

Motion trajectory illusion and eye movements*

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We describe a visual illusion where a moving target produces an illusory trajectory. Previously it has been suggested that this illusion is related to eye movements, but the exact nature of the relation, as well as relevant stimulus conditions and eye movement type were unknown. In two experiments, we varied critical stimulus conditions, recorded eye movements and judgments of trajectories. In Experiment 1, a visual cue led to a reduction of the illusion, however, only if a saccadic eye movements preceded the target's change of direction within a critical inter-

val, assessed by SacOA (Saccadic Onset Asynchrony). In Experiment 2, an analogous result was found under conditions of sudden velocity changes. The results are explained by a critical timing between smooth pursuit and different phases of saccadic eye movements.

Key words: *Smooth pursuit eye movement, saccadic eye movements, motion perception, perceived velocity, motion illusion, motion trajectory*

Judgment of the trajectory and velocity of a moving object is of great importance for analyzing and recognizing the dynamic visual world. Accurate judgment is difficult because the retinal image is not always stable during either saccadic eye movements or pursuit eye movement phases. Saccades tend to suppress visual inflow (Volkman, Riggs, White & Moor, 1978) and pursuit eye movements reduce correct motion information (Stoper, 1973). Several studies concerning the role of eye movements in the modification of visual motion perception have been published. These studies may be categorized into (1) those concerned with the relationship between eye movements and illusory velocity perception of targets moving with

constant velocity, and (2) those concerned with the perception of illusory motion trajectories and its relation to eye movements.

Studying illusory motion velocity perception, Dichgans et al. (1969) reported that a moving object is perceived to move more slowly when tracked by pursuit eye movement. The extent of reduction in velocity was 10 to 40 percent. Mack & Bachant (1969) examined this phenomenon using an afterimage on the retina which produced an illusory motion perception. When pursuit eye movements occurred, the afterimage appeared to move in the same direction as the pursuit eye movements. Mack & Herman (1972) compared the effect of eye movements (saccadic and pursuit eye movement) when apparent movement was observed. An apparent movement over the same distance produced longer distance estimates when observed by saccades rather than by pursuit eye movement. This illusory perception was investigated by Mack & Herman (1973) using composite velocity conditions of the target and background. The target appeared to move more slowly when tracked by pursuit eye movements. The authors compared this to the Filehne illusion (Filehne, 1922) which is observed when a stationary object appears to move in the opposite direction when a pursuit eye movement occurs. In a subsequent study, Mack &

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Herman (1978) examined the Filehne illusion by measuring position constancy during pursuit eye movement. They found that the stationary object appears to move in the direction opposite to the tracking eye movements. Miller (1980), investigating the same phenomenon, discussed it in relation to an afferent/efferent (perceptual/motor) neural interaction model. However Westheimer (1954) showed that these efferent interactions were of a more general nature and should rather be called extraretinal information.

A modulation effect of pursuit eye movements on motion perception was demonstrated with a non-moving stimulus by Koga & Groner (1990). When one of two visual targets moved laterally at a constant velocity, and the other stimulus remained stationary, the moving stimulus pursued by the eye was perceived as motionless. On the other hand, the stationary stimulus was perceived as a moving object. An explanation of these results was given in terms of two sources of motion information: a displacement detector which is based on retinal coordinates, the other arising from proprioceptive sensing units based on eye movements. As a consequence, a target moving with constant velocity produces different motion velocity perceptions compared to the objective movement of the target. This perception depends on the particular eye movement phase, such as fixation or smooth pursuit, which has a strong modulation effect on the perceived velocity. Koga et al. (1988) demonstrated such an effect using a composite scrolling visual stimulus which consisted of an object and a surround which moved at the same speed behind a slit. Two clearly different perceptions were obtained. The first was a slow velocity perception for the surround when it appeared together with the object. The second was a high velocity perception of the surround when it was presented without the object. When the object moved together with the surround at the same speed, the eye pursued the object smoothly while the object and surround remained in almost the same retinal position, thus producing a relatively slow velocity. On the other hand, when the surround appeared without the object, no pursuit eye movements were observed. Rather, a position somewhere around the edge of the slit was fix-

ated. In this situation, the surround traversed the central foveal area, producing the perception of a relatively high speed motion. It was concluded that the velocity difference between stimulus and surround motion produced different velocity perceptions, dependent on retinal position and eye movement phase (saccades vs. smooth pursuit). This, in turn, might result in non-veridical visual velocity perception.

The second aspect of the modulating effect of eye movements on motion perception has been discussed in terms of the perception of illusory motion trajectories. Fujii (1943) was probably the first author to examine systematically the non-veridical perception of motion trajectories. He reported large discrepancies between the actual path of a target motion and the visually perceived motion trajectory under a wide variety of target motions. Sumi (1964a, 1964b, 1966) interpreted this non-veridical perception as a motion aftereffect, but he did not deal with the modulation effect produced by eye movements. However, neither Fujii nor Sumi noticed the importance of eye movements for the perception of motion. Mack, Fendrich & Sirigatti (1973) examined the relationship between eye movement and illusory backward motion when an abrupt change of motion occurred. They concluded that this illusion, called "rebound illusion", was caused by an unmonitored overshoot of the target by the eye. They suggested that the position information during eye tracking is derived from neuronal efferent signals based on proprioceptive feedback from extraocular muscles. Festinger & Easton (1974) emphasized the important role of eye movements for this illusion which they called "Fujii illusion". Prior to their work, subjects were typically instructed to simply follow the moving target without any explicit control. Festinger and Easton monitored eye position during the target movement and recorded it simultaneously with the actual target position. From the composite signal between the target and eye position, the motion path was calculated and was shown to be similar to the perceived target motion trajectory, in particular at the location of the change in target direction. This implies that the composite retinal position signal is one of the factors that determines the non-veridical perception of the motion trajectories. Festinger

et al. (1976) emphasized the importance of the timing differences between efferent command for extraocular muscles and the change in the position of the eye itself.

In summary, a model of motion trajectory perception that accounts for both, veridical and non-veridical aspects should include both static and dynamic signals from the environment (surround and target) which then serve as stimuli for the saccadic and the smooth pursuit system. Motion trajectory perception is considered the result of a computation which combines both sources of information. In most natural situations, this leads to veridical perception. However, some situations can be constructed experimentally which cannot be handled by the two systems, leading to non-veridical perception.

The experiments described below were designed to create such situations and to examine the role of smooth pursuit and saccadic eye movements including fixation for the perception of motion trajectories. In our experiments, eye movements were recorded as concomitant events and there was no attempt to manipulate them experimentally. Some conditions were introduced which were expected to influence eye movements. We analyzed eye movement phases and compared them with the judgments of the perceived motion trajectories.

Experiment 1: Effects of a static cue

Method

Subjects

Ten subjects, 7 male and 3 female, with normal visual acuity and their age ranging from 20 to 26, participated in Experiment 1. The subjects had no previous experience with psychophysical experiments and were not aware of the purpose of the experiment.

Apparatus

Stimuli were generated on a high-resolution graphic display system (COMTEC-2555) under the control of MicroVAX-II. The eye position was registered by an automatic video image tracking system (Hamamatsu C1000 with NEC-

PC9801) using the infra-red first-Purkinje reflection method (Koga and Osaka, 1983). The sampling time was 16.7 ms in both the horizontal and vertical components of the eye position. Spatial resolution was 0.2 deg in both horizontal and vertical components. Prior to each session, a calibration was performed to linearize the horizontal and vertical components. The fixation points for the calibration in the two-dimensional area on the display screen were shown to the subject before the trial sessions.

Procedure

Motion targets were generated on the display screen. The starting position of the moving target was randomly assigned to one of four mid-points of the visible window edge on the display screen. The motion target had a diameter of 5 mm subtending 0.5 deg of arc and a brightness of 7 cd/m² against the display screen background of 1 cd/m². The target moved with a constant velocity of 5.7 deg/s for one second, traversing 6 cm on the screen which corresponds to 5.7 deg visual angle, and then changed its direction abruptly at the center of the screen at a right angle on either side. The distance for the observation from the subject and the center of the display was 60 cm. For half the trials, a visual cue was added which contained information, when and in what direction the target would change its trajectory (with-cue condition). The cue consisted of a thin bar having a length of 1 deg of arc at the center of the display, and it was slanted 45 degrees from the direction of the motion trajectory in order to indicate the location of the target's change of motion and its future trajectory direction. This cue could be used by the subjects as a predictor of the location where the target would turn, as well as of the direction in which its trajectory would continue. On the other hand, it could also be used as a stimulus for a saccadic eye movement and subsequent fixation.

Figure 1 shows schematically one example of the motion target trajectory pattern. In the with-cue condition, the visual cue was presented simultaneously with the moving target. In the without-cue condition, during the entire

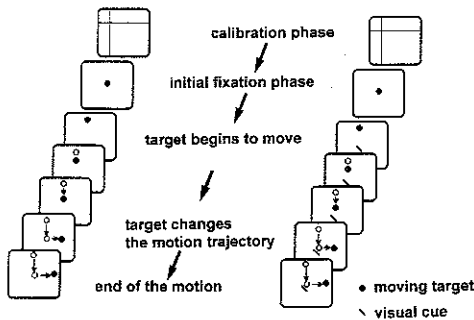


Figure 1: The stimulus configurations for both without-cue and with-cue conditions for one condition with the target motion trajectory in each condition. Each experimental condition included eight different motion trajectory patterns.

trial the cue was not present. By combining the four starting positions with the two directions of changing the trajectory, eight motion trajectory patterns were generated which, combined with cue condition, represented the full set of stimuli. For both, with-cue and without-cue condition, eight motion trajectory patterns were used in ten replications.

Before data acquisition, a training session of about one hour allowed subjects to become familiar with the procedure. They were shown several examples of both with-cue and without-cue trials, at first without being asked for any judgments. After a first block of trials with cue and one without cue they were instructed to press one button if the perceived path followed the simple pattern forward – turn 90° – forward, and the other button if it did not. Nothing was said about the true path of the trajectory, nor was any hint given about possible relations to the experimental conditions. In fact, none of the subjects noticed the relationship between judgment and cue condition. For convenience, we will use the terms “veridical” and “non-veridical”, although these words were actually never used in the communication with the subjects.

After the training session, each subject served in 2 test sessions. Each consisted of 10 trials of stimulus replications in random order. In a balanced order, the 2 sessions were performed by each subject, one of them consisting of the 80 with-cue condition trials, and the other entirely of the 80 without-cue condition trials.

The data consisted of individual calibration data, and for every trial, a continuous eye position recording (horizontal and vertical component), plus the corresponding veridicality judgment. In a computerized automatic procedure supervised by the experimenter, the eye movement recordings were first subjected to a linear transformation based on the off-line calibration data, and then analyzed with respect to phases of smooth pursuit versus saccades and fixations. The onset of saccades was determined, defined as a velocity change on the vertical and/or the horizontal component of the eye movement recordings larger than 40 deg arc/sec. This threshold value had been determined in previous studies using the same equipment (Koga & Osaka, 1983; Koga et al., 1988; Koga & Groner, 1990). Both horizontal and vertical components of the eye position data stored were differentiated digitally and the position data were converted into velocity components. Saccades were searched for automatically from the velocity component data using DSS (Digital Signal processing System) and Wave Master II (by Canopus Inc.). Once a saccade was detected, the time interval between the onset of the target's directional change and the initiation of the saccade was calculated. In the following, this time difference is referred to as saccade onset asynchrony (SacOA). Sign is negative if the saccade occurred before the direction change. If there was no saccade within 500 ms before the directional change, a saccade was searched within an interval of 500 ms after the target's direction change, and the SacOA was recorded as positive. If there was no saccade within this temporal windows of 1 sec, “No SacOA” was recorded.

For a statistical analysis of the interrelations between cue condition, SacOA, and veridicality of judgment, a loglinear analysis (Goodman, 1978) was performed using hierarchical loglinear models (Norusis, 1993). The models contained the factors a) two cue conditions, b) three signs of SacOA (positive, negative, or none), and c) two possible veridicality judgments. Separate frequency distributions of SacOAs were computed for all combinations of factors a and b.

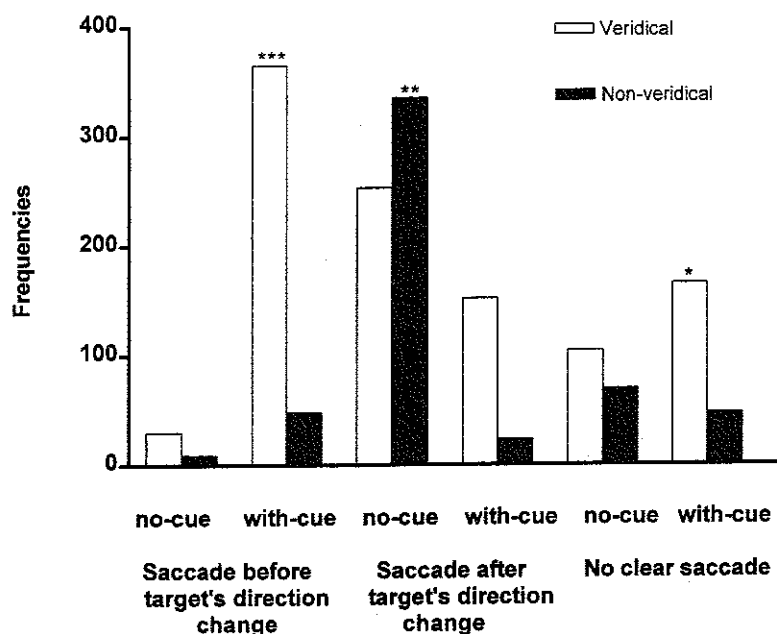


Figure 2: Frequencies of veridical and non-veridical judgments, dependent on cue condition and latency of first saccade; results of the loglinear statistical analysis.

Results

Figure 2 shows the pattern of results based on the analysis by categories. The three-way hierarchical loglinear analysis revealed a high degree of statistical dependency between all pairs of variables. There were more veridical judgments in the with-cue condition (85%) than in the without-cue condition (48%) (partial $\chi^2 = 113.05$; $df = 1$, $p < .001$), and there were more veridical judgments associated with negative SacOAs (87%) than with positive SacOAs (53%) and no saccades (69%) (partial $\chi^2 = 22.00$; $df = 2$, $p < .001$). In the with-cue condition, 91% negative SacOAs were observed, compared to 23% at positive SacOAs, and 55% for the observations without saccades (partial $\chi^2 = 457.19$; $df = 2$, $p < .0001$).

In Figure 2, there are three combinations of conditions that show much higher frequencies than are to be expected by chance: veridical judgments under with-cue conditions after negative SacOAs (observed frequency: 365, expected frequency: 151; $z = 24.04$, $p < .0001$), non-veridical judgments under without-cue condition after positive SacOAs (observed frequency: 335, expected: 127; $z = 23.99$, $p < .0001$), and veridical judgments under with-cue condition associated with no saccade (ob-

served frequency: 165, expected: 129; $z = 4.34$, $p < .001$).

Figure 3 shows the frequency polygons of the SacOAs. Their distribution around zero differs remarkably.

Discussion

For a better understanding of the patterns of results, we show an example of typical eye movements patterns for both the without-cue (upper panel) and with-cue condition (lower panel) in Figure 4.

Detailed inspection of both eye and stimulus position reveals an interesting relationship. When no visual cue was presented to the subject, the eye started to pursue the moving target after it had left its departure. Pursuit eye movement also continued in the same direction after the direction change of the target. In the without-cue condition, most of the smooth pursuit eye movement overshoot the center of the screen where the target changed its direction abruptly and continued the smooth eye movement. At the overshoot position, the smooth pursuit eye movement stopped, and the subject kept a short fixation. Thereafter, the subject made another saccade towards the moving target.

With-cue Condition

Without-cue Condition

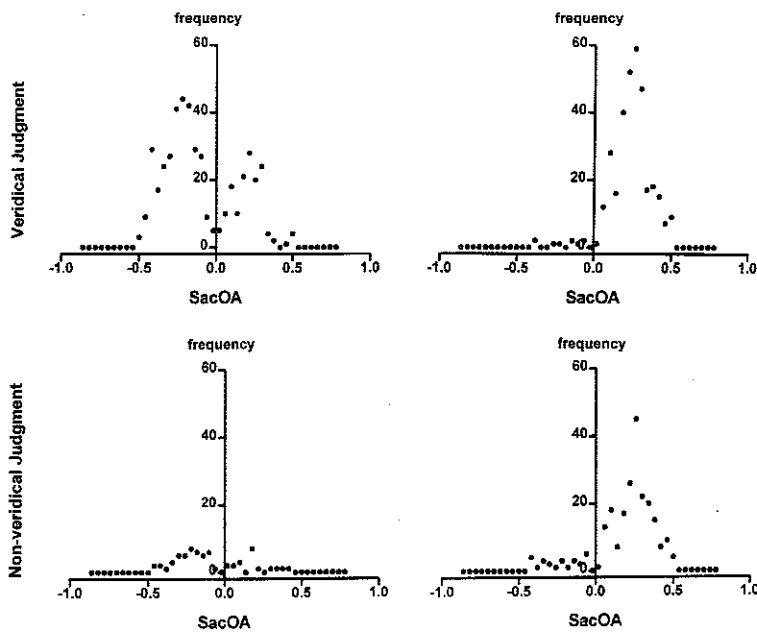


Figure 3: Absolute frequencies of SacOA in both with-cue and without-cue conditions for veridical and non-veridical judgments. In the with-cue condition, a peak for negative and another one for positive SacOA can be observed. In the without-cue condition, a peak is observed only for the positive SacOA, in both veridical and non-veridical judgments.

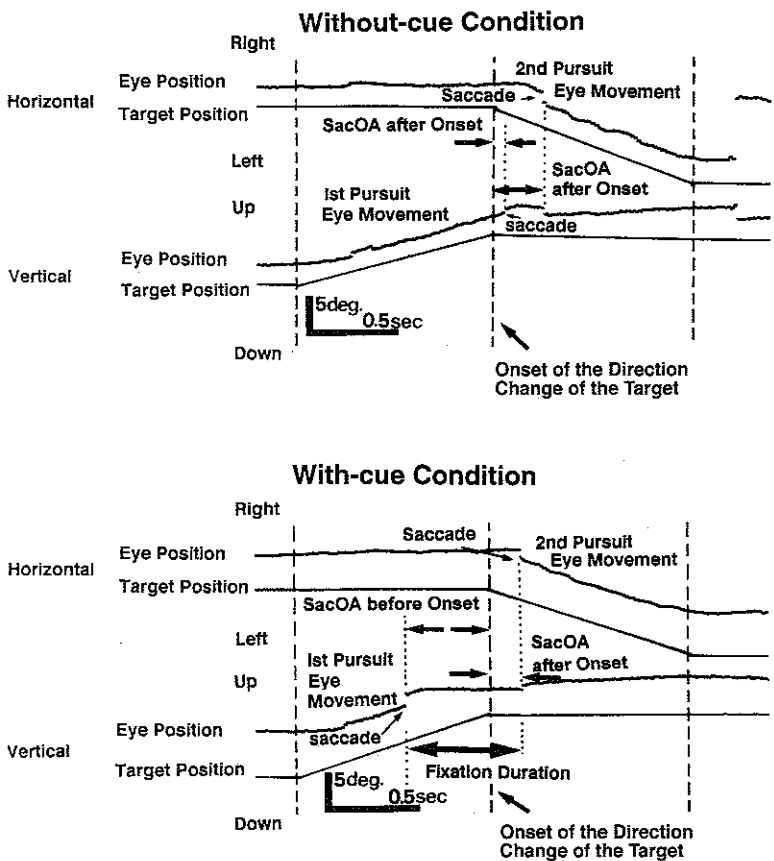


Figure 4: Typical eye movement for both horizontal and vertical positions in the without-cue and with-cue conditions. For an explanation see text.

On the other hand, in the with-cue condition, the eye stopped smooth pursuit before the target's change of direction at the midpoint between departure and the center of the screen; then it made a saccade to the visual cue at the center of the display screen when the target was still moving towards the visual cue. After the saccade, eye fixation continued at the location of the visual cue for a while, as if waiting for the moving target to arrive at the visual cue. After the onset of the target's change of direction, the eye made a saccade, then again continued pursuing the moving target. Figure 5 also shows the schematic diagram for two dimensional eye movements and target motion trajectory simultaneously.

This shows two interesting points: First, the Subject was unable to change the direction of the pursuit eye movement corresponding with the abrupt change of the target's direction. Second, the subject continued the pursuit eye movement – in the wrong direction – after the change of the target's direction. It is reasonable to hypothesize that the smooth pursuit eye movement predicts not only the target's velocity but also the target's motion trajectory.

In the with-cue condition, on the other hand, the subject stopped the smooth pursuit eye movement at the half way point of the motion trajectory without having been instructed, and made a saccade prior to the onset of the direction change, then made a longer fixation at the center of the screen where the visual cue was presented. After the change of target direction, the eye remained fixed at the position of the visual cue, and then made another saccade to follow the moving target that had changed its direction. Smooth pursuit eye movement continued until the end of the target motion. Between the first and second eye pursuit in the with-cue condition, the Subject kept fixation at the visual cue. Thus the target's trajectory pattern was kept fixed on the retina resulting in a more veridical motion trajectory perception. The difference of the eye behavior between without-cue (pursuit eye movements) and with-cue condition (fixation) at the moment of target's direction change corresponds to the non-veridical or veridical motion trajectory perception. Consequently, there was a strong relationship between subjective perception of the

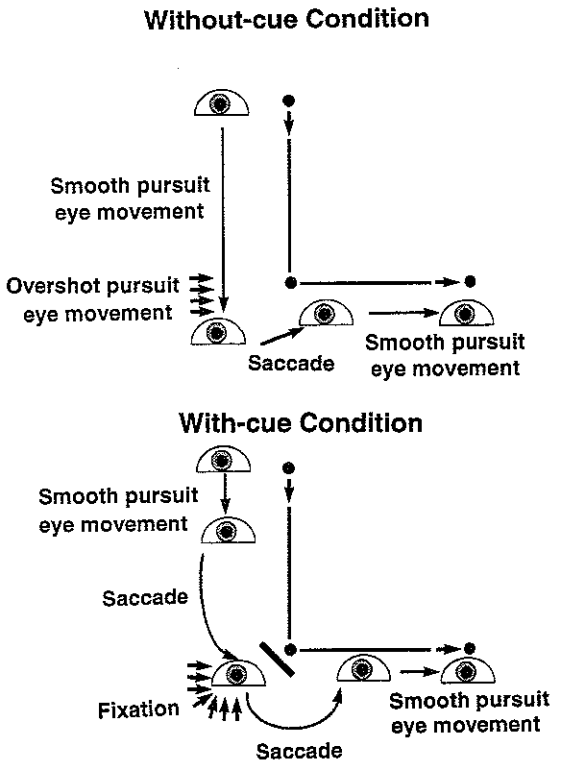


Figure 5: The relation between eye movement and target movement. Smooth pursuit eye movement mostly exceeds the position of the target's change of direction in the without-cue condition. In the with-cue condition, on the other hand, the eye quits the smooth pursuit before the target's change of direction, then makes a small saccade and keeps fixation as if waiting for the approaching target. After the change of target direction, eye again makes a saccade to catch up the moving target and then switches to the smooth pursuit mode again.

motion trajectory pattern and the mode of eye movement phase in experiment 1. It can be expected that, under eye fixation, the target's trajectory pattern is seen more veridically than under pursuit because, in the latter, the different direction of the eye and of the target leads to a composite trajectory. This may cause non-veridical perception of the target's motion.

Based on this hypothesis, a second experiment was designed to establish the relationship between non-veridical perception and eye movements. Different target velocity combinations, before and after the onset of the target's direction change, were introduced in order to examine whether the adaptation of the pursuit eye movement to different target velocities corresponds to the veridicality of the target motion

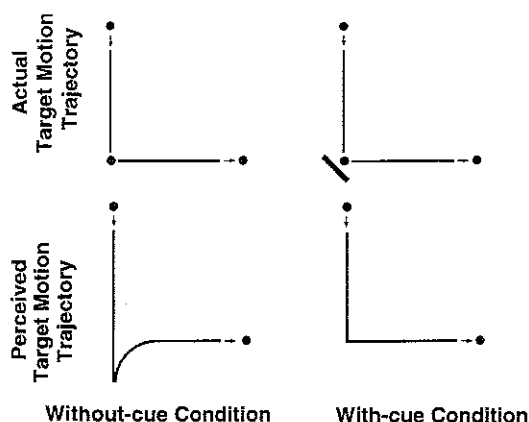


Figure 6: Actual and perceived target motion trajectory in the without-cue and with-cue condition, respectively. Where no visual cue for the moving target is shown, most of the perceived target motion trajectory was non-veridical.

trajectory perception. Figure 6 shows both veridical and non-veridical motion trajectory schematically, which were reported by the subjects after the experiments in both with-cue and without-cue conditions.

Experiment 2: Trajectory perception with changing target velocities

From the previous experiments it was concluded that different eye movement phases, fixation or pursuit eye movement, produced different motion trajectory perceptions. Specifically, when smooth pursuit eye movement continued after the target's direction change, non-veridical motion trajectory perception was most frequently observed. If a failure of the pursuit eye movement system causes non-veridical trajectories, we should also be able to increase non-veridical perception by introducing more difficult conditions for the smooth pursuit system, increase non-veridical perception. Velocity might affect the non-veridical target motion trajectory, because pursuit eye movement alone can follow only a limited range of target velocities, of approximately 5 deg/s up to 40 deg/s (Westheimer, 1954; Yarbus, 1967).

In Experiment 2, we used the without-cue condition (including conditions near the lower threshold of target velocity for pursuit eye

movements) to examine whether the pursuit eye movement contribute to the perception of motion trajectory. If the eye can pursue the target more easily, it may tend to exceed (overshoot) the location and timing for onset of target direction.

Method

Subjects

Six male and one female subjects, aged 25 to 48, participated in this study. They had normal or corrected-to-normal vision and were different from those who participated in Experiment 1.

Apparatus and stimuli

The stimuli were presented on a high-resolution graphic display system (ONYX, SG). They were generated in the same way as in the previous experiment. The target had a diameter of 3 mm subtending 0.3 deg of arc. The brightness of the target and background of the display screen were adjusted to 7 cd/m² and 1 cd/m², respectively. The moving target changed direction and velocity abruptly at the center of the screen perpendicularly in each trial in the same way as in Experiment 1. A cue was never shown. The velocity of the moving target was set differently before (at a velocity v_1) and after (v_2) the direction change of the target. Six velocity combinations of v_1 and v_2 were employed, and one condition of constant velocity was added, resulting in the following combinations of v_1/v_2 : 7.7/1.5, 7.7/3.1, 7.7/6.2; 1.5/7.7, 3.1/7.7, 6.2/7.7; and 7.7/7.7 deg of visual angle per second, respectively. The corresponding velocity ratio combinations were 5.0, 2.5, 1.25, 0.20, 0.40, 0.80, and 1.0, respectively. These velocities are near the lower threshold of the pursuable velocity of the eye (Westheimer, 1954).

Procedure and data analysis

As in Experiment 1, there were eight motion trajectory patterns, and now each pattern was duplicated in 5 trials for a total of 40 trials in

one session in random order. The time difference between the closest saccade compared with the onset of velocity change from v_1 to v_2 (SacOA) was measured in the same manner as in Experiment 1.

Eye movements were registered using DC-EOG whose signal were fed to a PC via 12 bit AD-converter with a 3 ms sampling rate. Data were calibrated with 17 random-position fixation prior to the trials and linearized after the experiments in the same manner as in Experiment 1.

Prior to the test session, subjects underwent a 1 hour training session to become accustomed to the situation. The subjects were seated at a distance of 60 cm from the screen. They were asked to pursue the moving target with both eyes and, after the target had disappeared, press one of two buttons, under the same instruction being used as in Experiment 1.

The processing of the data was done as in Experiment 1 with an extension of the SacOA analysis as described below. Again, a hierarchical loglinear analysis (Goodman, 1978) was computed with the variables a) two directions of velocity change (decreasing versus increasing), b) three amounts of velocity change (large: containing 7.7/1.5 and 1.5/7.7, respectively; versus medium: containing 7.7/3.1 and 3.1/7.7, respectively; versus small: containing 7.7/6.2 and 6.2/7.7, respectively), and c) veridicality of judgment (veridical versus non-veridical). The control condition (7.7/7.7) was left out from the loglinear analysis.

The SacOA analysis, i.e. the time delay of the last saccade that either preceded or followed the onset of velocity change, was performed in the same way as in Experiment 1, but in addition to the first saccade, the second one following immediately next was computed and analyzed, too. The difference between corresponding SacOAs reflects the duration of fixation at this moment.

Results

How does the sudden change of speed affect the perceived trajectory? One could expect that a decrease in velocity is more detrimental to veridicality since it will produce more over-

shoots and therefore will lead to more non-veridical judgments. Pooling the data over all trials with decreasing velocities from v_1 to v_2 results in 70% non-veridical judgments, as compared to 61% non-veridical judgments in all trials with increasing velocities. This difference is statistically significant (loglinear analysis: partial $\chi^2 = 54.09$; $df = 1$, $p < .001$). The amount of change plays also an important role: If there is a large change, by a factor of 5 or, vice versa, 0.2, we observe 59% non-veridical judgments; if there is a medium sized change (factor 2.5 or 0.4) non-veridical-judgments increase to 69%, and if the change is small (factor 1.25 or 0.80) non-veridical judgments reach their highest percentage of 80%. This increase in non-veridicality is statistically significant (partial $\chi^2 = 60.62$; $df = 2$, $p < .001$).

In addition to these main effects, there is an interaction between the experimental factors as represented in Figure 7, which shows the percentage of non-veridical judgment of the target motions in each velocity combination. The strongest discrepancy between random expectation (as defined by the residuals from the loglinear model that accounts for all possible two-way interactions) can be found in the group 1.5/7.7 with only 42% non-veridical judgments, as compared to a random expectation of 49.5% (statistically significant: $z = -4.92$, $p < .001$). On the other hand, the group with the same amount of velocity change but decreasing (i.e. 7.7/1.5), resulted in 76% non-veridical judgments, compared with a random expectation of 68.7% (significant: $z = -4.92$, $p < .001$). In summary, a strong sudden increase of the target's velocity leads to comparatively few non-veridical judgments, a decrease of the same amount results in a much high percentage (almost double the amount) of non-veridical judgments.

What are the typical eye movement patterns associated with these conditions? Figure 8 shows the mean SacOAs in each velocity combination, arranged in ascending order of v_2 and v_1 . While the SacOAs of the saccades after the target's directional change appear to be constant, the SacOAs before the target's direction change decrease gradually. When the v_1 decreased to 1.5 deg/s – which is almost impossible to pursue by eye tracking – the average

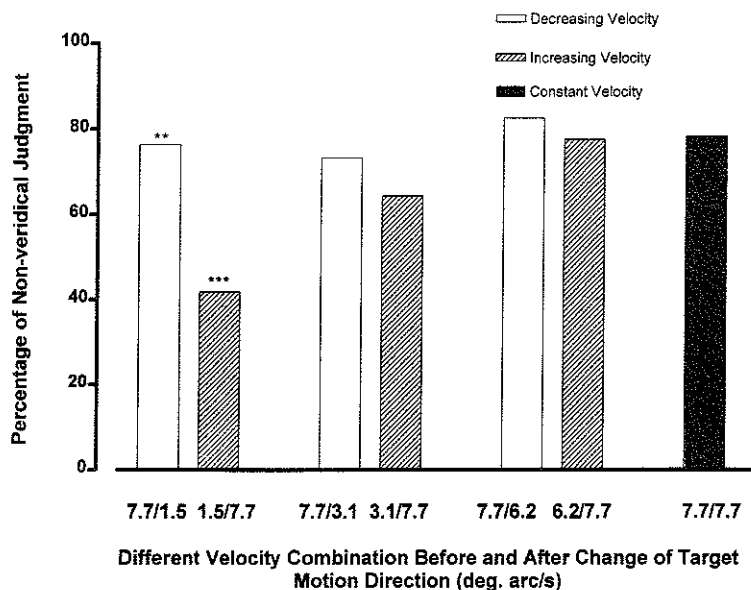


Figure 7: The percentage of non-veridical judgment of the target motion in each velocity combination before and after change of target motion direction. Velocity condition for the target motion was categorized into decreasing pair of v_1/v_2 , increasing pair of v_1/v_2 , and constant velocity pair of $7.7/7.7$.

SacOA of the first saccade showed negative values as was observed in the with-cue condition of Experiment 1.

Statistical tests were conducted on the SacOAs by means of an ANOVA. There was a significant main effect of the velocity combinations, $F(6,84) = 10.38$, $p < .001$, and also for the difference between the first and second saccade, $F(1,84) = 534.91$, $p < .001$. The interaction between velocity combinations and first versus second saccade was shown to be statistically significant, $F(6,84) = 3.50$, $p < .001$. The latter means, that the differences between the

SacOAs between second minus first saccade – corresponding to fixation durations – increase gradually, from 178 ms at velocity combination $7.7/1.5$ to 255.8 ms at $1.5/7.7$, and this increase was shown to be statistically significant by the test of the interaction.

Discussion

In the loglinear analysis, all three possible sources of variation – the main effects of direction change and of amount, as well as their

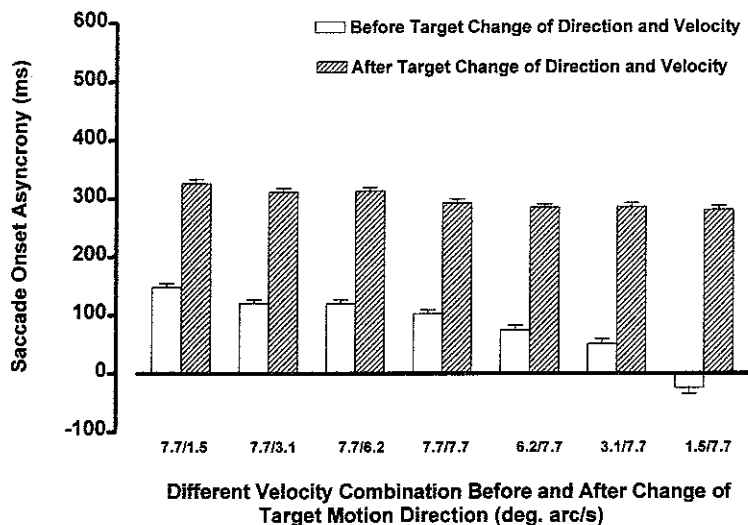


Figure 8: Average SacOA (± 1 SE) before and after the target change of direction shown for each velocity combination.

interaction were found to have a highly significant effect on frequencies of non-veridical judgments. A velocity change from fast to slow produced a 9% higher percentage of non-veridical judgments as the reversed change from slow to fast. Somewhat surprisingly, a small amount of change produces the lowest percentage of non-veridical judgments, a medium change decreases that percentage 11%, and a large amount of change reduces non-veridicality judgment for another 10%. However the interaction between direction and amount of change makes the picture even more complex: the combination of slowest velocity at v1 with highest velocity at v2 has with only 42% an even lower percentage of non-veridical judgments than expected by a linear combination of the two main effects.

This complex interaction between the two factors motivated us to perform the ANOVA of the SacOAs with one combined factor of velocity changes. This factor included the six experimental groups that resulted from all the combinations of the previously two factors, plus the constant velocity condition. The second factor of the ANOVA was the SacOA of the immediately next saccade. Since the difference of the second and the first saccade reflects the duration of the fixation which was closest to the target's direction change, it provides important additional information. In Figure 9, it can be noticed that the velocity combination 1.5/7.7 – which gave rise to the interaction in the loglinear analysis and had the smallest percentage (42%) of non-veridical judgments – is also the only one which produces a substantial amount of negative SacOAs. For this reason we plotted in Figure 9 the individual fixation durations as they occurred with respect to the time scale of direction change. We predict that those trials which start their fixation before the target's direction change will lead to a veridical judgment. In Figure 9, 60.3% of the trials start their fixation before the target's direction change which is almost identical with the percentage of veridical judgments in this condition, 58%. It can also be seen that, while the beginning of the fixation varies systematically with respect to the time of the target's direction change, the end of fixation is much less related to this event.

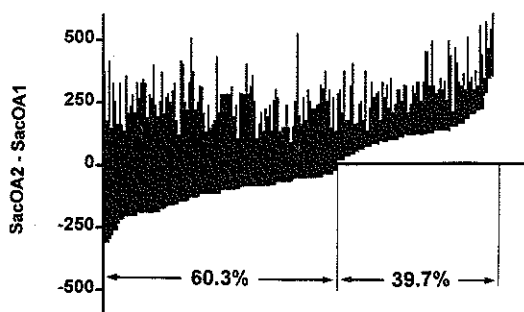


Figure 9: The difference of SacOA2 – SacOA1 in the condition of 1.5/7.7, plotted individually and arranged in ascending order of SacOA2.

This finding – which also results in the longer average duration in this condition – can be interpreted that, after the target's directional change, subsequent saccades were inhibited for a certain time in order to allow for a spatial orientation.

General discussion

There is an interesting connecting link between the results of the loglinear analysis of the veridicality judgments and the ANOVA of the SacOAs: The same condition which produced by far the smallest percentage of non-veridical judgments, is also the only one which has a considerable amount of negative SacOAs. This correspondence matches to the result of Experiment 1 where the with-cue condition produced the largest amount of negative SacOAs and also the smallest percentage of non-veridical judgments. Thus we might conclude that in Experiment 2, the small velocity v1 had a similar effect as the static cue in Experiment 1, to produce saccadic eye movements and fixations, which had a positive effect on veridical judgments about the target's trajectory. With respect to tracking, however, this condition of small velocity of v1 makes the task more difficult; in fact almost impossible, to follow such a slow stimulus by means of smooth pursuit eye movements.

Thus we arrive at the apparently paradoxical result that, conditions which make a task on the perceptual level almost impossible to solve, lead to a much better performance on the level of (veridical) judgments. The paradox disap-

pears, if we take into account, that the task is more difficult only for the smooth pursuit system, for the saccadic system it will become easier if there are static – or almost static – stimuli available which then can serve as fixation points for the saccadic system. However, there is another prerequisite for veridicality. For this, discrepancies between the results of the two experiments should be examined more closely.

The average percentage of non-veridical perception was greater in Experiment 2 than in Experiment 1. We observed in preliminary experiments that a smaller sized moving target increased the frequency of non-veridical perception. It should be noted that in Experiment 1 the diameter of the target was 0.5 mm and in Experiment 2 it was 0.3 mm. One possible explanation of this phenomenon can be discussed from the viewpoint of the visibility of moving targets; this, however, was not the main purpose of this study, and this hypothesis could be examined in more detail in the future.

We must also examine the effect of the initial target velocity condition, v_1 . When v_1 was slow and rather below eye pursuit threshold, the alternation of saccadic eye movement and fixation compensates for pursuit failure. However, only when the timing of alternating saccades and fixations happened in such a way, that one fixation bridged exactly the time interval before and after the target's change of direction, only under this condition a veridical perception of the trajectory is possible. The crucial issue is not just the saccadic system: in addition, the temporal relation between fixations and simultaneous target motion changes is most important.

Our stable visual world is usually made up by taking in visual information with successive fixations about the object's properties like shape, color and brightness, and object depth. Dynamic characteristics of visual information such as motion and changes in size are also important for properly recognizing the visual world. They are all processed at the different part of the visual cortex. On the other hand, the purpose of innate pursuit eye movement is to stabilize moving objects on the central part of the retina, not only to obtain temporal information, such as object velocity, but also to recognize more clearly spatial characteristics such as

shape or color. The above-mentioned results indicate that the pursuit eye movement may have the property of sacrificing the veridical motion perception of moving objects in terms of both velocity and motion trajectory. Thus, pursuit eye movements can capitalize more on information about the static characteristics of the object, but this happens on the costs of the dynamic aspects of visual information, such as object velocity and target motion trajectory.

References

- Dichgans, J., Koerner, F. & Voigt K. (1969). Vergleichende Skalierung des afferenten und efferenten Bewegungsssehens beim Menschen: Lineare Funktionen mit verschiedener Anstiegssteilheit. *Psychologische Forschung*, 32, 277–295.
- Festinger, L. & Easton, A. M. (1974). Inferences about the efferent system based on a perceptual illusion produced by eye movements. *Psychological Review*, 81, 44–58.
- Festinger, L., Sedgwick, H. A. & Holtzman, J. D. (1976). Visual perception during smooth pursuit eye movements. *Vision Research*, 16, 1377–1386.
- Filhene, W. (1922). Über das optische Wahrnehmen von Bewegungen. *Zeitschrift für Sinnesphysiologie*, 53, 134–145.
- Fujii, E. (1943). Forming a figure by movement of a luminous point. *Japanese Journal of Psychology*, 18, 196–232.
- Goodman, L. A. (1978). *Analyzing qualitative/categorical data*. Cambridge, Mass.: Abt Books.
- Koga, K. & Osaka, R. (1983). A comparison of triple recording methods of eye movement. *Japanese Psychological Research*, 25, 181–190.
- Koga, K., Makino, T., Sakata, K. & Takahashi, N. (1988). How can we know the veridical velocity of a moving object? In Lürer, G., Lass, U. & Shallo-Hoffmann, J. (Eds.), *Eye movement research – Physiological and psychological aspects* (pp. 320–336). Toronto: C.J. Hogrefe.
- Koga, K. & Groner, R. (1990). Pursuit eye movements and the perception of object motion. In Groner, R., d'Ydewalle, G. & Parham, R. (Eds.), *From eye to mind – Information acquisition in perception, search, and reading* (pp. 59–68). Amsterdam: North-Holland.
- Mack, A. & Bachant, J. (1969). Perceived movement of the afterimage during eye movements. *Perception & Psychophysics*, 6, 379–384.
- Mack, A., Fendrich, R., & Sirigatti, S. (1973). A rebound illusion in visual tracking. *American Journal of Psychology*, 86, 425–433.
- Mack, A. & Herman, E. (1972). A new illusion: The underestimation of distance during pursuit eye movements. *Perception & Psychophysics*, 12, 471–473.
- Mack, A. & Herman, E. (1973). Position constancy during pursuit eye movement: An investigation of the Filehne illusion. *Quarterly Journal of Experimental Psychology*, 25, 71–84.
- Mack, A. & Herman, E. (1978). The loss of position constancy during pursuit eye movements. *Vision Research*, 18, 55–62.

- Miller, J.M. (1980). Information used by the peripheral and oculomotor systems regarding the amplitude of saccadic and pursuit eye movements. *Vision Research*, 20, 59–68.
- Norusis, M.J. (1993). *SPSS for Windows. Advanced Statistics. Release 6.1*. Chicago, IL: SPSS Inc.
- Stoper, A.E. (1973). Apparent motion of stimuli presented stroboscopically during pursuit movement of the eye. *Perception & Psychophysics*, 13, 201–211.
- Sumi, S. (1964a). Further observation on the path of seen motion of two small light spots. *Perceptual and Motor Skills*, 19, 254.
- Sumi, S. (1964b). Path of seen motion of two small light spots. *Perceptual and Motor Skills*, 19, 226.
- Sumi, S. (1966). Paths of seen motion and motion after-effect. *Perceptual and Motor Skills*, 23, 1003–1008.
- Volkman, F., Riggs, L.A., White, K.D. & Moore, R.K. (1978). Contrast sensitivity during saccadic eye movements. *Vision Research*, 18, 1193–1199.
- Westheimer, G. (1954). Eye movement responses to a horizontally moving visual stimulus. *AMA Archives of Ophthalmology*, 52, 932–941.
- Yarbus, A.L. (1967). *Eye movements and vision*. Translated by B. Haigh. New York: Plenum Press.

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