In the present context, however, we are less concerned with negative mislocalizations than we are with the perception of action-generated and computer-generated vanishing points. Contrary to Experiment 1, the present results did not show a difference in this regard. Therefore it can be concluded from both experiments that localization judgements are not generally more accurate in the action-generated vanishing condition, but only in conjunction with pursuit eye movements.

EXPERIMENT 3

This experiment examines whether and how pursuit eye movements vary with the action-generated and computer-generated vanishing conditions. If different pursuit movements are found in the two conditions, the analysis will focus on possible relationships with regard to the localization judgement.

At least, two different eye-movement parameters might be critical for the location judgement. As mentioned before, one parameter is the drift of the eyes, after the target has vanished from the screen. This *overshoot* seems to move the persisting image of the target in the direction of movement. Kerzel (2000) suggested that the perceived vanishing position is determined by the position of the drifted eye at the point in time at which the persisting retinal image expires.

The second parameter is the position of the gaze at the point in time, when the target vanishes from the screen. In pursuit tasks the fovea often lags behind the target (*spatial lag*; e.g. Stork et al., 2002). Because of anticipating eye movements this lag is smaller than the assumed latency of the system would suggest (cf. Lisberger & Westbrook, 1985). Nevertheless, this spatial lag of the eyes could be important for the localization performance. Mateeff, Yakimoff, and Dimitrov (1981) emphasized that in a pursuit task retinal stimulation is not at the fovea but at a more peripheral position. Accordingly, they assume that the perceived localization emerges from the eye position when the target vanishes and the position of the target relative to the fovea.

In sum, two eye positions during pursuit of a moving target were suggested to influence target localization: the eye position when the target vanishes and the eye position after the persisting retinal stimulation expires. The aim of the present experiment is to look at both parameters and to relate them to the corresponding localization judgements.

Method

Participants. Six female and five male individuals who ranged in age from 20 to 30 years (mean age of 24.1 years) were paid to participate in the experiment.

Apparatus and stimuli. The experiment was carried out on a PC (Compaq Deskpro Pentium) and the stimuli were presented on a 17-inch colour monitor (ViewSonic 17PS) with a refresh rate of 75 Hz. The moving stimulus and its trajectory were similar to the stimulus presentation used so far (a circle with a radius of 5.5° visual angle, which corresponded to a radius of 53.3 mm at a viewing distance of 550 mm). The participant's head was placed on a chin and forehead rest in front of the monitor. The room was dimly lit.

Measuring of eye movements. Eye movements were gathered by a SMI Eye Link infrared video based eye-tracker (SensoMotoric Instruments GmbH). Each eye was measured with an infrared digital camera respectively. The reflection patterns on the cornea of two Light Emitting Diodes (LEDs), mounted beside each camera, were measured by the cameras. By isolating the pupil position, the point of gaze was calculated in *xy* coordinate pairs. The eye movements were sampled at a rate of 250 Hz with a second PC (Columbus Pentium). The trajectories were analysed offline by using MATLAB 5.0 scripts. A saccadic onset was defined as the point in time when ocular velocity exceeded 35°/s and the acceleration exceeded $9.500°/s^2$.

Before each block the system was calibrated by offering nine saccadic targets on the monitor. During the experiment, the calibration to the fixation cross was adjusted online and if necessary a drift correction was performed automatically in order to correct the drift in the calibration.

Design and procedure. Design and procedure were similar to Experiment 1, save for the following changes. Each trial began with an auditory warning signal. After 300 ms the central fixation cross changed its colour from red to green and the moving target appeared. Observers were instructed to immediately follow the target with the eyes until it vanished from the screen and then to make a saccade to the adjustment cursor. The adjustment cursor appeared 1.000 ms after the target had vanished from the screen.

Participants were confronted with 40 repetitions in the computer-generated and action-generated vanishing condition respectively. The two conditions were presented blockwise with the sequence of blocks counterbalanced between participants. The experiment lasted approximately 30 min, including the calibration, training trials, and short breaks.

Results and discussion

Trials were excluded from further analysis, if (1) the eye-movement algorithm was not able to detect a saccade at the end of pursuit (51 of 880 trials), (2) the localization error or the final eye position deviated more than $\pm 6^\circ$ visual angle from the actual vanishing position (32 of 829 trials), and (3) in the remaining trials the localization errors and eye positions were not in the range of ±2 standard deviations within participants. The data of one participant were completely excluded, because the mean values exceeded the criterion of ±2 standard deviations between participants.

The analysis of the location judgements revealed a significant localization error in movement direction in the computer-generated condition (0.71°), SE = .12, $t(9) = 5.92, p < .001$. In the action-generated condition only a tendency for a corresponding localization error was observed (0.28°), SE = .13, $t(9) = 2.1$, $p = .065$. However, the difference between the conditions was again significant, $t(9) = 2.65$, SE = .13, $p = .027$ (cf. Figure 3, panel A). This pattern of results replicates the findings of Experiment 1.

In each trial the offset of the pursuit movement was considered as the eye position at the point in time when the onset of the saccade to the adjustment cursor occurred. Figure 4 shows the eye trajectories of a typical observer for the two conditions. The plot nicely demonstrates the more pronounced overshoots of the eye in the computer-generated condition. Moreover, the trajectories seem to be flexed in anticipation of the stimulus path (cf. also Stork et al., 2002).

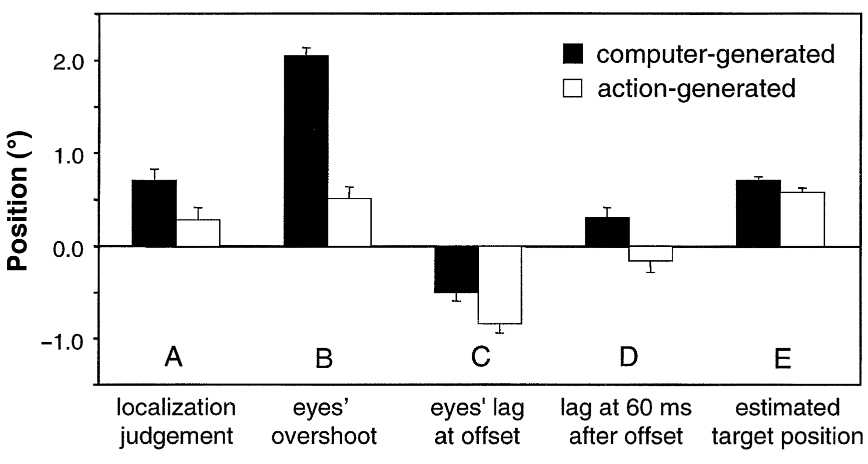

Figure 3. Mean localization judgements (A), eye positions (B: eyes' overshoot; C: eyes' lag at targets' offset; D: 60 ms after targets' offset) and estimated target positions (E) with a computer-generated or action-generated vanishing point (Experiment 3).

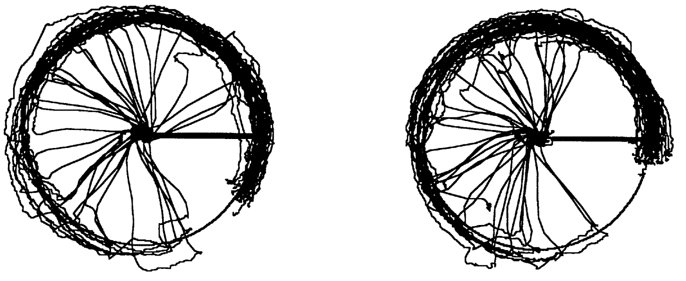

Figure 4. Eyes' overshoot of one typical observer in the computer-generated vanishing condition (left) and the action-generated vanishing condition (right). The targets' offset was arbitrarily rotated to the 3 o'clock position in order to compare different offset positions (horizontal line; Experiment 3).

The amount of eyes' overshoot was computed as the angular difference between the final target position and the position at the offset of the pursuit movement. This value represents a tangential displacement expressed in visual angle. Positive values indicate that the eyes overshot the offset position; negative values indicate that the eyes stopped before. Over all participants, mean overshoots different from zero were observed in both conditions; with the computer-generated vanishing condition: 2.05°, $SE = .08$, $t(9) = 24.79$, $p < .001$; with the action-generated vanishing condition: 0.51°, $SE = .12$, $t(9) = 4.41$, $p = .002$. A t-test revealed a significant difference between conditions, $t(9) = 8.49$, $SE = .18$, $p < .001$ (cf. Figure 3, panel B).

Analysing the eye positions at the point in time when the target vanishes from the screen revealed a spatial lag different from zero in both conditions; with the action-generated condition: –0.84°, $SE = .1$, $t(9) = 8.85$, $p < .001$; with the computer-generated condition: –0.51, $SE = .08$, $t(9) = 6.31$, $p < .001$. However, the eyes lagged further behind the target in the action-generated than in the computer-generated condition, $t(9) = 5.63$, $SE = .06$, $p < .001$ (cf. Figure 3, panel C).

Comparing the overshoot and the spatial lag of the eyes with the location judgements revealed corresponding effects between conditions (i.e., comparing panels A–C of Figure 3). Mean values were always larger in the computer-generated vanishing condition than compared with the action-generated vanishing condition. However, it is obvious that the perceived locations did neither correspond with the eyes' overshoot (cf. also Kerzel, 2003) nor with the spatial lag in absolute terms. In panel C the position of the fovea at the point in time when the target vanishes from the screen is shown, but there is no reason to assume that the perceived target position corresponds with the position of the fovea. The same is true with panel B. Of course, the fact that the eyes overshot a target does not indicate that the target is perceived at these locations.

According to Kerzel (2000), to get an estimation of the perceived target positions, the retinal persistence has to be taken into account. Kerzel assumed that the eyes move the retinal image in the direction of the movement for the time of visual persistence. The observed overshoot of the eyes in the present study clearly support this idea. Further, the author estimated the visual persistence of the moving stimuli in his experiments to last about 60 ms. Figure 3, panel D depicts the eye positions at the point in time of 60 ms after targets' offset in our experiment. A positive value was observed in the computer-generated condition (0.31°), SE = .09, $t(9) = 3.47$, $p = .007$, and a negative value in the action-generated condition (–0.17°), SE = .1, $t(9) = 1.75$, $p = .114$. The difference between conditions was also significant, $t(9) = 5.08$, SE = .09, p = .001.

Note, however, that in this last calculation of the eye positions the spatial lag observed in panel C of Figure 3 is also shifted with the eyes. In other words, the target still precedes the fovea in the shifted retinal image. To get an estimation of the perceived target position, one has further to add to these calculations the spatial lag of the eyes. The resulting values are shown in panel E. Now the estimated perceived positions of the computer-generated condition fit nicely the mean localization judgement (0.73°), SE = .03, $t(9) = 24.68$, $p < .001$. In the action-generated condition the estimated positions are somewhat smaller than the mean localization judgements (0.58°), SE = .05, $t(9) = 12.44$, $p < .001$, but the difference between estimations is still significant, $t(9) = 3.25$, SE = .05, $p = .01$.

In summary, the observed eye-movement parameters differed significantly between the two conditions. Due to predictive pursuit eye movements, which use anticipations of the ongoing stimulus movement, the eyes were more shifted in movement direction in the computer-generated condition than in the action-generated condition. With the action-generated offset, the prediction of the vanishing point enables eye movements to stop faster and to attain a greater spatial accuracy. Additionally, the assumed visual persistence of 60 ms and the observed spatial lag yielded eye positions that correspond nicely with the location judgements. This is further evidence for the assumption that the perceived stimulus positions depend on the overshoot of the eyes.

GENERAL DISCUSSION

The present findings showed crucial differences in the perceived locations of moving targets with action-generated and computer-generated vanishing points. In Experiment 1 with pursuit eye movements, localization errors were in movement direction, but more pronounced in the computer-generated condition than in the action-generated condition. In contrast, in Experiment 2 with fixation instruction, localization errors were opposite movement direction and independent from conditions. This pattern of results pointed at the role of eye movements for the perceived final positions (see also Jordan et al., 2001; Kerzel, 2000; Kerzel et al., 2001). Therefore, eye-movement trajectories were gathered in Experiment 3. They showed that the eyes lagged behind the target at the point in time when it vanished from the screen, but that then the eyes continued to move on the targets' virtual trajectory for some time. Comparing the spatial lag and the overshoot of the eyes with the localization judgements revealed corresponding effects with regard to the computer-generated and action-generated conditions. However, the absolute amount of mislocalization was not reflected in the eye-movement parameters. For an adequate correspondence, the visual persistence and the position of the target relative to the fovea had to be taken into account.

The suggested mechanism is as follows. The eye-movement trajectories have shown that the eyes lagged behind the target at stimulus offset. Therefore, a retinal image existed with a peripheral target preceding the fovea. The overshooting eye drifted this persisting image in movement direction for approximately 60 ms (cf. Kerzel, 2000). Accordingly, the last perceived position resulted from the drift of the eyes and last retinal position of the target relative to the fovea.

Previous eye-movement studies have already shown that the eyes tend to overshoot the vanishing point of a moving target (e.g., Becker & Fuchs, 1985; Mitrani & Dimitrov, 1978). We were able to demonstrate that this overshoot did not simply originate from inertia of the eyes, but instead seems to originate from some kind of anticipation of future target positions (Stork et al., 2002). Such anticipations need not necessarily be implemented as higher order anticipations. Also low-level implementations are conceivable (see, e.g., Erlhagen & Jancke, 2004; Müsseler, Stork, & Kerzel, 2002). Irrespective of the level of implementation, anticipations might cause the perceived mislocalization in movement direction, but they also enable the compensation of neural delays and therefore are able to minimize the spatial lag of the fovea (for details see Stork et al., 2002).

In the present context it is important to note that the eye-movement parameters and the localization judgements were modulated in the same way by the intentional control over the vanishing point. The result that the overshoot of the eyes was reduced in the action-generated condition is in accordance with comparable findings with predetermined final positions (Mitrani et al., 1979). Our result additionally demonstrated that not only anticipations based on external stimulus characteristics could be used to guide the eye, but also anticipations based on internally generated events (see also Lazzari et al., 1997; Steinbach, 1969; Vercher et al., 1997). The key press allowed the very precise prediction of the vanishing position, offering the possibility of reducing the eye velocity in advance and thereby reducing the overshoot. The fact that these reductions are accompanied by a decreased localization error suggests a strong dependency between these measures.

The suggested relationship between the eye-movement system and the localization behaviour is also observed with other phenomena of moving stimuli (for an overview see Ebenholtz, 2001). An early example stems from an observation of

Hazelhoff and Wiersma (1924). They reported that a stimulus, which is flashed above a moving stimulus, is mislocalized in movement direction when the moving target is tracked with the eyes. Metzger (1932) examined the same phenomenon with fixation and observed that the flashed target is now perceived at its objective position but that the moving target is mislocalized in movement direction with regard to the flash. This phenomenon, recently known as the flash-lag effect (e.g., Nijhawan, 1994; Nijhawan, Watanabe, Khurana, & Shimojo, 2004), already demonstrated that eye movements can modulate the localizations and that these modulations do not exclusively occur at the final position.

To conclude, the present paper started with the notion that the mislocalizations at the final position of a moving stimulus are often conceptualized in terms of representational momentum. The present findings disagree with a simple version of this idea. If at the vanishing position an internalized dynamic of an external stimulus representation would be sufficient to evoke the mislocalization, it should be independent from eye movements and from internally generated key presses, but it is. This is further evidence that action-control mechanisms are able to exert an elementary influence on perceptual processes.

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