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Systematic distortion of perceived 2D shape during smooth pursuit eye movements

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Abstract

Even when the retinal image of a static scene is constantly shifting, as occurs when the viewer pursues a small moving object with his or her eyes, the scene is usually correctly perceived to be static. Following early suggestions by von Helmholtz, it is commonly believed that this spatial stability is achieved by combining retinal and extra-retinal signals. Here, we report a perceptually salient 2D shape distortion that can arise during pursuit. We provide evidence that the perceived 2D shape reflects retinal image contents alone, implying that the extra-retinal signal is ignored when judging 2D shape.

Keywords: Eye movements; Spatial vision; 2D shape; Pursuit; Extra-retinal signal

1. Introduction

When a viewer pursues a small moving object with his or her eyes, the image of the surrounding static scene shifts across his or her retina. Despite this the surrounding scene is usually correctly perceived to be static. Following early suggestions by von Helmholtz it is commonly believed that this spatial stability is achieved by subtracting an internal reference signal, such as a copy of the eye movement command, from the retinal motion signal. This notion has received substantial experimental support, but it is evident that the mechanism itself is not perfect.

Filehne (1922) reported that a briefly visible stationary object, whose image shifted over the retinas because the eyes were tracking a second, moving object, appears to move in the opposite direction than the pursued object. This apparent failure of position constancy is now known as the Filehne illusion. Similarly, a moving object appears to move more slowly when pursued than when viewed with the eye static: the Aubert–Fleischl phenomenon (Aubert, 1886; Fleischl, 1882). Both effects can be explained by assuming that the internal reference signal underestimates the eye's velocity (see Howard, 1982 and Wertheim, 1994, for reviews). Alternatively, the retinal signal could over-estimate the motion on the retina (Howard, 1982), the critical factor being the relative magnitudes of the retinal and extra-retinal velocity signals (Freeman & Banks, 1998).

Perceptual errors during smooth pursuit eye movements have been reported for judgments about whether a background is stationary (Ehrenstein, Mateef, & Hohnsbein, 1986; Haarmeier & Their, 1996; Mack & Herman, 1973; Wertheim, 1981), about the velocity of a moving object (Brenner & van den Berg, 1994; Turano & Heidenreich, 1999), and about the positions of flashed objects (Brenner & Cornelissen, 2000; Mateeff, Yakimoff, & Dimirtrov, 1981; Mita, Hironaka, & Koike, 1950). In the present study we examined whether there are also errors in 2D shape perception during smooth pursuit. We developed a paradigm for studying the effect of pursuit eye movements on 2D shape perception, and found that the extra-retinal signal is ignored altogether under such conditions.

2. Experiment 1

One way to evaluate the extent to which extra-retinal signals are considered in perceptual judgments is by

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presenting retinal information sequentially while the subject's eyes are moving (Brenner & Cornelissen, 2000; Stoper, 1967). A complication when trying to use this method for studying shape perception is that most sequences of retinal images give rise to a percept of motion rather than of shape. This is not surprising because a moving object would produce the same sequence of images. When two images are presented sequentially for judging their relative positions, this complication can be avoided by using very different images that are seen as separate entities. When such entities are combined to form a single apparent shape, the only uncertainty is in their relative positions. For true sequential shape perception one would want the contours of a single shape to gradually unfold, so that each image provides very little information about the integrated shape. To achieve this, without having a contour that will appear to move itself, we defined objects by the sequential pattern of occlusion of a moving line. In that case the shape of the invisible virtual object emerges as the line moves behind the object. The line is perceived to move, but the missing part is perceived as an extended occluding shape rather than as a moving occluder. We examined how the apparent 2D shape of the object defined by the occlusion of the moving line is distorted during pursuit eye movements.

2.1. Methods

2.1.1. Subjects

Three observers who did not know the purpose of the research and one author each judged the perceived shape for every condition. All participants had normal (corrected) vision.

2.1.2. The stimuli

The stimuli were generated with a PowerMac G4/450 and displayed on a 17″ LG Flatron 795 FT Plus video monitor (1268 H × 768 V pixel resolution; 85 Hz frame rate). A white (70 cd/m^2) horizontal line (7.9° × 0.08°) passed behind a virtual target object (always a rectangle in Experiment 1). The line moved down the screen at a velocity of 3.4, 6.7 or 10.1°/s. The virtual object had the same luminance as the background (20 cd/m^2), so that the pattern of occlusion of the line provided the only information about the object's shape (see Fig. 1A). The virtual rectangle had one of three heights: 0.8°, 1.6° or 2.4°. Its width was 1.6°. A dot that was to be tracked by the subject's eyes moved horizontally across the center of the target rectangle at the same speed as the line was moving vertically. The time delay between the onset of the tracking dot and the first appearance of the virtual rectangle depended on the speed at which the tracking dot was moving and the height of the target, and varied between 149 and 682 ms. We do not expect this to be of any significance other than perhaps influencing the gain of pursuit at the moment that the target appeared. The time that it took to present the whole virtual rectangle was between 78 and 702 ms, depending on the speed of the line and the height of the rectangle. A constantly visible white (70 cd/m^2) parallelogram served as a comparison shape. This shape was presented 5° to the left of the target stimulus. Subjects could adjust the shape of the comparison to match that of the virtual target seen during pursuit. The initial shape of the comparison was always a square (1.58° × 1.58°).

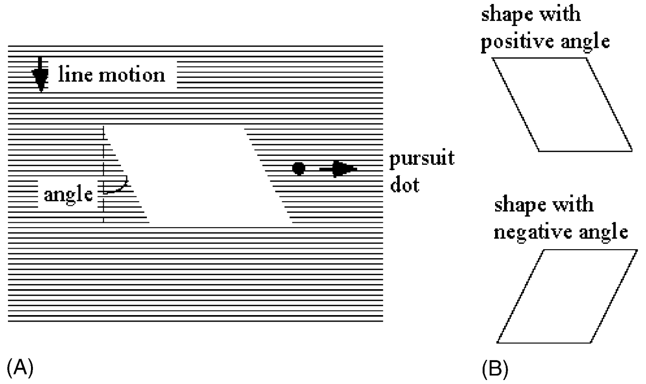

Fig. 1. (A) Schematic diagram of the stimulus. The pursuit dot moves horizontally across the screen. The line moves downwards and is occluded by the otherwise invisible target. The target's shape is represented by the deviation of the sides' angles from vertical (in Experiment 2; in Experiment 1 the target was always a rectangle: angle = 0°; see http://daisy.kwangwoon.ac.kr/~hyung/demo.htm for demonstrations). (B) The angle on the retina and the set angle could differ from 0° in both experiments, and could be either positive or negative.

2.1.3. Procedure

Each session consisted of 54 trials: two tracking directions (leftward and rightward), three target heights, three tracking speeds, three repetitions. The conditions were presented in random order. During target presentations subjects were instructed to track the dot with their eyes. They were allowed to see the target as often as they wanted. When the target was not being presented, the comparison shape was visible. Subjects were to report the perceived target shape by modifying the comparison shape using keyboard buttons. They pressed another button to indicate that they were satisfied with the modified comparison shape. Each subject completed four sessions, resulting in 12 repetitions for each of the 18 conditions. Only the data from the last three sessions were analyzed. A chin rest was used to help minimize the subject's head movements. The viewing distance was 45 cm. The amount of perceptual distortion was quantified by determining the angle of the modified comparison shape (see Fig. 1B).

2.2. Results

If subjects take full consideration of their eye movements they will obviously always set the angle defined in

Fig. 1 to 0°, because the virtual target was always a rectangle. Since the pursuit dot and the horizontal line always move at the same speed and in orthogonal directions, the shape on the retina, assuming that pursuit is perfect, is a parallelogram with an angle (see Fig. 1) of 45° or −45°. If subjects altogether ignore the fact that their eyes are moving they will match the retinal images. Thus they would set an angle of −45° for pursuit from the left to the right, and 45° for pursuit from the right to the left. In fact the average set angles of the four subjects, three different tracking 2D speeds and three different heights of the target stimulus were −29.4 and 29.2, respectively. This means that about 35% of the eye movement during pursuit was accounted for when interpreting the retinal image (still assuming perfect pursuit). The perceptual distortion in 2D shape was symmetrical with respect to the direction of pursuit, and increased with increasing tracking speed and with decreasing height of the target stimulus (see Fig. 2).

2.3. Discussion

As was found for judgments of position and speed, we found that subjects make systematic errors in judgments of 2D shape for stimuli presented during smooth pursuit eye movements. The errors were largest for small targets presented during fast pursuit, which are the conditions for which the duration of the target presentation is shortest, so that the gain of pursuit is least likely to have been influenced by the presence of the target. In these conditions so little of the eye movement that is required to track the dot is accounted for, that we cannot be certain that the apparent consideration of eye orientation is not simply caused by subjects not pursuing the dot perfectly. We therefore decided to repeat the experiment while monitoring the subjects' eye movements.

3. Experiment 2

Apart from the fact that eye movements were recorded, the second experiment also differed from the first in that the actual shape on the screen was no longer always a rectangle but could also be a parallelogram. Moreover, we asked two of our subjects to also make settings while fixating a static dot. These conditions made it possible to evaluate whether the subjects had any biases that have nothing to do with pursuit when comparing occlusion-defined and luminance-defined shapes. We used a single speed, direction of pursuit and target size. Pursuit and fixation trials were presented in separate sessions. The different shapes were presented in random order within each session. The use of a single speed and direction of pursuit on all trials within a session may help subjects to achieve a high pursuit gain.

3.1. Methods

The basic paradigm was very similar to that of Experiment 1, except that eye movements were recorded. However, a number of details were slightly different.

3.1.1. Subjects

Two authors and two observers who did not know the purpose of the research each judged the perceived shape for the pursuit condition. One author and one naïve observer also made judgments for the fixation condition. All participants had normal (corrected) vision.

3.1.2. The stimuli

Stimuli were now presented on a 20″ CRT-monitor (subtending 31° by 23° at the 71.5 cm viewing distance) and generated by a Power Macintosh computer using software routines provided in the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; see http://psychtoolbox.org/). Screen resolution was set to 1152 × 870 with a

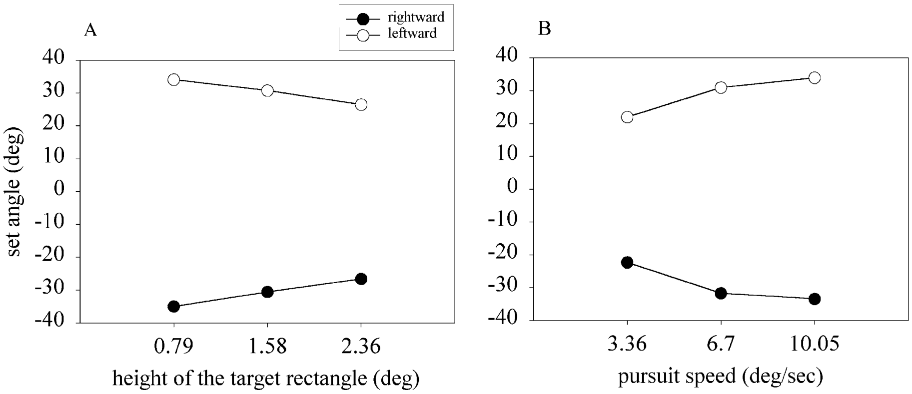

Fig. 2. Results of Experiment 1. Averages with standard errors (between subjects; $n = 4$). Error bars are smaller than symbols. (A) Set angle as a function of target size. (B) Set angle as a function of pursuit speed.

refresh frequency of 75 Hz. The background luminance of the screen was 25 cd/m^2. The luminance of the vertically moving white line was 75 cd/m^2. The line's width was 31° and its height 0.1°. It moved downwards at 6°/s (three pixels per frame). Luminance of the 0.25° red dot that was to be pursued with ones' eyes was 30 cd/m^2. The dot moved from left to right, also at 6°/s (three pixels per frame). Its starting position was always 11° to the left of the center of the screen. In the fixation condition a similar static dot appeared at the center of the screen. The target appeared approximately at the center of the screen (position randomized within ±0.7°, both horizontally and vertically) and about 1800 ms after onset of the pursuit target (depending on the target's randomly chosen horizontal position). The target could have one of six shapes on the screen: angles of 0°, 18°, 34°, 45°, 53° and 59° for the pursuit condition, and −45°, −34°, −18°, 0°, 18° and 34° for the fixation condition. These angles were chosen because they correspond with horizontal shifts of the 'occluded' part of the line by a whole number of pixels per frame. Different sets were chosen for the two conditions so that the images on the retina would be similar for both, and would include both positive and negative angles. The height of the target and the length of the occluded part of the line were both 1.1°. The comparison shape had exactly the same dimensions. Subjects' heads were restrained with a chin-rest.

3.1.3. Eye movements

Eye movements were recorded at 250 Hz with an infrared video-based eyetracker (Eyelink Gazetracker; SensoMotoric Instruments, Teltow, Germany) and software routines from the Eyelink Toolbox (Cornelissen, Peters, & Palmer, 2002; see http://psychtoolbox.org/). For our further analysis trials were only considered valid if subjects adhered to the instructions concerning eye movements and did not make saccades while the target was being presented. We only analyzed the eye movements during target presentation. The velocity of the eye was determined by fitting a straight line to the measured eye orientations. For the pursuit condition the pursuit gain had to be larger than 0.7 (eye velocity > 4.2°/s). For the fixation condition the horizontal eye velocity had to be between −0.3 and 0.3 times the velocity of the pursuit target in the pursuit condition (i.e., <1.8°/s). In both cases the vertical eye velocity had to be between −0.3 and 0.3 times the vertical velocity of the line (i.e., also <1.8°/s). Moreover, it had to be certain that there were no saccades while the target was presented. We considered it possible that there had been a saccade whenever the mean velocity of the eye during any 36 ms interval was more than twice the velocity of the pursuit target. This corresponds with a velocity threshold of 12°/s, whereby the velocity was determined by fitting a straight line to a moving window of 10 samples. The percentage of trials that were considered valid and the median values for the eye movements (including rejected trials) are shown in Table 1. Rejected trials were included in the list of median values in order to give an impression of subjects' overall performance.

Table 1
Median eye velocity[a] and percentage of valid trials in Experiment 2

Subject	FC	HS	EB	HB
Horizontal eye velocity during pursuit	0.96	0.78	0.90	0.94
Horizontal eye velocity during fixation	0.00	−0.02		
Vertical eye velocity during pursuit	0.06	0.18	0.15	0.04
Vertical eye velocity during fixation	0.00	0.13		
Percentage of trials valid during pursuit	98	73	77	95
Percentage of trials valid during fixation	97	98		

[a] Horizontal eye velocity is expressed as a gain with respect to the moving dot in the pursuit condition (this measure is also used for the fixation condition to facilitate direct comparisons). Vertical eye velocity is expressed as a gain for pursuit of the line. The two gains are equivalent because the dot and line move at the same speed.

3.1.4. Procedure

After each target was shown, subjects set a white, 75 cd/m^2 parallelogram to the same shape using the computer's mouse. The comparison parallelogram only appeared after the target was shown. The height of the parallelogram remained constant. Moving the mouse shifted the top and bottom edges laterally in opposite directions, thereby changing the slant of the other two sides. Again we used the slant angle (see Fig. 1B) as our measure of shape. The parallelogram was presented 2.7° below the center of the screen. The angle of its initial shape was randomized. Subjects pressed the mouse button when satisfied with their setting. Each of the six targets was presented 20 times, in random order.

3.2. Results

Table 1 provides some general information about the eye movements. As was to be expected, the average gain of ocular pursuit (top row) was slightly below 1, while there was no systematic horizontal eye motion during fixation (second row). There was a clear tendency to move the eyes downwards, in pursuit of the line, but the gain of this pursuit was modest (third and fourth rows). We consider the number of trials that had to be discarded to be acceptable (last two rows).

Fig. 3A and B shows the set angle as a function of the angle presented on the screen for the two subjects who participated in both conditions. The open symbols show the settings for targets presented during fixation. The

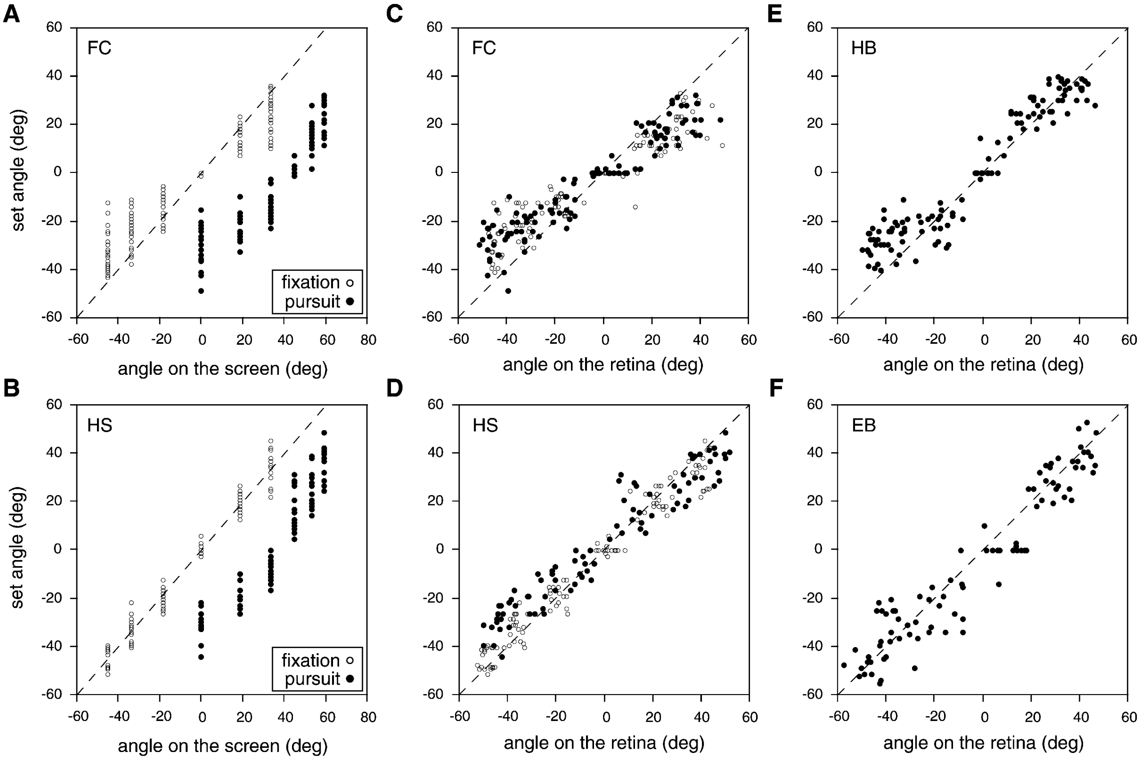

Fig. 3. The settings on all valid trials in Experiment 2. (A, B) Set angles for two subjects as a function of the angle presented on the screen. Open symbols: target presented while subjects fixated a static dot at the center of the screen. Solid symbols: target presented while subjects pursued a dot moving rightward across the screen. The dashed diagonal line indicates a perfect match. (C, D) The same settings for the same subjects, but now as a function of the angle in the image on the retina. (E, F) Similar data for two more subjects with the targets presented during pursuit.

solid symbols those for targets presented during pursuit. The dashed diagonal line indicates a perfect match. For the fixation condition the naïve subject HS's settings were almost a perfect match of the angle on the screen. Author FC had a slight bias towards setting smaller angles (i.e., a tendency to set a more rectangular shape). For the pursuit condition both subjects set angles that were very different from those that had been presented on the screen. They set considerably more negative angles than had been presented, in a similar way as the subjects had in Experiment 1 for rightward pursuit.

Fig. 3B and C shows the same set angles as a function of the angle on the retina. To determine the latter we considered both the horizontal and vertical eye movements on each trial. The dashed diagonal line now represents setting an angle that perfectly matches the target's retinal image. Subject HS appears to match the retinal image almost perfectly, irrespective of whether the eye is moving or not (no difference between open and solid symbols). Subject FC also appears to match the retinal image, irrespective of whether the eye is moving, but with a small bias toward right angles. The other two subjects, who only made settings in the critical, pursuit condition, also appear to set an angle that matches the retinal image, totally ignoring the fact that their eyes are moving (Fig. 3E and F).

3.3. Discussion

The 2D shape of the object defined by the pattern of occlusion of the moving line was systematically distorted during pursuit: the perceived 2D shape reflects the retinal image. Thus, the eye's orientation is not accounted for when judging shape. From the results of Experiment 1 we could not conclude that eye orientation was ignored altogether, because we did not measure eye movements. For the set angles in Experiment 1 (Fig. 2) to be consistent with purely retinal matching requires a lower pursuit gain in the first experiment (about 0.65, average set angle about 29°) than in the second experiment (about 0.9, average set angle about 34° for the rectangular targets). Pursuit gain differs between subjects, and the predictable direction and velocity of the pursuit dot in the second experiment may have made it easier to follow. Moreover, subjects were allowed to look at the presentations as often as they liked in the first experiment, and may have based their settings on the trials with the lowest pursuit gains. In contrast, excluding trials with saccades in the second experiment will tend to select trials with higher pursuit gains. Finally, some subjects have biases that are not related to pursuit when comparing the occlusion and luminance defined targets. For example, the leftmost solid points in

Fig. 3 correspond with the conditions in Experiment 1, and the set angles are clearly smaller for two subjects (FC, HB) than one would predict for a true match to the retinal image. For subject FC we are sure that this bias is not related to pursuit because it is also present during fixation (open symbols). Thus we do not consider the smaller errors during pursuit in Experiment 1 to be inconsistent with the conclusion from Experiment 2 that eye orientation is ignored. Eye movements appear to be ignored irrespective of target shape (Experiment 2) and size (Experiment 1), and of pursuit velocity and direction (Experiment 1).

We used the angle defined in Fig. 1B as our measure of shape. This appears to us to be the most intuitive measure. However, we must note that this choice is not completely irrelevant, because subjects made small vertical eye movements, which reduce the retinal height of the target. Thus if subjects were actually comparing the horizontal offset of the base of the parallelogram relative to its upper edge, we would expect a slightly different retinal match. The difference however would be very small (about 5° for the most extreme angles for subject HS who had the highest vertical eye velocity during pursuit), so it would not change our conclusions.

In the experiments, the virtual shape was defined by the occlusion of a vertically moving horizontal line during horizontal pursuit. There are other ways to construct stimuli. Using a different line orientation (e.g., diagonal) with horizontal pursuit will result in a different retinal image, and therefore presumably in a different perceived shape. We see no reason to expect changes in eye orientation to be considered for lines of some orientations, but not of others. We also see no reason to expect the principle that eye movements are ignored to only apply to horizontal pursuit or vertical line motion. However, it is possible that eye orientation cannot be ignored for certain combinations of retinal motion and eye movements, such as if the line moves in the same direction as the eye. Whether this is so remains to be examined.

There have been several previous studies showing that the visual system completely ignores extra-retinal information about eye movements for certain judgments. Stoper (1967) reported that the perception of stroboscopic motion during pursuit depends on the stimulation of two separate retinal loci. If the flashes emanated from two different places in space, but fell on the same retinal position, no stroboscopic motion was perceived. Brenner and Cornelissen (2000) recently showed that during pursuit the perceived distance between two successively presented flashing objects reflected the retinal separation rather than their actual separation. The results of the present experiments show that extra-retinal information about eye orientation is also completely ignored for judgments of 2D shape. Normally, shape can be detected from simultaneous retinal information, so there is no need to consider eye movements. Only when different parts of the image are visible sequentially as the eye moves, and these cannot be related to other structures that are not occluded, as in our strange way of specifying the shape, would it be useful to consider eye movements. This probably occurs so seldom in real life that eye movements can simply be ignored. Thus we expect our conclusion to apply to shape perception in general, not only to the illusory shape used in the present study. In this sense it would appear that shape and relative positions are processed in a similar manner, possibly involving common pathways.

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