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Distortion of Visual Space During Pursuit Eye Movements

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We measured perceived positions of flash stimuli arranged two-dimensionally in the peripheral visual field during pursuit eye movement to examine the influence of displacement of the eye position on localization in the peripheral visual field. The horizontal mislocalization of the flash stimulus during the horizontal pursuit eye movement was found toward the pursuit direction. The magnitude of this mislocalization was asymmetrical around the central visual field, and the asymmetry depended on the pursuit direction. As the eye position changed, the magnitude of the horizontal mislocalization gradually decreased. It was also observed that the vertical mislocalization of the flash stimulus was constant regardless of the eye position displacement. These results show that the visual space during the horizontal pursuit eye movement is expanded horizontally and then gradually returns to the normal state. It is suggested that the visual space is dynamically distorted during the pursuit eye movement.

Key words: visual psychophysics, mislocalization, pursuit eye movement, peripheral visual field, visual space

1. Introduction

We move our eyes to place an object in the center of our field of vision. When the object moves within our visual field, our eyes track it to keep it in the center. This is called pursuit eye movement (PEM). Tracking the moving object to keep it in the central visual field improves its visibility,[1,2] but produces the retinal image motion of the background in the peripheral visual field. For that reason, the improved visibility seems to be at the cost of visual information in the peripheral visual field.

One important question is whether the visual system can make use of the visual information acquired in the peripheral visual field during PEM. It is well known that stationary background objects appear to move against a moving target during PEM[3–6]; this phenomenon is called the Filehne illusion. Movement of the tracking target during PEM is also known to be perceived more slowly than the same target moving on the retina during fixation;[3,4,7,8] this is called the Aubert-Fleischl paradox. Mack and Herman (1973) reported that the amount of perception by which the stationary background was perceived to move during PEM was equal to the amount of perception by which the movement of the tracking target was underestimated. They concluded that the role of the Filehne illusion was to compensate for mismatch between a registered underestimation of the speed of eye movement during PEM and the speed of retinal displacements of the stationary background caused by PEM. Their conclusion means that the visual system makes good use of motion information acquired in the peripheral visual field during PEM. Thus, the motion information in the peripheral visual field during PEM seems to have an important role in linking to the eye movement information.

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On the other hand, position of an object in the peripheral visual field during PEM is also expected to link with eye movement information. The visual system must consider eye position to localize the position of an object with respect to the observer during eye movement.[9] Therefore, the relationship between the localization in the peripheral visual field and PEM must be understood to clarify the role of the visual information in the peripheral visual field; some studies have examined this relationship.[10,11]

Mitrani and Dimitrov (1982) investigated visual localization of a brief flash in the peripheral visual field during PEM. They reported that the perceived location of the flash was systematically mislocalized in the same direction as the eye movement, and that the magnitude of the mislocalization in the peripheral visual field was asymmetrical around the fovea, depending on the direction of the eye movement. Until then it had been believed that the mislocalization during PEM resulted from the perceptual latency of the brief flash.[12] According to the explanation of perceptual latency, time is required for the visual system to transmit information of the flash. During this time interval, the eyes continue to track a moving target. When the flash is finally perceived, the eyes shift in the direction of the eye movement. The flash is localized using the retinal location of the flash compensated by the eye position, so that the flash is mislocalized to the direction of the eye movement.[12] However, Mitrani and Dimitrov (1982) concluded from their results that the perceptual latency of the brief flash was not the only determinant of the mislocalization during PEM. Another study suggested that the asymmetry of the mislocalization in the peripheral visual field they had found was related to the direction toward or away from the fovea of a reference stimulus movement in the background. When the reference stimulus moved toward the fovea, a brief flash around the reference stimulus was mislocal-

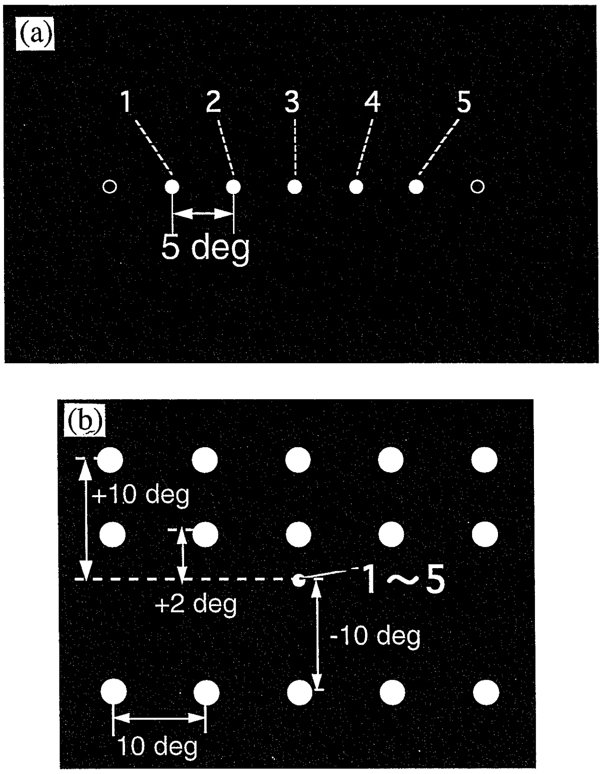

Fig. 1. (a) Triggering positions, pursuit starting position, and pursuit stopping position. Five disks indicate the positions at which presentation of the flash stimulus is triggered when the moving target passes through one of these positions selected at random; two circles indicate a pursuit starting position and a pursuit stopping position (horizontally −15 and 15 deg from the display center). When the observer moves his eye from left to right, the left circle indicates the pursuit starting position. (b) Positions of the flash stimuli. Fifteen large disks indicate the presented positions of the flashed stimuli. One small disk indicates the position selected at random from the five triggering positions.

ized in the direction away from the fovea. When the reference stimulus moved away from the fovea, a brief flash around the stimulus was only slightly mislocalized.[11] However, these studies measured the localization of the brief flash only at the moment eye position was carried to the center of the display by PEM. They did not consider the effect of time from the onset of PEM on the mislocalization of the flash in the peripheral visual field. Several studies suggested that the mislocalization of the target tracked by PEM depended on the time from onset of PEM.[13-15] Therefore, the mislocalization of a brief flash in the peripheral visual field may also depend on the time from the pursuit onset.

Here, we investigated how PEM affects the perceived position of a brief flash in the peripheral visual field depending on the time from PEM onset. Our experiment was designed to measure the perceived position of a flash presented at a position in the surrounding area of the target being tracked by PEM. We represented the visual space during PEM by plotting the perceived position of the brief flash on two dimensional coordinate, because there had been no attempt to investigate the perceived position in both horizontal and vertical directions. This representation enabled us to observe how the perceived positions arranged two-dimensionally over the peripheral visual field during PEM were modified by the eye position.

2. Methods

2.1 *Apparatus*

The observer sat in the dark. His head was fixed by a bite bar and a forehead rest. The visual stimuli were presented on a CRT display with a refresh rate of 60 Hz (SONY GDM-2000TC). The display was controlled by a computer (Apple Power Macintosh 7100/66AV). The display size was 74.3 × 58.5 deg of visual angle. Viewing distance was 25 cm.

A photoelectric limbus tracking device measured horizontal eye-movement with an accuracy of about 0.5 deg. The eye position was recorded by the computer via an A/D converter (MacADIOS II) with a sampling rate of 60 Hz. The eye-movement data were used to determine the horizontal retinal location of a flash stimulus, and to detect saccadic eye movement in order to eliminate the observer's response to a flash stimulus during the saccadic eye movement which interrupted PEM.

2.2 *Calibration of Eye-Movement*

Each trial started with a calibration procedure as follows: the observer had to sequentially fixate five dots presented in sequence on a horizontal line of the display center. When he had fixated a dot, he pushed a button. That dot disappeared and the next one appeared. The horizontal eye positions, expressed in terms of voltage, and the display position were recorded in the computer. A regression line was used to convert the voltage to the display position.

2.3 *Stimuli*

A visual target (0.5 deg in diameter, 1.0 cd/m^2) moved for a distance of 30 deg horizontally at a velocity of 16.0 or 32.0 deg/s. A stationary flash stimulus (1.0 deg in diameter, 1.0 cd/m^2) was presented for 16.7 ms at a position in the area surrounding the target. In Fig. 1(a), the disks show the five positions triggering the presentation of the flash stimulus when the moving target passed through one of the positions selected at random, and the two circles show a pursuit starting position and a pursuit stopping position placed −15 and 15 deg horizontally from the display center. When the observer moved his eye from left to right, the left circle indicates the pursuit starting position. In Fig. 1(b), the large disk shows the position at which the flash stimulus was presented and had one of the 15 positions multiplied the five types of horizontally −20, −10, 0, 10, 20 deg from the triggering position by the three types of vertically −10, 2, 10 deg from triggering position, and the one small disk shows the position selected at random from the five triggering positions. The observer viewed the moving target and the flash stimulus with his left eye, and tracked the moving target with PEM.

2.4 Procedure

Figure 2 shows an example of stimulus presentation sequence in a single trial. A moving target appeared at a pursuit starting position on the left or right side of the display. The observer fixated the target. When he pushed a button, the target began to move horizontally. The observer was tracking the moving target by PEM. When the target passed through the triggering position selected at random from 5 positions, the flash stimulus appeared for 16.7 ms at one of the 15 positions around the triggering position (see Fig. 1). After the moving target arrived at the pursuit stopping position, the observer localized the position of the flash stimulus by pointing a mouse cursor at that position. If he could not perceive the flash stimulus, the trial was cancelled. For a control trial, the observer fixated one of 5 triggering dots. When he pushed a button, a flash stimulus appeared for 16.7 ms at one of 15 positions around the fixation point. The observer localized the apparent position in the same way as in the pursuit trial. Each observer performed eight sessions; a session consisted of 300 single trials.

2.5 Observers

Two male observers (KM, 27 years old, and TS, 24 years old) participated in the experiments.

3. Results

Figures 3 and 4 show the horizontal and vertical mislocalization of the flash stimulus, which is presented 2.0 deg above the horizontal meridian when the tracking target passes through the display center, as a function of the retinal location, respectively. The mislocalization represents the difference between the response and the real location. For the horizontal mislocalization, its positive value means that the flash stimulus is mislocalized in the same direction as PEM, and for the vertical mislocalization, its positive value means that the flash stimulus is mislocalized in the upper direction. The symbols ● and ○ represent the condition of target velocity of 32.0 and 16.0 deg/s, respectively. The symbol + represents the fixation condition.

In Figs. 3 and 4, the top and bottom panels represent right and left pursuit conditions for the two observers. The direction of gaze was obtained by analyzing eye-movement data, and the position of the flash stimulus was corrected as the retinal location using its gaze direction.

Figure 3 shows large mislocalizations in the pursuit direction. When the eye moved to the right, the magnitude of the mislocalization in the right side field was larger than that in the left side field. When the direction of eye-movement was the opposite, the side having larger magnitude was reversed. These results agreed well with those obtained by Mitrani and Dimitrov (1982). In addition, the horizontal mislocalization of the flash stimulus, which was presented 10.0 deg above or −10.0 deg below the horizontal meridian, had the same tendency as when the flash stimulus was presented 2.0 deg above the horizontal meridian. These results suggest that the asymmetry of the mislocalization in the peripheral visual field is common in the wide range of the visual field. There was no data at the range of 15 deg to 20 deg in the left side field. This is because of the blind spot where the flash stimulus was presented.

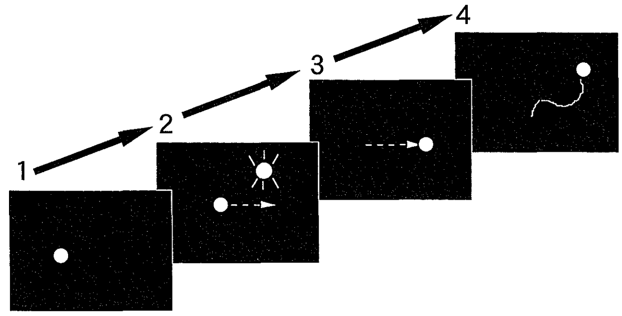

Fig. 2. An example of stimulus presentation sequence. 1: a moving target is presented on the left or right side. After the observer fixates the target, he pushes a button. 2: when he is tracking the moving target with pursuit eye movement, a flash stimulus is presented for 16.7 ms at a position in the surrounding area of the target. 3: the moving target arrives at the pursuit stopping position. 4: the observer localizes the apparent position of the flash stimulus by moving the mouse pointer presented on the display.

Figure 4 shows the vertical mislocalization. For observer TS, the vertical mislocalization in the peripheral visual field tended to shift toward the lower direction. This tendency was found under the fixation condition as well as the pursuit conditions. Observer TS seemed to have a bias in reporting the lower direction. For observer KM, there were no significant mislocalizations in the vertical direction.

Figures 5 and 6 show mean perceived positions of the flash stimulus during the right and left PEM at the five eye positions. The symbols ● and ○ represent the perceived position during pursuits and fixation, respectively. In calculating the mean perceived position, the range of the horizontal retinal locations was divided into 5 equal subintervals: [−25.0 deg, −15.0 deg), [−15.0 deg, −5.0 deg), [−5.0 deg, +5.0 deg), [+5.0 deg, +15.0 deg), and [+15.0 deg, +25.0 deg). Horizontal and vertical perceived positions in each interval were averaged and plotted on the two dimensional coordinate. The eye velocity of 32.0 and 16.0 deg/s, and observers KM and TS are shown in Figs. 5 and 6. The eye position is indicated on the right side of the figures (cf. Fig. 1).

In Fig. 5, when the observer's eye was at triggering position 1, the perceived positions of the flash stimulus during pursuits were shifted dramatically in the direction of pursuit in the right side field as compared with that during fixation. The magnitude of the shifts of the perceived positions in the right side field was larger than that in the left side field. As the eye approached triggering position 5, the magnitude of the shifts of the perceived positions gradually became small. The effect of the triggering position on the perceived positions is also described in Fig. 7.

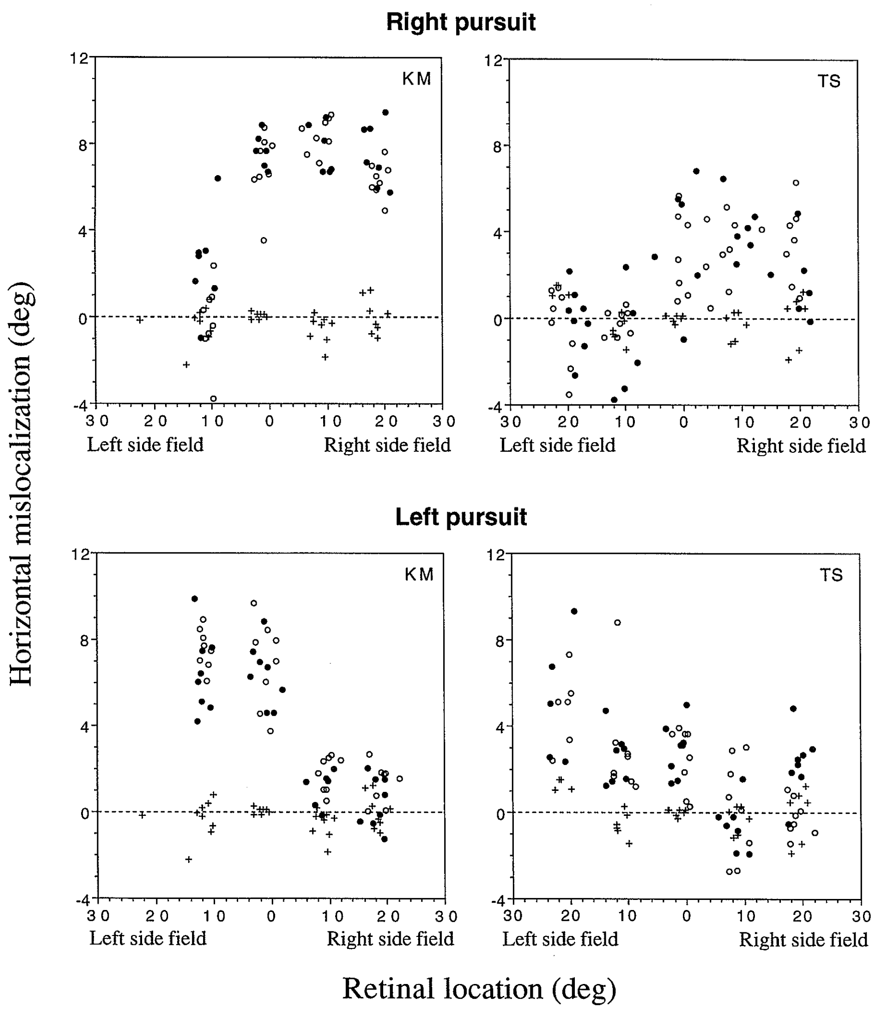

Fig. 3. Horizontal mislocalization of the flash stimulus as a function of retinal location (the flash stimulus is presented at 2.0 deg above the horizontal meridian when the tracking target passes through the display center). Positive values in the ordinate show mislocalization in the pursuit direction. ●, target velocity 32.0 deg/s; ○, target velocity 16.0 deg/s; +, fixation condition. The top and bottom panels represent the right and left pursuit eye movement conditions, respectively. Left and right columns represent observers KM and TS, respectively.

For observer KM, the perceived positions during pursuits in the upper and lower field shifted toward the horizontal 0 deg line. For both observers, the magnitude of those shifts in the vertical direction tended to be constant regardless of the eye position. There were no differences in perceived positions between target velocities under 32.0 and 16.0 deg/s conditions.

Figure 6 shows that, when the observer's eye was at triggering position 5, the perceived positions during pursuits shifted dramatically in the direction of the pursuits. The magnitude of the shifts was larger in the left side field than in the right side field. The shifts in the vertical direction had the same tendency as in Fig. 5.

Figure 7 shows mean perceived positions during the right PEM and fixation as a function of triggering position when the flash stimulus was presented 2.0 deg above the horizontal meridian. The symbols ● and ○ represent the condition of target velocity of 32.0 and 16.0 deg/s, respectively. The symbol △ represents the fixation condition. The way of calculating the mean perceived position is the same as in Fig. 5.

In Fig. 7, it is shown that the magnitude of the shifts of the perceived positions in the right side field gradually became small as the eye approached triggering position 5. The magnitude of the shifts of the perceived positions in the left side field tended to be constant regardless of the displacement of the triggering position. The magnitude of the shifts of the perceived positions at 0 deg enlarged as the eye approached triggering position 5. The horizontal perceived positions, which were presented 10.0 deg above or -10.0 deg below the horizontal meridian, had the same tendency as the case of 2.0 deg above the horizontal meridian. When the direction of the eye movement was opposite, the side affected by the triggering position was reversed.

4. Discussion

The present study showed that the displacement of

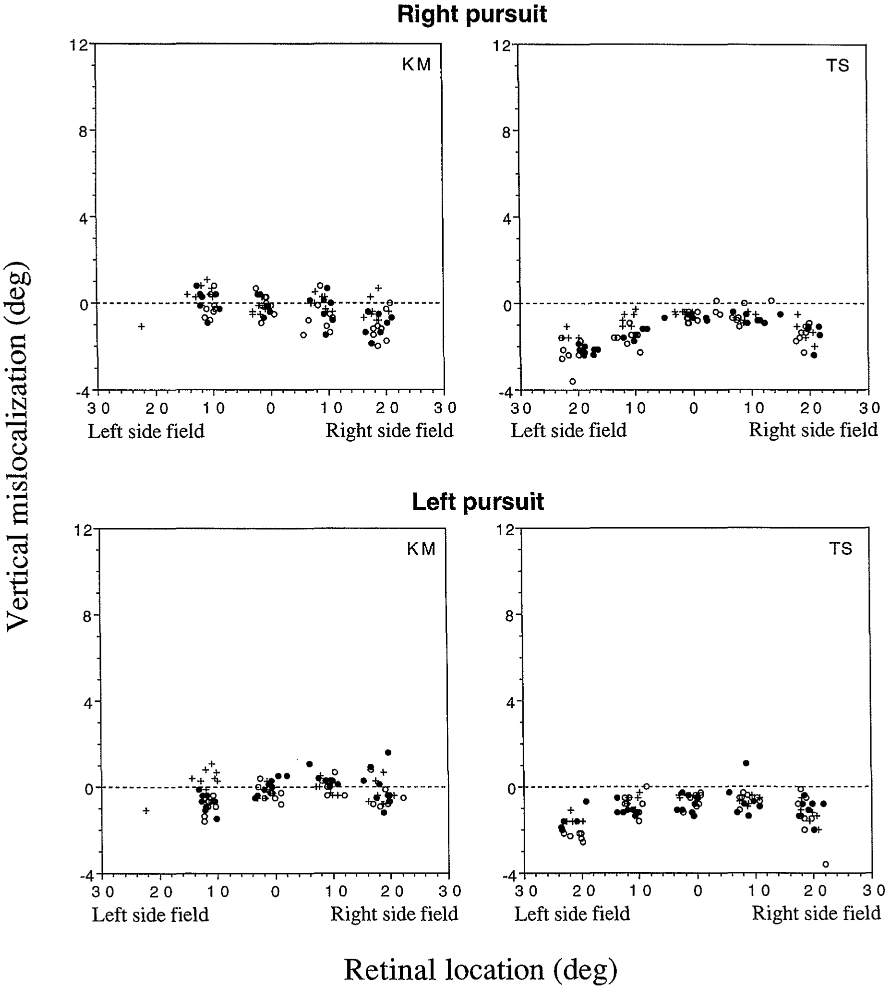

Fig. 4. Vertical mislocalization of the flash stimulus as a function of retinal location (the flash stimulus is presented 2.0 deg above the horizontal meridian when the tracking target passes through the display center). Positive values in the ordinate show mislocalization in the upper direction. ●, target velocity 32.0 deg/s; ○, target velocity 16.0 deg/s; +, fixation condition. The top and bottom panels represent the right and left pursuit eye movement conditions, respectively. Left and right columns represent observers KM and TS, respectively.

eye position during PEM affected the perceived position of a flash stimulus in the peripheral visual field. That is, the horizontal shift of the flash stimulus occurred during the horizontal pursuit and was dependent on the direction of PEM. The magnitude of the shift decreased gradually as PEM continued. In addition, the perceived positions in the vertical direction turned out to be constant regardless of displacement of the eye position. The observers judged the location of a flash stimulus with respect to head-centric coordinates during PEM, and then localized the apparent position of the flash stimulus with respect to the head-centric coordinates following PEM. The head-centric coordinates were fixed relative to the display while the observer performed the experiment, because his head was fixed by a bite-bar and a forehead rest. Head-centric judgment is possible only if the eye position is taken into account together with the retinal location of the flash stimulus, and visual space is structured by combining the eye position and the retinal position.[9] Hence, these findings suggest that visual space during the horizontal pursuit is horizontally distorted depending on the eye position.

How can we explain these findings? These shifts might be explained by considering motion signal generated by extraretinal signal.

As shown in Fig. 3, the magnitude of the shifts depended on the direction of PEM, not on the side of the visual fields. These results agreed with the previous studies which showed that mislocalization in the peripheral visual field was influenced by motion of a reference stimulus in the background.[10,11] Mateeff & Hohnsbein (1988) concluded that a reference stimulus movement toward or away from the fovea in the background was an important factor in the magnitude of the mislocalization. However, in our experiment, it was difficult for the observer to judge a flash position by using the edge of the display which might serve as a reference background; he could not see the display edge in our experimental setup and judged the flash position using the head-centric direction. Therefore, our results could not be explained by the

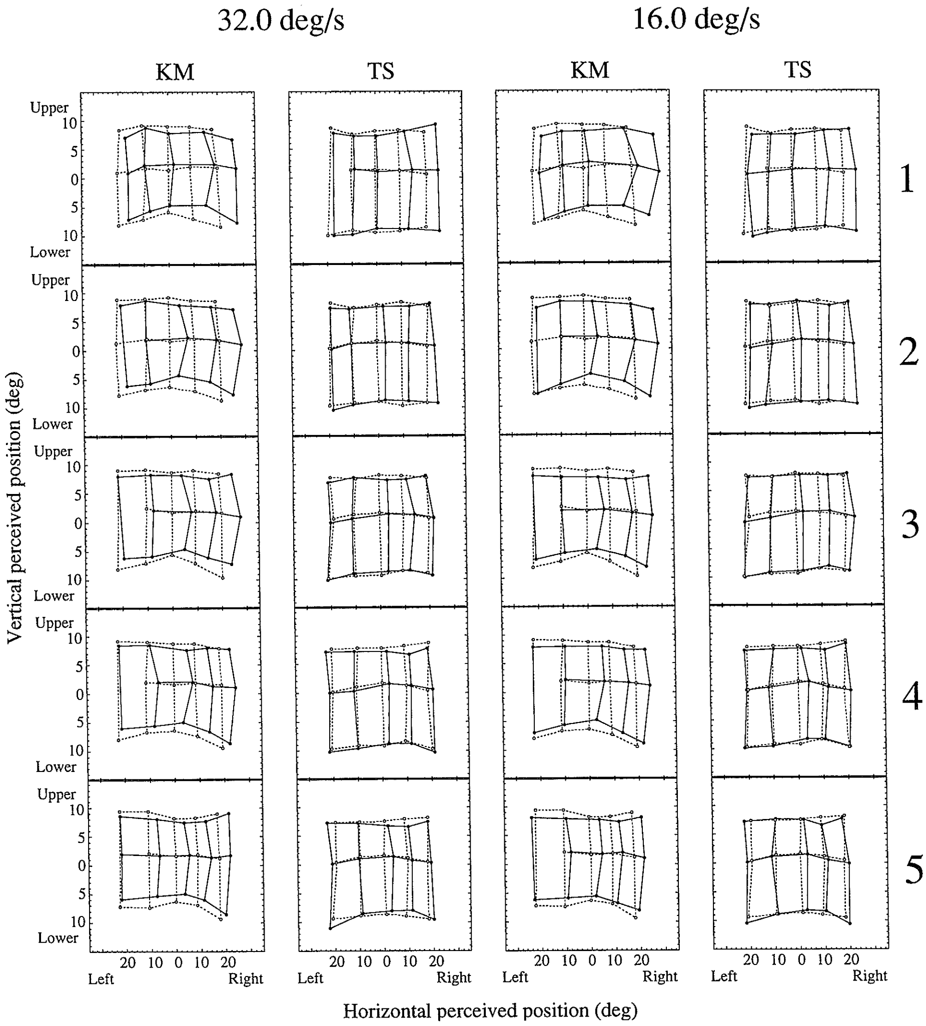

Fig. 5. Mean perceived positions during the right pursuit eye movement and fixation on the two dimensional coordinate, separately for five eye positions. ●, the right pursuit condition; ○, the fixation condition. Two left and two right columns represent the eye velocity of 32.0 and 16.0 deg/s. Left and right columns out of the two left or the two right represent observers KM and TS, respectively. The number on the right side of the figure indicates eye position (cf. Fig. 1).

motion of a reference stimulus in the background.

Furthermore, the memory of a flash position relative to the head-centric coordinates might be uncertain after PEM. However, our results could not be explained by the uncertainty of memory either, because this uncertainty was the same among all retinal locations.

One possible explanation for our results is that the motion signal generated by the extraretinal signal during PEM may cause the mislocalization in the peripheral visual field. Some neurophysiological studies[16,17] seem to support the possibility of relating our results to the motion signal from extraretinal signal input. The activity of the cells in the medial superior temporal (MST) areas of primates is increased by extraretinal inputs during PEM. In addition, some of the MST cells have large receptive field in the left-side visual field, and these cells respond strongly during the leftward PEM but are inhibited during the rightward PEM.[16] At the same time, the MST cells are sensitive to the movement of the visual stimulus field.[16,17] These findings suggest that MST cells are closely related with the motion signal generated by the extraretinal signal at the half area of the visual field depending on the pursuit direction.

Consider what happened to these cells during the localization task. They had been activated by PEM, and their activation was related to the motion signal. At the same time, the motion signal may cause the mislocalization of a flash stimulus. A study by Nishida and Johnston (1999) seems to support this possibility.[18] They reported that, after adaptation to motion, the perceived position of a stationary pattern shifted in the direction of the motion aftereffect. Therefore, we speculate that the extraretinal signal during PEM generated activation of the MST cells, which was related with the motion signal, in half the area of the visual field depending on the pursuit direction; this resulted in the asymmetrical mislocalization in the peripheral visual field depending on the pursuit direction as shown in Fig. 3.

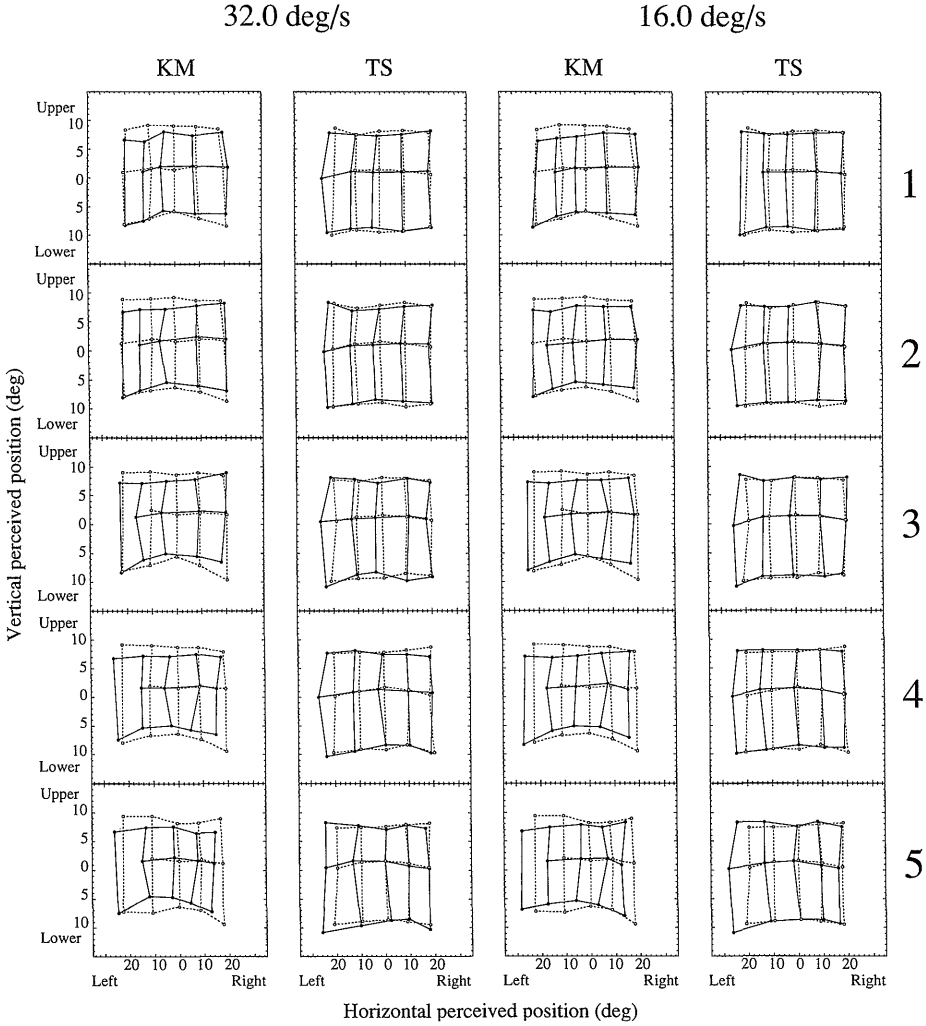

Fig. 6. Mean perceived positions during the left pursuit eye movement and fixation on the two dimensional coordinate, separately for the five eye positions. The way of viewing this figure is the same as in Fig. 5 except ●, which is the left pursuit condition.

Alternatively, if the observer judged the location of the flash stimulus relative to his eye position, the asymmetry of the mislocalization in the peripheral visual field might be explained by considering that a flash stimulus presented at the half area of the visual field in the same direction as PEM was at the half area opposite the pursuit direction following the eye movement.

It is known that mislocalization also occurs during fixation and that the apparent position of a flash presented in the peripheral visual field tends to shift toward the central visual field.[10] Therefore, if the observer perceives a flash stimulus, which is presented in the same direction as PEM, as shifted toward the central visual field during the eye movement, then the flash will be mislocalized in the direction opposite to the eye movement. However, after the eye movement, the absolute position of the flash shifts in the direction opposite the visual field, and the flash will be mislocalized in the same direction as the eye movement when the observer confirms the perceived position of the flash in order to localize its position. As a result, the direction of the mislocalization of the flash during the eye movement is different from that of the mislocalization of the flash after the eye movement. Conversely, a flash stimulus presented in the direction opposite to PEM is perceived as shifted in the same direction as the eye movement during the eye movement. After the eye movement, the absolute position of the flash is in the same visual field, and the flash will be mislocalized in the same direction as the eye movement when the observer confirms the perceived position of the flash in order to localize its position. As a result, the direction of the mislocalization of the flash during the eye movement is the same direction as the mislocalization of the flash after the eye movement. Therefore, mislocalization in the visual field opposite the pursuit direction may be different from that in the same visual field as the pursuit direction.

However, the observer judged the location of the flash stimulus relative to his head position, not his eye position. The location of his head position did not change during or after the eye movement, because his head was

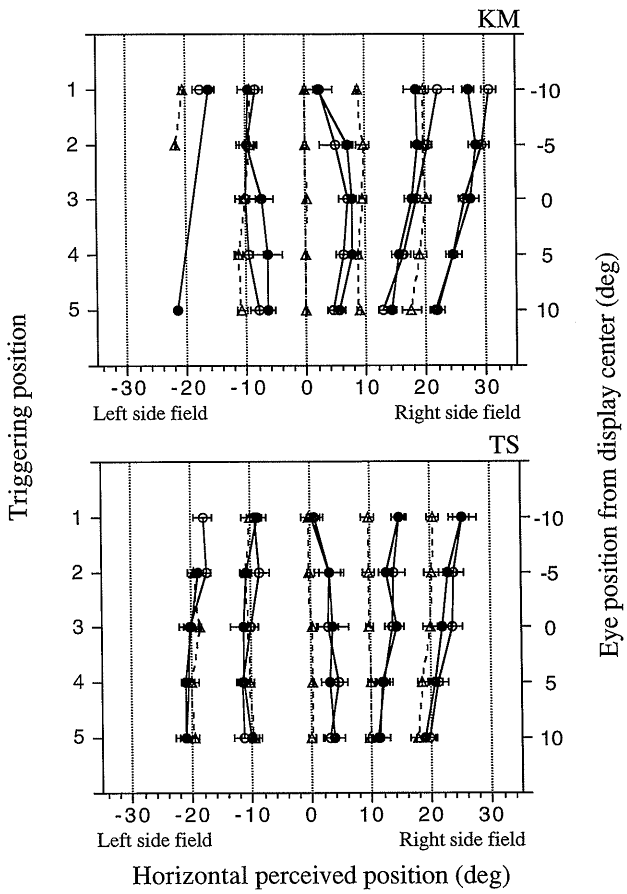

Fig. 7. Mean perceived positions during the right pursuit eye movement and fixation as a function of triggering position (the flash stimulus is presented at 2.0 deg above the horizontal meridian). ●, target velocity 32.0 deg/s; ○, target velocity 16.0 deg/s; △, fixation condition. A plus sign in the left ordinate shows eye position on the right side of the display.

fixed by a bite-bar and a forehead rest. Therefore, the second explanation may be inappropriate for the present study.

As shown in Figs. 5 and 6, the visual space was distorted during PEM. The expansion of the visual space was maximum in the same direction as PEM just after PEM began, then decreased gradually as the eye moved. Finally, the visual space during PEM became normal. This dynamics could be explained by assuming that not only the Filehne illusion, which is the apparent movement of stationary background objects,[3,4] but also the apparent displacement of their positions occurred during PEM.

The visual system makes use of the apparent movement of stationary background objects in order to compensate for the underestimation of the speed of PEM.[3,4] In addition, MST cells are activated in half the area of the visual field depending on the pursuit direction.[16] Therefore, the apparent movement of stationary background objects may occur in half the area of the visual field depending on the pursuit direction. At the same time, according to their apparent movement, the positions of stationary background objects may be displaced in the direction opposite the PEM from their real positions. Consequently, we speculate that, because the displacement of the stationary background objects also occurred as well as their apparent movement in half the area of the visual field depending on the pursuit direction, the visual system had their positions shifted in the same direction as PEM by expansion of the visual space at the beginning of the pursuit and then had their positions gradually displaced from the shifted positions toward the real positions during PEM. That is, the visual system might have the visual space distorted during PEM in order to be consistent with the real positions of the stationary background objects in half the area of the visual field depending on the pursuit direction after completion of PEM.

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